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Cod and Climate Change

A Symposium held in Reykjavík,
23–27 August 1993

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

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Cod and Climate Change

Proceedings of a Symposium held in Reykjavík,
23–27 August 1993

Edited by Jakob Jakobsson
and
Olafur S. Astthorsson, R. J. H. Beverton, Björn Björnsson,
Niels Daan, Kenneth T. Frank, Jens Meincke,
Brian Rothschild, Svein Sundby, and Snorre Tilseth

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Cod and Climate Change Symposium Proceedings

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Cod and Climate Change

Introduction

Jakob Jakobsson

Convener and Editor

At the Statutory Meeting held in Copenhagen in 1990, the International Council for the Exploration of the Sea decided to convene a Symposium on Cod and Climate Change in Reykjavík, Iceland, for five days in August 1993. In accordance with this resolution and in consultation with the Chairmen of the relevant Subject/Area Committees and the Chairman of the Consultative Committee, a Steering Group was formed with Jakob Jakobsson as the Convener. The members of the Steering Group were: Niels Daan (The Netherlands), David Garrod (United Kingdom), Bogi Hansen (Faroe Islands, Denmark), Jens Meincke (Germany), Brian J. Rothschild (USA), Sigfús A. Schopka (Iceland), Michael M. Sinclair (Canada), and Svein Sundby (Norway). The Steering Group met in Hamburg in April 1991 and agreed on the main features of the programme for the Symposium. Otherwise, members of the committee worked by correspondence.

The Symposium was held during the period 23–27 August 1993 at the University of Iceland in Reykjavík. At the opening ceremony, the President of Iceland, Vigdís Finnbogadóttir, gave a welcome address, and the President of ICES, David de G. Griffith, delivered an opening address. In addition, a children's choir entertained the more than 200 participants with folksongs from various ICES countries.

Registration and the day-to-day information service were handled most efficiently by Gillian Post of the ICES Secretariat. She was assisted by staff members of the Iceland Travel Bureau, who also organized a tour to Thingvellir and an enjoyable conference dinner.

The Symposium was conducted in nine consecutive sessions, with no parallel sessions. Of the 108 titles submitted, 59 papers were selected for oral presentation and 24 posters for display at special poster sessions.

Three joint meetings of the Steering Group and Session Chairmen were held during the Symposium, and an Editorial Committee was formed, comprising Jakob Jakobsson (Editor-in-chief), Olafur S. Astthorsson, R. J. H. Beverton, Björn Björnsson, Niels Daan, Kenneth T. Frank, Jens Meincke, Brian J. Rothschild, Svein Sundby, and Snorre Tilseth.

From the papers and posters submitted, a total of 59 manuscripts were divided among the editors, evaluated by at least two reviewers, and accepted for publication.

I take this opportunity to thank the Steering Group and the other Editors, as well as all the people who worked so hard and efficiently at reviewing the papers (see following page). Without their devotion this volume of the *ICES Marine Science Symposia* series would not have reached the scientific standard aimed at by the editorial board. Cordial thanks are extended to Olafur S. Astthorsson for his invaluable help and support throughout the editorial process. Sincere thanks are also extended to the ICES Technical Editor, Judith Rosenmeier, who has once again excelled at her difficult task.

The Symposium and the coordination of the editorial work received financial support from the Icelandic Ministry of Fisheries and the Marine Research Institute.

Jakob Jakobsson: Marine Research Institute, Skúlagata 4, PO Box 1390, 121 Reykjavík, Iceland.

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List of referees

Material presented at the Symposium on Cod and Climate Change and submitted for publication in this volume of *ICES Marine Science Symposia* was reviewed by the following scientists:

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O. S. Astthorsson
A. Árnason
O. Bagge
J. Bartsch
R. J. H. Beverton
C. Bishop
B. Björnsson
K. Brander
E. Buch
S. Carlberg
J. Carscadden
G. Chouinard
S. Coombs
T. Cross
N. Daan
A. Daníelsdóttir
W. Dekker
B. Ellertsen
J. G. Evans
E. Fahrbach
K. Frank
H. Friedrich
H. J. Fyhn
J. C. Gascard
J. Giske
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M. Grosslein
G. Guðmundsson
H. J. L. Heessen
C. Heinze
J. R. G. Hislop
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J. Jakobsson
S. Jónsson
T. Kjørbo
G. Lilly
H. Loeng
J. J. Maguire
P. Mälkki
G. Marteinsdóttir
S. Mehl
J. Meincke
R. Mohn
P. Munk
G. Nævdal
F. Page
P. Pepin
K. Pittman
J. Rice
S. A. Schopka
D. Schnack
F. M. Serchuk
A. Sinclair
D. Slagstad
H. Sparholt
M. Stein
G. Stefánsson
S. Sundby
C. Taggart
S. Tilseth
A. V. Tyler
J. H. Vølstad
K. E. Zakariassen
K. Zwanenburg

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Fisheries off Iceland, 1600–1900

J. Jónsson

Jónsson, J. 1994. Fisheries off Iceland, 1600–1900. – ICES mar. Sci. Symp., 198: 3–16.

This paper describes the importance of fish to the people of Iceland, where for centuries dried cod has taken the place of bread. The main methods of fishing and fish processing are mentioned, including available export figures. The English started fishing off Iceland at the beginning of the fifteenth century, but few published statistics are available about their landings. The Dutch, and especially the French, fisheries off Iceland are better documented. The Dutch statistics cover the years 1751–1786 and 1802–1852, while French statistics, in addition to tonnes landed, include number of vessels and fishermen in the years 1763–1792 and 1814–1900. The combined average Icelandic, Dutch, and French annual landings (ungutted fish) are estimated at 34 000 t in 1766–1772 and 56 000 t in the 1860s compared with an annual average of around 390 000 t in the 1960s. In the "Icelandic Annals", which contain accounts of main annual events, the yearly output of the winter fishery on spawning cod is characterized by the average lot (share) of the fishermen, sometimes expressed as the actual number of fish caught, but mainly reported using expressions like lots *very high*, lots *very small*, *medium* and such like. In the absence of actual statistics the average yearly lots have been evaluated and expressed on a scale ranging from one to six. The smoothed annual lots are believed to indicate the fluctuations in landings from 1600 to 1882. The yearly number of months with drift ice off Iceland in the years mentioned above has been estimated from various Icelandic sources. There is a correlation between these and the average yearly temperature. The yearly catch indices show distinct – if irregular – fluctuations, probably caused by variations in year-class strength. The smoothed curve shows fluctuations of 50–60 years, coinciding with the estimated variations in temperature, and thus indicating its effect on long-term recruitment.

Jón Jónsson: Marine Research Institute, Skúlagata 4, PO Box 1390, 121 Reykjavík, Iceland.

Introduction

The "Icelandic Annals" contain considerable information on fisheries in earlier times. The output of the winter fishery on spawning cod is given for each year; weather conditions are likewise mentioned and so is the incredible number of fishermen drowned at sea. The Annals, however, have to be interpreted carefully, the main reason being that the various annalists were not equally close in time and space to the events reported. The extension and duration of the drift ice in various coastal areas is also documented in the Annals, as well as its effect on fishing and farming.

The oldest published export statistics from Iceland are from 1624. There is information for most years from 1733 to 1796, but nineteenth-century export figures are few.

The most important publication about the eighteenth century Icelandic fisheries is that of Skúli Magnússon (1785), dealing with the winter fishery in the Reykjanes area (southwest coast). Ólafur Olavius (1780) also made a valuable contribution to the socio-economic aspect of the Icelandic fisheries. The diaries of Sveinn Pálsson (1791–1794) contain some observations on cod behaviour and so does Eggert Ólafsson's and Bjarni Pálsson's (1772) well-known work on the life of the Icelandic people. Bjarni Sæmundsson's work on the Icelandic fisheries (1930) also contains a historical review. Lúðvík Kristjánsson's (1980–1986) momentous five-volume work on the open-boat fisheries is an invaluable source of information on the cultural, social, economic, and technical aspects of these fisheries. Páll Bergthórsson (1969) studied the climatic variations in Iceland based on drift-ice records in the Annals. The present author has dealt with the history of marine research in Icelandic waters in various publications (Jónsson, 1988, 1990).

Published statistics on the English fishery off Iceland are sparse, but Edgar J. March (1970), A. R. Mitchell

(1977), and Hervey Benham (1979) mention some interesting details. Marie Simon Thomas (1935) deals with the history of the Dutch fishery off Iceland in the seventeenth and eighteenth centuries and lists Dutch landings in 1751–1786 and 1802–1852. Elín Pálmadóttir (1989) mentions some of the more important publications dealing with French fisheries off Iceland and summarizes the yearly data regarding number of ships, number of fishermen, and the amount of fish landed in the periods 1763–1792 and 1814–1938. Also, the director of the Icelandic Weather Bureau, Páll Bergthórsson (1969), supplied valuable and partly unpublished data on temperature changes in past centuries. The Statistical Bureau of Iceland provided unpublished information on the fish export from Iceland in the eighteenth and nineteenth centuries, and Lúðvík Kristjánsson and Jón Th. Thór furnished the author with additional references regarding the history of fisheries off Iceland.

Icelandic fisheries

Fishing methods

Farming and fishing constituted the basis of the Icelandic economy during the first millennium. They still do, but until relatively recently most farms were too small and unproductive to sustain an average family. Fish was therefore important nourishment and for a long time dried cod substituted for corn in the daily diet.

In the fishing seasons, people living inland made their way to the fishing stations in the south and southwest, frequently a long and hazardous journey on foot in the middle of winter across mountains and unbridged rivers, carrying all their provisions on their backs.

The fishing seasons were based on the migration of the cod, and accordingly very much the same as today. Haymaking, too, was an important part of the farmer's work, with everyone taking part. Furthermore, the catching of seabirds, salmon, and trout also took place at much the same time, and so there was no fishing from July to September, except for home consumption.

Up until the middle of the nineteenth century, the Icelandic fishery was almost exclusively carried out in open boats. The oldest complete boat records date from 1770, when the fishing fleet mainly consisted of four- to eight-oared boats with a substantial number of two-men boats, adding up to a total of 1869 fishing craft (Table 1). During the next seventy years there was a considerable increase in the number of fishing vessels, particularly in the two- to six-oared category. Between 1840 and 1869 there was a further increase in six-oared boats and smaller craft, reaching a total of 2037 by 1900. Two years later a motor was installed in an Icelandic fishing vessel for the first time, thus marking the end of the rowboat era.

Table 1. Types and number of rowboats 1770–1900.

Type of boat	1770	1840	1900
10–8 oars	408	275	122
6–4 oars	811	1138	1152
<4 oars	650	1415	763
Total	1869	2828	2037

Fishing from rowboats was confined to a rather restricted area, as the catch had to be landed every evening and these boats were not as seaworthy as the bigger decked vessels which superseded them.

The accumulated knowledge of the best fishing grounds and time of fishing was passed on from one generation to the next. However, some of this information could be kept within the family, e.g. the location of the halibut grounds. The oldest documental reference to fishing grounds can be found in a manuscript dating from the fourteenth century.

Homespun material was used for sails until the nineteenth century, when canvas became quite common. In several places in the south, however, sails were not used until late in the nineteenth century. Lúðvík Kristjánsson (1982) mentions that sometimes sails were even hired out at a rental of two fish per season for each member of the crew.

In the absence of any harbour facilities, boats had to be beached every time they returned from fishing. Rollers for this back-breaking work were generally made of whale ribs.

At the beginning of the nineteenth century the Icelanders started a modest decked sailing vessel fishery. In 1816 the estimated number of such vessels was 16, but by 1859 it had increased to 61; this fishery culminated in 1906 with 172 ships taking part (Gils Guðmundsson, 1979, III).

The *hand-line* has been used in the Icelandic fishery since the settlement, the oldest description of this gear being contained in the history of bishop Guðmundur góði (the good) from the middle of the fourteenth century. Until the end of the nineteenth century hooks were handmade from imported iron. Despite a successful experiment in 1750, in which an artificial fish was attached to the hook, the Icelanders continued to use hooks with plain shanks for the next hundred years, thus fishing far less effectively than their foreign colleagues alongside (Kristjánsson, 1983). The common length of the hand-line was 40–60 fathoms. It was weighted with lead, through which there was a bar with a hook on each end. The hooks were baited with fish like small halibut and catfish. Shellfish, especially the common mussel (*Mytilus edulis*), was also in widespread use as bait.

The first Icelandic records of *long-lines* are from 1482 in the fjords on the east coast, where this gear was probably copied from the English fishing in that area. The long-lines were set on the seabed. Off the northwest coast there were usually twelve lines with a total of 1200 hooks, the lines being set twice a day. Off the east coast, however, the line was set once a day, with a total of only 90–100 hooks. This, however, became a controversial method of fishing, and in the important fishing area around the Westman Islands it was not used until 1897. This particular gear was actually bought from a British long-liner which had gone aground on the islands the year before.

In the Westman Islands the long-lines brought such excellent results, that 1897 has been considered the turning-point in the history of fishing in this area (Kristjánsson, 1983). In other fishing areas, such as those off the Snæfellsnes peninsula and the western fjords, long-lines have been in use, more or less continuously since 1500.

In 1752 Skúli Magnússon was shipwrecked in Norway, where he became acquainted with the use of cod gillnets. He brought some of them home to Iceland and had them tested in Faxa Bay the following summer. Gradually, this fishing method came more into use in Faxa Bay, but elsewhere not until the beginning of this century. Cod gillnets were first employed in the Westman Islands in 1916 and, ten years later, on the northwest coast.

When fishing with hooks, the bait is of great importance and well into this century it was customary for each fisherman to supply his own bait. If the bait was provided by someone else, he would claim his share of the catch – the so-called bait-lot.

Fish processing and export

The prominence of the cod in the Icelandic economy is reflected by the coat of arms introduced by Christian III in 1591, picturing a gutted cod with a crown. In the latter part of the regime of Christian IV this emblem was changed to a split cod with a crown (Fig. 1).

Stockfish or dried cod was processed in several ways. The most important was the production of flatfish. In winter, the fish was preserved for several weeks in heaps of 4–6 layers and then dried on specially constructed stone walls, the skin facing down at day and up during the night or in rainy weather.

Around the middle of the eighteenth century the flatfish contributed to three-quarters of the total Icelandic fish export. This was a high quality product, fetching about 60% higher prices than the common Norwegian skrei (Gunnarsson, 1983). Other types of stockfish were the so-called "hangfish" and "rowshear", by which two fish were either tied together or one fish was split apart from the tail and hung up for drying on a bar.

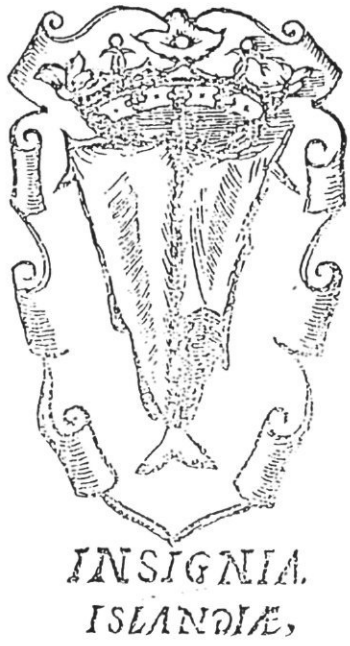


Figure 1. The old Icelandic coat of arms.

In the 1830s the stockfish export was superseded by the production of dry salted fish or klipfish. The oldest trade accounts of saltfish are from 1624 (Table 2). The curing of saltfish was similar to that of the flatfish, except for the salting.

In Table 2 the various fish products have been converted into ungutted fish, using modern conversion factors. It is interesting to note that as early as 1785, Skúli Magnússon stated that 80 pounds of ungutted cod gave 10 pounds of flatfish, which gives a conversion factor of 7.7, i.e. very similar to the present factor. The small difference is due to the fact that the present Icelandic stockfish is the so-called hangfish, which does not have its backbone removed.

As mentioned above, stockfish was an important part of the Icelandic diet for a thousand years. According to Skúli Magnússon (1786), in the years 1764–1773 the domestic fish consumption was about 63% of the total catch. This figure has been used to calculate the total Icelandic landings in Table 2. He also mentions variations in the yearly landings of middle-sized cod, an indication of variations in year-class strength.

Until the 1870s almost all the fish exported came from fishing stations on the south and west coasts and only a very small fraction from the north and east. There was a limited summer fishing off the north and east coasts, but only for local consumption because, as mentioned above, this fishery coincided with the haymaking season.

Table 2. Icelandic landings and export 1624–1871.

Year	Stockfish Skp	Saltfish Skp	Barrels (salted)		Total exported		Estimated landed Tonnes ungutted
			Number	Skp	Skp	Tonnes	
1624	5817	843	445	356	7016	1123	21 217
25	1148	–	380	304	11 792	1887	38 610
30	2823	207	142	114	3144	503	9885
55	10 151	–	280	224	10 375	1660	34 055
1733	4493	586	593	474	5553	888	15 185
34	5884	813	645	516	7213	1154	21 589
35	4867	391	491	393	5651	904	17 361
36	5298	341	420	336	5975	956	18 641
37	4519	458	616	493	5470	875	16 430
38	5942	383	575	460	6785	1086	21 087
39	6686	250	276	221	7157	1144	22 945
40	5530	376	651	521	6427	1028	19 688
41	5322	293	404	323	7027	1124	18 622
42	5593	861	716	573	7027	1124	20 787
43	5380	392	658	526	6298	1008	19 238
53	3007	238	481	385	3630	581	10 897
59	2860	109	128	102	3071	491	9828
60	5238	374	539	431	6043	967	18 611
61	2874	293	420	336	3503	560	10 490
62	3318	229	237	190	3737	598	13 109
63	5048	298	297	238	5584	893	17 607
64	5626	200	513	410	6236	998	19 578
65	6762	344	394	315	7421	1187	23 471
66	8695	906	728	582	10 183	1629	31 180
67	7136	510	587	470	8116	1299	25 202
68	4798	1270	569	455	6523	1044	18 671
69	6461	1403	1072	858	8722	1396	24 935
70	5381	1473	690	550	7404	1185	21 068
71	6060	2441	514	411	8892	1423	24 764
72	7204	2311	1111	889	10 404	1665	28 968
73	7536	2594	1178	942	11 072	1772	30 610
74	7409	2465	844	675	10 549	1695	29 608
75	5673	1966	1016	813	8452	1352	23 207
76	5185	2652	1117	894	8731	1397	22 820
77	5251	2571	706	565	8387	1342	22 464
78	5257	4065	630	504	9826	1572	24 897
79	5214	3686	693	554	9454	1513	24 195
80	1787	2703	606	485	4975	796	11 067
81	4256	3495	600	480	8331	1333	20 593
82	3604	4204	237	190	7998	1280	19 235
83	4573	3590	676	541	8704	1393	21 889
84	3781	3598	201	161	7540	1206	18 779
88	5331	–	361	289	5620	899	18 106
89	7223	–	461	369	7592	1215	24 511
90	4305	–	767	614	4919	787	15 117
91	3536	–	395	316	3852	616	12 180
92	5191	–	492	394	5585	894	17 788
93	4362	–	608	486	4848	776	15 144
94	3146	–	489	391	3635	582	10 967
95	5972	–	468	374	6346	1015	20 361
96	6534	–	472	378	6912	1106	22 280
1806	2334	2011	150	120	4465	714	11 256
16	2485	1304	190	152	3941	631	10 643
19	2925	3361	52	42	6328	1012	15 379
49	3244	16 400	–	–	19 644	3143	38 065
55	3090	20 989	–	–	24 079	3853	45 176
62	2076	18 812	–	–	20 888	3342	38 192
65	39	8287	–	–	8326	1332	13 908
66	227	10 952	–	–	11 179	1789	18 959
67	965	22 803	–	–	23 768	3803	41 124
68	757	11 750	–	–	12 507	2001	22 059
69	1258	14 897	–	–	16 155	2585	28 960
71	778	26 009	–	–	26 787	4286	45 833

1 skippund (skp) = 160 kg; 1 barrel = 128 kg = 0.8 skp.
Conversion factors for ungutted fish: stockfish 7.7, saltfish 3.85, in barrels 3.0.

The fish export from Iceland in the sixteenth and seventeenth centuries was very modest compared with that of the other main fishing countries in the North Atlantic. In 1790–1798 the average annual export from New England was about 22 000 t and 23 000 t were exported from Newfoundland in 1792. The export from the French colonies in North America varied from 5000 to 22 000 t in the seventeenth century, and the yearly export from Bergen of Norwegian stockfish was in the order of 6000 to 7000 t in the period 1750 to 1800. In the first half of the eighteenth century the yearly average export of stockfish and saltfish from Iceland was not quite 1000 t and barely 1100 t in the last quarter of that century. By 1855–1871 the yearly average had increased to 2874 t.

Fisheries and climatic changes 1600–1900

The author has assembled all the available information on fisheries contained in some 24 Icelandic Annals covering the period 1564 to 1882. These Annals record fisheries in various coastal areas, but the most complete records are from the winter and spring fisheries off the south and west coasts. Accordingly, I deal with the area between the Westman Islands and the Snæfellsnes peninsula, which also today is the most important spawning area of the cod.

Reconstructing old catch records

When on shore, the captain separated the catch into heaps of equal size, one for each of two fishermen. Each heap was then divided into two lots and various methods were used to ensure a random division between the fishermen. For example, a knife or a foot was put between the two lots and the man who looked away would then choose either the blade or the handle, the heel or the toe and so on. Besides the lots to the fishermen, other parts of the catch, which usually were called dead lots, were taken for the boat, the gear, the bait, and so on.

Most of the annalists were educated men, clergymen, including a bishop, county sheriffs or intelligent farmers with a firm knowledge of the people's livelihood. The main prerequisite with regard to the credibility of the events described in the Annals is the writer's or his informants nearness to them in time and space.

In the Annals, the yearly output of the winter and spring fishery was evaluated as the average lot of the fisherman. In some instances the actual number of fish is given, but in most cases the outcome is described by expressions like lots "very high", lots "very small", lots "medium", and so on. These estimates, however, are relative. In the middle of the seventeenth century a lot of 500 fish was considered about average, but a hundred years later a lot of 300 was thought to be quite good.

The estimates of the annual output of the fishery are in general fairly concordant, but in the case of disagreement, the record of a writer living in the vicinity of the main fishing grounds in the south and west carries more weight than for instance the county sheriff in the east, some 600 km away.

As a rule, there is quite good agreement between the various annal writers regarding their evaluation of the average yearly lots. Significant variations between the different fishing stations in any one season are probably in the main caused by the weather conditions.

In the absence of actual statistics the average yearly lots or catch indices have been evaluated and arranged on a scale ranging from one to six. Figure 3 shows the resulting annual and smoothed catch indices. The yearly catch indices are listed in Table 3. The smoother used is a smoothing spline implemented in the S-plus software (Chambers and Hastie, 1992).

Climatic influences

Systematic meteorological observations are available in Iceland as far back as 1823. Páll Bergthórsson (1969) compared the mean annual average temperatures from 1846 to 1919 with the number of months in which drift ice had been observed during the same period. He then calculated the annual variation in temperature since 1600 based on information on the yearly number of ice months in the same period. Bergthórsson (pers. comm.) has now calculated the mean temperature in each decade in the years 1851 to 1990 using the formula

$$t = \log [(120 - n)/n]/0.88 + 2.19$$

where t is the temperature in °C and n the number of ice months in a decade. The correlation between the values predicted from this formula and those actually measured was 0.85 with a standard deviation of ±0.3°C. In periods with much drift ice the standard deviation decreased to ±0.2°C.

The normal climate of Iceland is very near the limit of endurance of a European people maintaining their cultural standard, any deteriorations therefore being of major consequence for the people, livestock, and fisheries. Accordingly, it is readily understandable why the annalists were so careful recording them.

As shown in Figure 2, there was a distinct increase in the output of the fishery during the first half of the seventeenth century, concurrent with a marked rise in temperature. The decreasing catches during the second half of the seventeenth century similarly closely coincide with the deterioration in the climate, until terminated by improved weather conditions and landings in the first four years of the 1670s and another similar increase in the 1680s. Fishing was exceptionally good in 1684, a year rightly named the "winter of the big lots" (hlutaveturinn

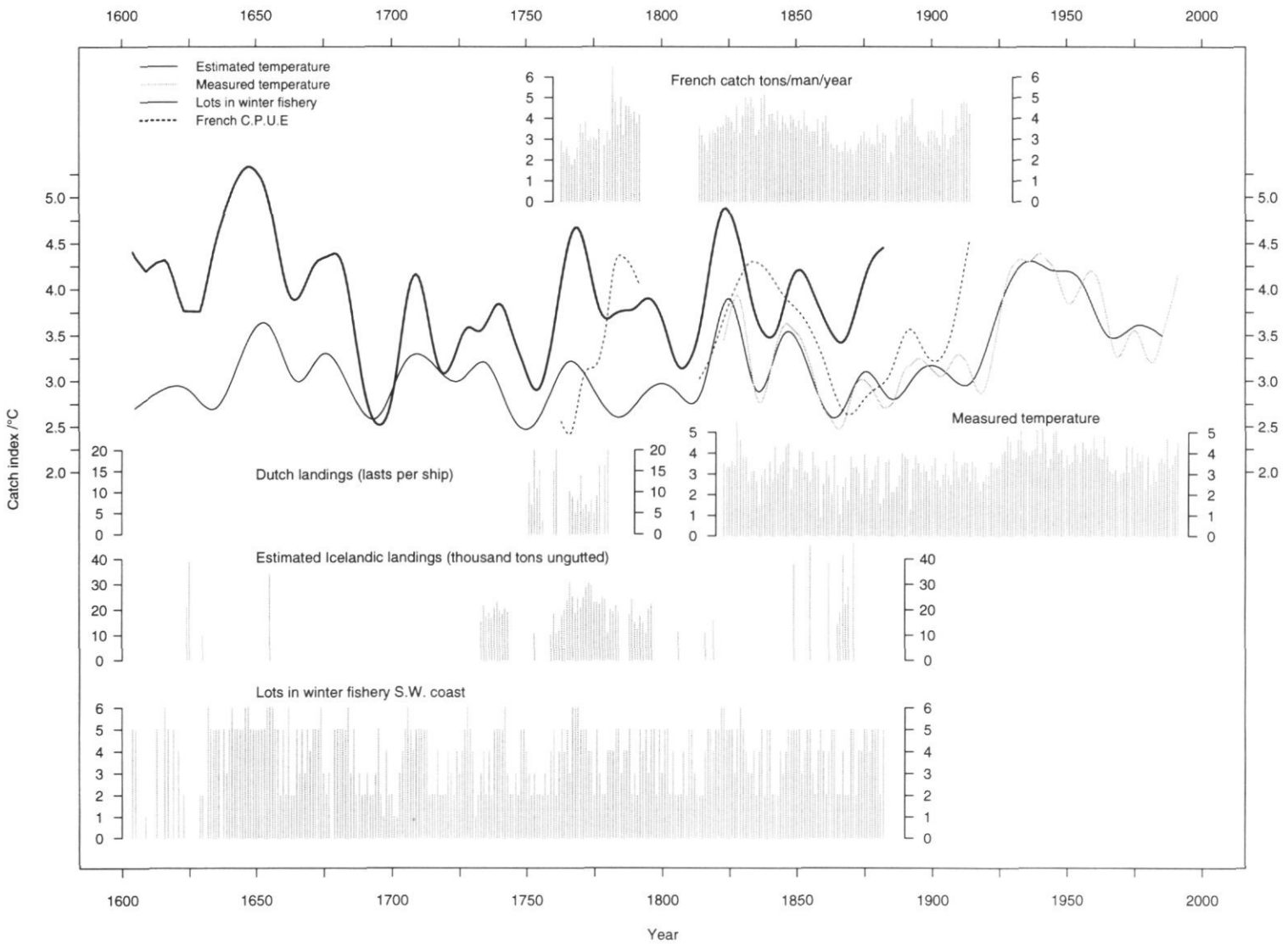


Figure 2. Icelandic waters, cod fisheries and climate changes 1600–1900.

Table 3. Estimated yearly lots in the winter fishery 1604–1882.

1601	–	1651	5	1701	1	1751	3	1801	5	1851	5
1602	–	1652	5	1702	1	1752	2	1802	5	1852	3
1603	–	1653	5	1703	3	1753	3	1803	2	1853	4
1604	5	1654	6	1704	4	1754	2	1804	4	1854	5
1605	5	1655	6	1705	5	1755	2	1805	2	1855	5
1606	–	1656	6	1706	6	1756	2	1806	2	1856	3
1607	–	1657	5	1707	5	1757	3	1807	2	1857	2
1608	–	1658	5	1708	4	1758	2	1808	4	1858	4
1609	1	1659	2	1709	5	1759	4	1809	2	1859	5
1610	–	1660	5	1710	5	1760	5	1810	5	1860	4
1611	–	1661	2	1711	5	1761	2	1811	5	1861	2
1612	–	1662	6	1712	5	1762	4	1812	3	1862	4
1613	5	1663	2	1713	5	1763	5	1813	2	1863	5
1614	–	1664	2	1714	2	1764	4	1814	2	1864	5
1615	–	1665	5	1715	2	1765	5	1815	2	1865	2
1616	6	1666	3	1716	2	1766	3	1816	4	1866	2
1617	5	1667	5	1717	4	1767	6	1817	5	1867	4
1618	–	1668	3	1718	2	1768	6	1818	5	1868	2
1619	5	1669	5	1719	2	1769	6	1819	4	1869	2
1620	–	1670	4	1720	2	1770	5	1820	5	1870	5
1621	4	1671	5	1721	4	1771	5	1821	5	1871	5
1622	–	1672	5	1722	3	1772	5	1822	6	1872	2
1623	2	1673	5	1723	2	1773	4	1823	6	1873	4
1624	–	1674	6	1724	4	1774	4	1824	5	1874	4
1625	–	1675	3	1725	3	1775	2	1825	5	1875	5
1626	–	1676	2	1726	4	1776	5	1826	5	1876	5
1627	–	1677	3	1727	5	1777	3	1827	3	1877	4
1628	–	1678	–	1728	6	1778	2	1828	5	1878	5
1629	2	1679	5	1729	5	1779	2	1829	6	1879	5
1630	2	1680	5	1730	4	1780	4	1830	5	1880	5
1631	–	1681	5	1731	1	1781	4	1831	4	1881	2
1632	6	1682	5	1732	2	1782	4	1832	3	1882	5
1633	5	1683	5	1733	3	1783	5	1833	3		
1634	5	1684	6	1734	4	1784	5	1834	4		
1635	5	1685	3	1735	2	1785	3	1835	2		
1636	5	1686	5	1736	4	1786	4	1836	4		
1637	–	1687	2	1737	2	1787	4	1837	5		
1638	5	1688	3	1738	5	1788	5	1838	2		
1639	3	1689	2	1739	5	1789	2	1839	5		
1640	5	1690	2	1740	5	1790	3	1840	5		
1641	6	1691	3	1741	5	1791	2	1841	2		
1642	5	1692	2	1742	6	1792	5	1842	2		
1643	5	1693	2	1743	3	1793	4	1843	2		
1644	5	1694	3	1744	2	1794	5	1844	4		
1645	5	1695	5	1745	2	1795	3	1845	3		
1646	6	1696	2	1746	3	1796	5	1846	4		
1647	6	1697	1	1747	2	1797	5	1847	5		
1648	5	1698	4	1748	5	1798	2	1848	5		
1649	5	1699	2	1749	5	1799	5	1849	5		
1650	5	1700	2	1750	4	1800	3	1850	5		

1 = very small lots, 2 = small lots, 3 = average lots, 4 = considerable lots, 5 = great lots, 6 = very great lots.

mikli). During the next two decades catches fell to a very low level coupled with greatly deteriorating weather conditions. The last five years of the century were exceptionally hard. In April 1695, for example, Faxa Bay filled with ice which had drifted from the north in a clockwise direction along the east and south coasts. As an example of the low catches, one boat-owner in the Faxa Bay area received 306 fishes from 30 lots in the year 1700, and in the same year the total catch of 12 men from the bishopric of Hólar in the north was only 300 fishes.

Hubert H. Lamb (1979) quotes Norwegian sources recording that in 1695 the fisheries also failed totally along the Norwegian coast south to Stavanger, except for a small stock in the inner part of the Trondheim fjord. To Lamb this indicated that in 1695 the Polar water spread across the entire surface of the Norwegian

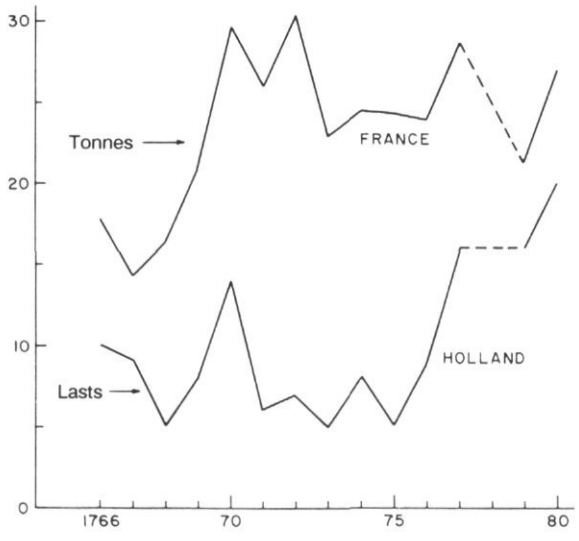


Figure 3. Dutch and French landings per ship per year from Iceland 1766–1780.

Sea and south past the Faroes. This was also a bad year for cod off the Shetland Islands.

According to C. Pfister (1992), drought was the most characteristic condition of seventeenth-century Swiss weather. The summers during the first three decades were wet, and so also was the weather in the 1670s and in the period 1685–1699. After 1685, temperatures dropped sharply in all seasons. In the 1690s the mean annual temperature in central Europe was almost 1.0°C lower than in the 1901–1960 reference period; in central England it was 0.8°C lower (Manley, 1974).

The temperature rose sharply during the first two decades of the eighteenth century, duly followed by increased catches at Iceland, according to the Annals. There was then a gradual worsening of the climate during the 1730s and 1740s, although interrupted by three or four good spells which are reflected in the landings. Statistical information for 1733 to 1743 (Table 2) does not show any clear-cut downward trend, the landings varying from 15 000 to 23 000 t, with an average of 19 000 t and average lots index of 4.0.

The temperature was at its lowest in the 1750s, a decade of very great hardship for the Icelanders. From 1756 to 1758 many people died of hunger. The yearly stockfish export in 1759–1762 fell to 3600 skippund (570 t) compared with the average of 5400 skippund (864 t) in the 1733–1743 period.

The Annals mention good fishing and many small cod off the north coast in 1758, followed by a good winter fishery in the subsequent years. In the seven preceding years (1751–1757), however, this fishery had been at a very low level. Furthermore, the Annals report good fishing off the north coast during most years from 1765 to 1780, and in several of them great numbers of small fish were observed and caught. Similarly, "blood sea" (algal blooms and possibly *Calanus*) was observed at various places off the north and east coasts, e.g. in 1765, 1767, and 1776. In 1768, fishermen of the central north coast had daily lots of 60–70 cod, and there were good catches of haddock and halibut. Great numbers of squid were also driven on shore and used as bait. Many Dutch doggers were noticed in Skagafjörður and Eyjafjörður and the years 1766–1770 were also very good for the Dutch fishery.

All this points to a great improvement in the environmental conditions in this area and to increased cod recruitment giving rise to a good winter fishery for mature fish in most years in the period 1766–1779. There was also a similar increase in French landings from Iceland, where the catch per man per year increased from 2.3 t in 1764 to 3.4 t in 1777.

As given in Table 2, the total Icelandic catch in 1764 to 1779 varied from 18 500 to 30 900 t, with a yearly average of 24 400 t. The Annals report good winter fishing in 1768 but heavy rainfall, especially in the Snæfellsnes area, and so a good deal of the dried fish was spoiled and could not be exported. The estimated total landings in this year is therefore too low.

In the 1760s, 1770s, and 1780s the temperatures dropped significantly, with a similar reduction in the Icelandic lots indices and the French c.p.u.e.s. The low Icelandic export figures in 1806, 1816, and 1819 confirm the low state of the stock at the beginning of the nineteenth century.

There was a gradual, but irregular, increase in temperatures during the first half of the nineteenth century, and this is reflected in an increase in both the French and Icelandic landings. The temperatures peaked in the 1820s and 1840s and then dropped to a low level in the 1860s and 1880s. The Icelandic lots indices seem to follow this fairly closely, and these changes are also largely reflected in the French c.p.u.e.s.

Foreign fisheries at Iceland

Britain

Fishermen from England are first mentioned in the Icelandic Nýji annáll (the New Annal), which deals with the period 1393–1430. For the year 1412 it states: "Came a ship from England east of Dyrhólmaey (Portland), people rowed out to them and they were fishermen from England."

English fishing vessels were soon followed by scores of merchantmen starting a business profitable for both nations. One reason was that the Norwegians often

failed to send to Iceland the six ships per year which they had agreed to in 1263 when the two nations were united under the King of Norway.

According to Icelandic annals, 25 English fishing vessels were lost on Maundy Thursday, 13th April 1425, indicating a substantial English fishery at that time. A. R. Mitchell (1977) mentions that, in 1528, 149 ships from ports along the east coast from London to Boston sailed to Iceland for the fishing of cod and ling, compared with 222 ships for the North Sea fishing grounds and 78 more to fish for cod in Scottish waters.

According to Edgar J. March (1970), the fleet which used to sail to Iceland in March and return in August was usually accompanied by one or more of the King's ships for protection. The trip from King's Lynn took about 14 days, which meant that some 70 miles were covered per day. In the opinion of March (1970), this compares favourably with the time taken by cod smacks sailing from Grimsby to Iceland 350 years later.

Icelandic sources confirm that English fishermen were using long-lines off east Iceland in the fifteenth century. Furthermore, the Annals state that the local people complained that the large craft and long-lines of the English were spoiling their fishing.

After the abolition of Catholicism in England, and thus also the compulsory eating of fish on days of fasting, the demand for salted fish declined and in 1553 only 43 ships went to Iceland and 10 to the Shetlands. In 1593, 8 ships are known to have left for fishing around Iceland and a mere three ships in 1665.

There was a revival of English fishing around Iceland at the end of the Napoleonic Wars in 1815. A typical smack from the 1860s was 60–80 t with a crew of 9 to 11 men plus 4–5 boys as apprentices.

The gears used at Iceland were either hand-lines or long-lines. A hand-line was about 45 fathoms in length. In the 1860s a complete long-line set consisted of 180 lines, each 40 fathoms in length. There were 26 snoods of 1 fathom on each line, with baited hooks 1.5 fathoms apart. The total length of such a line was over 7 nautical miles, with 4650 hooks.

No information on the English landings from Iceland in the nineteenth century is available to the author. In the 1870s steamships were introduced in the British fisheries, ending the long era of sailing vessels. According to Jón Th. Thór (1992) the first English trawlers went to Iceland in 1889 starting a very profitable fishery which was to last for the next 87 years.

Holland

The first documented information on the Dutch fishery off Iceland originates from 1655, when a captain named Jelle Alberts from Vlieland landed a cargo of salted cod after eleven weeks of fishing off Iceland. In the condition for this sale it was stated that the fish should measure at least 22 inches with the tail; two fish of less than this length were counted as one (Thomas, 1935).

The Icelandic Annals first recall a Dutch ship in Breidafjördur (W) in 1661. Prior to 1682 Dutch statistics do not distinguish between the herring vessels fishing in the North Sea and those fishing off Iceland, but in 1683 seven vessels were listed as fishing off Iceland, 26 in 1684, 20 in 1685, 14 in 1686, 9 in 1687, 5 in 1688, 7 in 1689 and 9 in 1690.

In her book about the Dutch fishery off Iceland in the

Table 4. Dutch fishery at Iceland.

Year	No. of ships	Average no. of lasts per ship	Year	No. of ships
1751	73	12	1811	2
1752	64	7	1812	–
1753	56	20	1813	–
1754	95	11	1814	4
1755	76	15	1815	5
1756	95	2–4	1816	7
1757	111	few	1817	–
1758	94	many	1818	10
1759	124	moderate	1819	15
1760	?	15	1820	13
1761	123	20	1821	12
1762	142	reasonable	1822	13
1763	148	reasonable	1823	8
1764	113	reasonable	1824	11
1765	140	reasonable	1825	15
1766	155	10	1826	9
1767	157	9	1827	12
1768	160	5	1828	11
1769	137	8	1829	15
1770	126	14	1830	15
1771	145	6	1831	17
1772	121	7	1832	18
1773	107	5	1833	17
1774	83	8	1834	9
1775	78	5	1835	14
1776	36	9	1836	10
1777	22	16	1837	4
1778	24	many	1838	–
1779	61	16	1839	4
1780	63	20	1840	3
1781	–	–	1841	5
1782	–	–	1842	1
1783	41	few	1843	2
1784	49	few	1844	2
1785	52	moderate	1845	2
1786	58	?	1846	2
1802	24		1847	3
1803	13		1848	5
1804	22		1849	6
1805	20		1850	3
1806	4		1851	3
1807	2		1852	5
1808	6			
1809	3			
1810	2			

seventeenth and eighteenth centuries, Marie Simon Thomas (1935) lists the annual number of Dutch vessels fishing off Iceland in the years 1751–1786 and 1802–1852 together with the yearly average landed per ship in the first period (Table 4).

The ships usually left for Iceland towards the end of March and came home at the end of September. Since the fish often deteriorated in quality during the long voyage from Iceland, the Dutch built fast carriers (jagers) to take the fish home, and to allow the other ships to go on fishing.

As given in Table 4, there was a gradual increase in the number of Dutch vessels fishing off Iceland in the second half of the eighteenth century, culminating in 1768 with 160 vessels. Thereafter, the number of fishing craft gradually decreased, and by the middle of the nineteenth century only 3–5 Dutch vessels were fishing off Iceland. In some years the fishery was interrupted by wars, while variations in export prices also greatly affected the yearly fishing effort. The yearly output reached a maximum in 1760 when 1764 lasts were landed (last is a measurement of volume estimated at 2 t).

There were considerable variations in the c.p.u.e.: from 2 to 4 lasts per voyage in 1756 to 20 lasts in 1761 and 1780. These variations are similar to those in the French fisheries in the same years (Fig. 3).

Dutch sources attribute the very low catch in 1756 to the ice conditions off Iceland, and this is confirmed by the Icelandic Annals. As mentioned earlier, great masses of ice filled all the bays and fjords of the north coast in that year, the ice even drifting along the east and south coasts all the way into Faxa Bay; 1756 was also a very bad year for the Icelandic fisheries.

According to Marie Simon Thomas (1935), a catch of 15 lasts per voyage was sufficient to cover all expenses of a Dutch ship fishing off Iceland.

France

The history of the French fishery off Iceland is better documented than any other foreign fishery. In 1614 Jean de Clerc from Dunkirk sent his ships to Greenland and Iceland to look for whales. Encouraged by the great number of cod they had seen off Iceland, he sent seven ships two years later to fish for cod. These fisheries grew fairly slowly, because of the many wars at that time. In 1681 Louis XIV decided to pay a bonus of 3000 francs to each ship fishing off Iceland, realizing the importance of these fisheries as a food supply and also as a means of training able seamen for his Navy. At the beginning of the eighteenth century the ships were 50–60 tons with a crew of seven to eight men. In her book about the French fishermen at Iceland, Elín Pálmadóttir (1989) collected all the available statistical information on these fisheries since 1763 (Table 5).

Information on the yearly number of fishermen is available from 1814, but as there were only seven or eight men on the smaller eighteenth-century ships, the figure of eight has been used for the pre-1814 data. There was a gradual increase in the average number of fishermen per ship during the nineteenth century, from fifteen in 1821–1830 to nineteen in the last decade of the century. This is correlated with the increased size of the fishing craft. These vessels were gradually adapted to the severe weather conditions in Icelandic waters. A typical golette from the 1850s was a wooden ship with a displacement of 180 t, 35 m long, 7.5 m beam, and 3–5 m draught. In the 1780s the average yearly number of French fishing vessels off Iceland was about 60, the same as in the 1820s. This was followed by a gradual increase in the fishing effort, culminating in 1884 with 347 ships manned by 6084 fishermen.

On their way to Iceland the crew drew lots for the position on board ship at which they would start their hand-lining, before moving on weekly to the next position behind them.

Figure 4 shows the main French fishing grounds off Iceland, with the fishing season usually lasting from mid-March to mid-August. Up to mid-May the ships fished in the area from Eystrahorn to Reykjavík, which includes the main spawning area of the cod. In spring and summer they operated off the northwest, northeast, and east coasts in accordance with the summer migration and distribution of the cod.

The lot of each fisherman was calculated by the number of fish tongues he gave to the captain at the end of each watch. In a good season, a fisherman would catch 3000–4000 fish. The Breton fishermen salted their catch directly in the hold, but those from Flanders used barrels, of which the hold could accommodate around 400. The conversion factor from wet salted to ungutted fish is estimated at about 3.0.

The data in Table 5 were used to calculate the catch per man per year, as shown in Figure 2. The general c.p.u.e. trend was upwards until 1787, although there was a temporary decline in the 1770s, which is also clearly reflected in the Icelandic fisheries and seems to have correlated with the worsening climatic conditions during that decade. After that, the c.p.u.e. increased again to a maximum in the middle of the 1780s, only to decline until the fishery came to an end in 1793.

The French fishery resumed in 1814 and until 1839 there was a general increase in the c.p.u.e., interrupted by a couple of setbacks at the end of the 1820s and middle of the 1830s. In the 1840s and 1850s the c.p.u.e. varied between 3.3 and 4.3 t but then decreased in the 1860s coincident with the cooling in that decade. The increasing temperatures in the 1870s seem to have been beneficial to the fishery, but in the early 1880s the temperatures fell to an all-time low level and in 1884 the

Table 5. French fisheries at Iceland 1763–1900.

Year	No. of ships	No. of men	Tonnes landed	Tonnes/ ship	Tonnes/ man	Year	No. of ships	No. of men	Tonnes landed	Tonnes/ ship	Tonnes/ man
1763	6	48	141	23.5	2.9	1842	73	1065	4171	57.1	3.9
1764	23	184	441	19.2	2.3	1843	79	1127	4874	61.7	4.0
1765	42	336	877	20.9	2.6	1844	87	1268	4275	49.1	3.3
1766	64	512	1131	17.7	2.2	1845	79	1127	4618	58.4	4.0
1767	66	528	945	14.3	1.7	1846	91	1493	5553	61.0	3.7
1768	63	504	1036	16.4	2.0	1847	87	1339	4691	53.9	3.5
1769	56	448	1166	20.8	2.6	1848	78	1315	5508	70.6	4.1
1770	42	336	1248	29.7	3.7	1849	68	1197	4689	68.9	3.9
1771	48	384	1248	26.0	3.2	1850	88	1602	5778	65.6	3.6
1772	57	456	1728	30.3	3.7	1851	122	1709	6664	54.6	3.8
1773	58	464	1329	22.9	2.8	1852	131	1854	6419	49.0	3.4
1774	66	528	1620	24.5	3.0	1853	109	1553	6700	61.5	4.3
1775	65	520	1579	24.3	3.0	1854	109	1577	5673	52.0	3.5
1776	60	480	1431	23.8	2.9	1855	101	1500	5013	49.6	3.3
1777	60	480	1660	27.7	3.4	1856	128	1511	5025	39.2	3.3
1778	–	–	297	–	–	1857	176	2695	8887	50.5	3.2
1779	70	560	1485	21.2	2.6	1858	191	3055	11 877	62.2	3.8
1780	70	560	1890	27.0	3.3	1859	222	3424	8937	40.2	2.6
1781	70	560	1653	23.6	2.9	1861	226	3582	14 737	65.2	4.1
1782	86	688	4468	51.9	6.4	1862	231	3731	12 302	53.2	3.2
1783	70	560	2651	37.9	4.7	1863	235	3814	10 565	44.9	2.7
1784	72	576	2110	29.3	3.6	1864	260	4337	10 892	41.9	2.5
1785	62	496	2475	39.9	4.9	1865	247	4031	10 663	43.2	2.6
1786	60	480	1532	25.5	3.1	1866	221	3708	8822	39.9	2.3
1787	51	408	1875	36.8	4.5	1867	232	3800	9075	39.1	2.3
1788	59	472	2125	36.0	4.5	1868	262	4000	11522	44.0	2.8
1789	58	464	1957	33.7	4.2	1869	289	4984	11825	40.9	2.3
1790	45	360	1552	34.5	4.3	1870	299	5128	12897	43.1	2.5
1791	36	288	1080	30.0	3.7	1871	226	3847	8536	37.8	2.2
1792	40	320	1330	33.2	4.1	1872	252	4394	10 809	42.9	2.4
1814	4	63	229	57.2	3.6	1873	230	4035	11 051	48.0	2.7
1815	27	393	1238	45.8	3.1	1874	208	3856	12 246	58.9	3.1
1816	60	863	2435	40.6	2.8	1875	220	4000	13 438	61.1	3.3
1817	52	768	1854	35.6	2.4	1876	228	3942	11 589	50.8	2.9
1818	31	417	1370	44.2	3.2	1877	244	4314	13 102	53.6	3.9
1819	30	442	1516	50.5	3.4	1878	267	4723	12 951	48.5	2.3
1820	42	600	1961	46.7	3.2	1879	321	5628	15 305	47.6	2.9
1821	44	613	2211	50.2	3.6	1880	269	4556	16 827	62.5	3.1
1822	43	559	2010	46.7	3.5	1881	202	3436	9695	47.9	2.5
1823	41	570	2062	50.3	3.6	1882	211	3696	12 013	57.0	3.1
1824	50	692	2881	57.6	4.1	1883	236	4148	13 082	55.4	3.9
1825	49	696	2812	57.4	4.0	1884	347	6084	11 193	32.3	1.4
1826	67	1089	4157	62.0	3.8	1885	314	5576	12 913	41.1	2.8
1827	76	1107	3750	49.3	3.8	1886	205	5327	11 629	56.7	2.0
1828	82	1253	5738	70.0	4.5	1887	149	2619	10 196	68.4	3.9
1829	77	1223	3949	51.3	3.2	1888	219	3723	11 654	53.2	3.1
1830	71	1185	4892	68.9	4.1	1889	178	3123	12 764	71.7	4.6
1831	63	795	3927	62.3	4.9	1890	153	2808	10 669	69.7	3.1
1832	73	926	4347	59.5	4.6	1891	163	2958	11 561	71.0	3.4
1833	70	881	4435	63.3	5.0	1892	167	3171	13 195	79.1	4.8
1834	84	1088	4927	58.6	4.5	1893	175	3362	16 623	95.0	4.8
1835	112	1429	4575	40.8	3.2	1894	212	4003	14 568	68.8	3.1
1836	114	1350	4628	40.6	3.4	1895	238	4252	13 293	55.8	3.4
1837	85	992	4895	57.6	4.9	1896	214	4052	11 852	55.4	2.5
1838	106	1243	6365	60.0	5.1	1897	190	3733	10 542	55.4	2.2
1839	102	1257	4577	44.9	3.6	1898	186	3534	9239	49.6	2.8
1840	76	930	3910	51.4	4.2	1899	158	3111	10 491	66.3	3.8
1841	66	924	3917	59.3	4.2	1900	149	3191	11 115	74.5	3.4

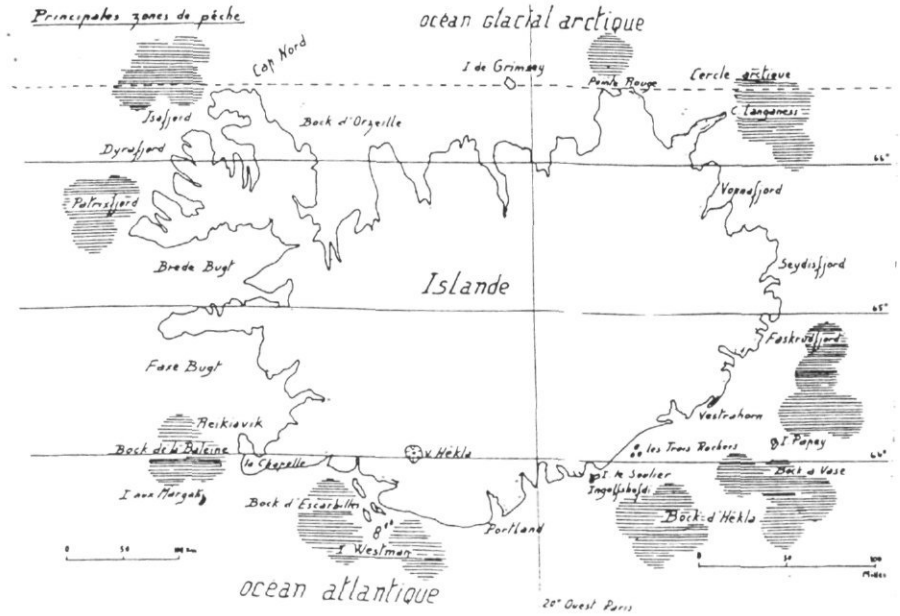


Figure 4. The main French fishing grounds off Iceland (from Pálmadóttir, 1989).

French catch per man per year was down to a minimum of 1.4 t (Table 5). In the next ten years the c.p.u.e. rose rapidly, culminating in 1892 and 1893 with 4.8 t per man.

Discussion and conclusions

The Icelandic fisheries were carried out exclusively with open rowboats until the beginning of the nineteenth century, and so the weather was one of the most important factors determining yearly landings. Loss of life during the stormy Icelandic winters was quite appalling. In the bad winter of 1685 a total of 136 fishermen were drowned in one day in the Westman Island–Reykjanes area, and the Annals report even greater losses.

Information on the English fishing effort is insufficient. The intensity of this fishery seems to have been at its greatest in the first half of the sixteenth century, and again after the Napoleonic wars. The Dutch fishing effort reached a maximum in the 1760s, with an average of 141 vessels taking part, and after a gradual decline came to an end in the middle of the nineteenth century. The French fishery, on the other hand, grew very rapidly in the course of the nineteenth century and was at its maximum in the mid 1880s with 347 ships taking part. In the first decade of this century participation in this fishery was down to an average of 154 ships.

The combined landings of Icelandic, Dutch, and French fishing vessels is estimated to have been in the order of 34 000 t (ungutted fish) annually in the period 1766–1777, varying from 29 000 to 43 000 t. About 75% was taken by the Icelanders, 15% by the Dutch, and the rest by the French. One hundred years later, in 1865 to 1869, the French and Icelandic landings together averaged about 56 000 t annually, the French share of which was 56%. This is only 14% of the 390 000 t average landings of cod in the 1960s and could not have had any significant influence on stock size.

The Icelandic fishery was based mainly on the mature part of the cod stock, whereas the Dutch and French also fished outside the spawning areas in summer and autumn. Despite this, exploitation of the immature part was certainly very limited.

Just as now, the eggs and larvae were carried to the colder waters off the north and east coasts, an area vulnerable to changes in hydrographic conditions. A recent example is the cooling off north and east Iceland during the latter part of the 1960s, when the East Icelandic Current changed from being an ice-free Arctic current in 1948–1958 to a Polar current in the cold years 1965–1969, transporting ice and preserving it (Dickson *et al.*, 1988). In this period Polar water covered all the north coast area and the northern part of the east coast. The primary production of phytoplankton was only 25% of the normal and, similarly, the zooplankton populations collapsed. Possibly similar events took place during the cold spells in the seventeenth, eighteenth and nineteenth centuries.

As the records show, the Icelandic winter fishery was at a low level during the very cold years in the 1740s and

1750s. The Annals, however, mention several signs of improved hydrographic conditions off the north coast of Iceland after the mid-1750s, as evidenced by "blood sea" (algal blooms and *Calanus*), great numbers of small cod, and increased catches of cod, haddock, and halibut. This is clearly borne out by improved recruitment, subsequent good winter fishery in 1766 to 1774, and also the French catches.

The yearly Icelandic catch indices reflect distinct fluctuations, probably caused by varying year-class strength. This is supported by Icelandic records from the 1770s and 1780s, which note yearly variations in the amount of middle-sized cod landed.

The smoothed catch-indices curve is in fairly good agreement with estimated temperature variations, showing long-term fluctuations of 50–60 years. The drift ice occurring in the warm water area off the south and southwest coasts is a sign of long-time cooling of the water masses north of Iceland. The ice affected the local fishery in the warm water area for only a short time and when it drifted away good fishing sometimes followed.

The long-term decline in the catches, e.g. in the second half of the seventeenth century and around the middle of the nineteenth century, was probably the result of reduced recruitment caused by adverse hydrographic conditions in the main nursery areas of the cod. As shown in Figure 2 there is a certain time lag between the temperature variations and the catch maxima and minima, as changes in the environment first affect the size of the immature part of the stock and later reflect the state of the spawning fishery.

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The author thanks his colleagues at the Marine Research Institute (MRI) for stimulating discussion and critical comments while working on this paper. Special thanks are extended to Gunnar Stefánsson and Höskuldur Björnsson for their help computing the data and in calculating and graphically presenting the yearly catch indices from the Icelandic Annals, the French c.p.u.e.'s, and the temperature variations. All are gratefully acknowledged along with Kristín Jóhannsdóttir (MRI), who typed the text and the tables.

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ICES mar. Sci. Symp., 198: 17–30. 1994

Historic changes in cod stocks and cod fisheries: Northeast Arctic cod

Victor Øiestad

Øiestad, V. 1994. Historic changes in cod stocks and cod fisheries: Northeast Arctic cod. – ICES mar. Sci. Symp., 198: 17–30.

Observations made in Norwegian waters in this century have been used to interpret the fragmentary fishery and climate data from the period 1500 to 1900. During the Little Ice Age, lasting from about 1550 to 1850, the Northeast Arctic cod stock went through large fluctuations in stock size, as reflected in catch per unit of effort and in overall catch. Behind these fluctuations may have been faltering recruitment in periods with very cold climate and lack of herring or capelin in the Barents Sea, two main prey organisms, as both these species also experienced stock fluctuations. The potential detrimental influence of young herring on the capelin stock in the Barents Sea is also considered. The quantity of drift ice around Iceland is considered as an indicator of both the general climate influencing cod recruitment and of the productivity in the main summer-feeding area for Norwegian spring-spawning herring, northeast of Iceland. The deterioration of this area's productivity has coincided repeatedly with sudden collapses in the herring stock. In all cases, except after the fast decline in the 1960s, a recovery of the Bohuslän herring fishery followed these collapses. The fished quantities of cod and herring has increased almost 10-fold for every century during the Little Ice Age, from 5000 t of herring in the 1640s to 1.2 million tonnes in the 1950s; and from 10 000 t of cod in 1590 to 1.2 million tonnes in 1960s. These catch values may indicate an underexploitation of the cod and herring stock at least until the turn of the twentieth century.

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Introduction

The Northeast Arctic (NA) cod stock has been through a severe decline followed by a recent and sharp build-up (ICES, 1993). It is tempting to blame fishing for this type of decline and the restrictive actions of the regulation authorities for the recovery. This is only part of the picture, however, as a heavy blow also came from the ecosystem itself, and not for the first time (Jakobsen, 1992; Nakken, 1994). The recovery, on the other hand, is basically brought about by a number of strong year classes in a situation with significantly improved feeding conditions (ICES, 1992, 1993).

The NA cod stock is not the only one experiencing drastic changes. The Baltic cod stock went through an abrupt build-up from the late 1970s due probably to a shift in the hydrographic conditions promoting egg and larval survival. The decline from the mid-1980s has brought that cod stock back to a level more in line with that experienced throughout this century (Otterlind, 1984; Bagge and Thurow, 1994).

Even more peculiar was the increase of the West Greenland cod stock starting in about 1920 and culminating in about 1965 with a fished quantity of more than 400 000 t yearly during peak catches (Jensen, 1939; Buch and Hansen, 1988). A shift in the Northeast Atlantic current system, influencing the Irminger Current dominating that area, frequently raised the water temperature enough to dramatically improve the survival rate of cod eggs and larvae. A return to the previous current pattern in about 1960 sharply reduced recruitment and the foundation for the fishery eroded rapidly, similar to the situation experienced by the Norse settlements in medieval times (Grove, 1988).

The NA cod stock has been through a number of declines and recoveries in addition to the most recent one (Otterstad, 1960). One decline often commented on occurred at the turn of the century, when ICES was in its formative years and little was yet known about the reason behind fluctuations in fish stocks (Pettersson, 1905; Helland-Hansen and Nansen, 1909). An abortive recovery after that crisis was followed by an even deeper

decline; catches in Lofoten hit the lowest recorded values, i.e. since 1864 (Rollefsen, 1954). A lasting recovery started about 1925 and continued for more than 20 years until the stock reached a level of around 5 million tonnes about 1950 (Lee, 1949; Sætersdal and Hylen, 1964; ICES, 1993).

Detailed landing statistics concerning NA cod, including liver and roe, go back to 1864. There are fairly good records back to 1815, the year following the Norwegian breakaway from 400 years of Danish rule, but information before then is far more obscure and fragmented (Solhaug, 1976). Nevertheless, this paper deals mainly with that early period, back to about 1500.

Intensive fishery and oceanographic research during the last 100 years in Norwegian waters has elucidated inter- and intraspecific relationships, and underscored the influence of short- and long-term variations in ocean currents and water temperature on processes starting with the broodstock and leading on to the next generation. This knowledge will be used to throw light on old records. The main working hypotheses applied will be these:

- Strong year classes of cod are produced when above-normal water temperatures occur around Lofoten and the southwestern parts of the Barents Sea.
- Large populations of young Norwegian spring-spawning (NSS) herring, distributed in the Barents Sea on a regular basis, are a prerequisite for a strong build-up of the NA cod population.
- Strong year classes of young herring distributed in the Barents Sea may for a while severely reduce the recruitment of the capelin population in that region, and might cause one or more years with almost no spawning capelin along the Norwegian coast.
- Expansion of Arctic water with reduced salinity may severely reduce productivity within the summer-feeding areas for NSS herring northeast of Iceland for years, and this might contribute to and even cause severe declines in this herring stock.

The Norwegian cod fishery from 1500 to 1900

The main fish product exported from Norway for hundreds of years was dried cod[1] or stockfish, and the principal region for the production of stockfish was northern Norway. The main season for the spawning NA cod or *skrei* fishery off Nordland and Troms counties was during springtime, and for the young cod fishery in Finnmark in early summer, when the young cod followed the migration of spawning capelin. A minor and variable skrei fishery also took place off the Møre coast (62°N) at the same time as the one off Lofoten (Fig. 1). Cod prepared with salt ("klippfish") had a later introduction as an export article from Norway than in the competing Newfoundland cod fishery, which introduced salted and dried cod to Europe as early as about 1520 (Cushing, 1988).

Quantitative information about the cod fishery is available from about 1300 (Helle, 1967; Nedkvitne, 1978). In the aftermath of the Great Plague (Black death), dried cod was highly priced. During the fifteenth century there was a church-building boom in the main cod fishery districts in Norway, indicating solid income from the fishery to the Church as tithes (Kårstad, 1981). At the end of that century, debt in the region of Nordland began to increase simultaneously with the falling prices of dried cod (Nedkvitne, 1988). The special taxation introduced by the Danish king in 1522 taxed the fishery districts in North Norway at a rate two to three times higher than farmers in mid-Norway (Trøndelag), supporting the view that incomes from the cod fishery were still good (Dybdahl, 1971; Holmsen, 1975; Lunden, 1976; Kårstad, 1981; Nedkvitne, 1988). However, the exchange rate continued to erode in favour of grain, the main product the fishermen had to buy (Fig. 5c; Lindbekk, 1974a; Lunden, 1976; Nedkvitne, 1988).

In 1536, Norway changed from being Catholic to Lutheran. However, the church continued to receive income from tithes for the coming centuries. Information from the tithe paid as dried cod is one of the basic data available[2] about the quantity of cod caught (Nedkvitne, 1988). The other source of information is export data from Bergen and some other main fish-export ports (Dyrvik *et al.*, 1979; Fossen, 1979; Ertresvaag, 1982), including export quantities of other fish types. Although data are incomplete with respect to quantities and destinations, they give a general picture of the trade and the quantities landed and exported to Hanseatic cities on the continent and cities outside the Hansa monopoly in a number of European countries.

General overview of the cod fishery from 1570 to 1900

The production of stockfish during the sixteenth century has been calculated at about 120 000 våger (1 våg = 18.5 kg) per year, or about 10 000 t roundfish (based on data from 1567 and 1577; Dyrvik *et al.*, 1979). By the end of the century, exports doubled and continued to increase, with large annual variations, to 350 000 våger about 1650 or between 25 000 and 30 000 t of roundfish (Fig. 2a and Fig. 3). A lengthy decline followed, reaching less than 5000 t in the 1680s. The decline in the cod stock had started about 1660 in the southern cod district, off Møre (Dyrvik *et al.*, 1979). During the 1680s and 1690s almost every year was a failure in the fishery along most of the coast, as also in Icelandic and Faeroe waters (Lamb, 1979; Nedkvitne, 1988). The capelin cod-fishery off the

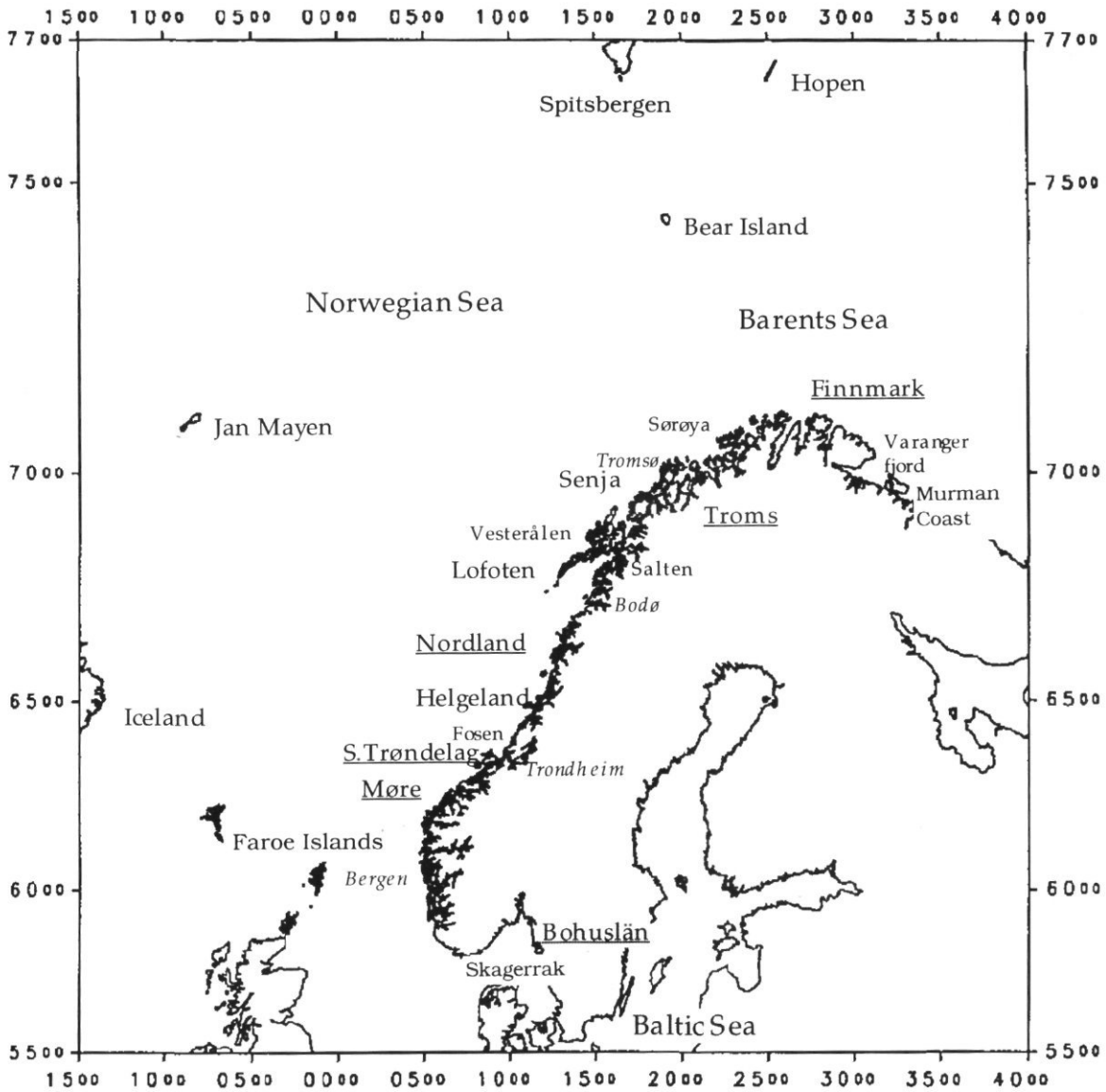


Figure 1. Geographical names used. Names of counties are underlined while cities are in italic.

coast of Finnmark, however, was reasonably good in the 1690s (Fossen, 1979; Nedkvitne, 1988).

The new century started off poorly, but a minor recovery in the cod fishery from 1713 was followed by a more significant recovery from the mid-1720s. During the crop failure of the 1740s, the fishery was good and improved even more in the 1750s (Fossen, 1979).

In about 1750, the export attained in 1650 was again reached, or even exceeded. Salted cod in barrels and, gradually from the mid-1700s, klippfish increased in importance as trading articles. After a new decline in about 1775 came a strong recovery, with an export in 1800 of more than 700 000 våger (i.e. about 60 000 t) roundfish. Of this, klippfish contributed an equivalent of about 14 000 t roundfish. The decline in export during the Napoleonic Wars (1807 to 1814) was partly caused by failure of the fishery in the Lofoten. This failure also hit the Møre skrei fishery from 1790 to about 1820, bringing to a stop a fishery that had been outstandingly good for some decades (Friele, 1877; Dyrvik *et al.*, 1979).

The high export level from 1800 was surpassed in 1825, but by about 1830 the cod fishery stabilized at about 75 000 t roundfish, remaining at this level for 15 years. A new period of expansion started about 1845,

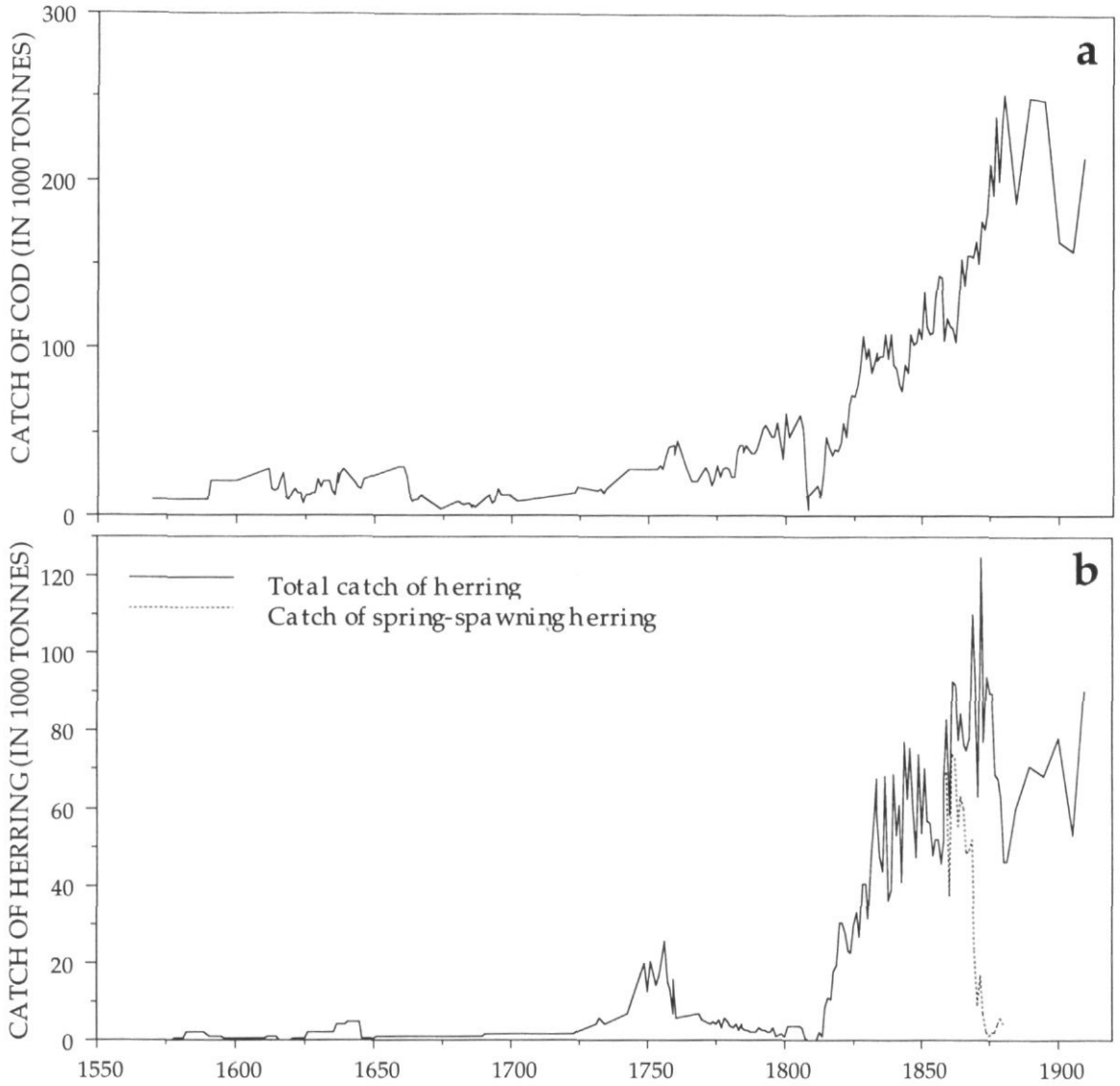


Figure 2. Landings in tonnes of NA cod (a) and herring (b); all types, but with catches of spring-spawning herring indicated for 1860 to 1880, hatched curve) along the west coast of Norway. From 1815 the values are the total for Norway; before that time the data are largely based on export records from Bergen, the main port of exportation. The cod data for 1610 to 1695 are based on tithe records from the Lofoten district adjusted to the level of export from Bergen in 1655. The cod records also include coastal cod catches and catches from the capelin-cod fishery (Dyrvik *et al.*, 1979; Fossen, 1979; Ertresvaag, 1982; Nedkvitne, 1988).

and catches reached a maximum of about 200 000 t roundfish during the 1890s (Fig. 2a). A new decline occurred at the turn of the century (Helland-Hansen and Nansen, 1909).

Stock size and availability

For centuries the skrei fishery was carried out by angling. The first change in the Lofoten region came with gillnets and long-line, from the 1790s (Dyrvik *et al.*, 1979). The dominance of angling makes it easier to compare the catch per unit of effort (c.p.u.e.) during most of the Little Ice Age.

A drawback with angling is that it does not operate well below 100–150 m. When a strong expansion of cold Baltic water dominates the Norwegian coastal current, the migrating and spawning skrei might be forced to stay deeper, becoming less available to angler fishery. A similar effect has been observed on spring-spawning herring (Soleim, 1940).

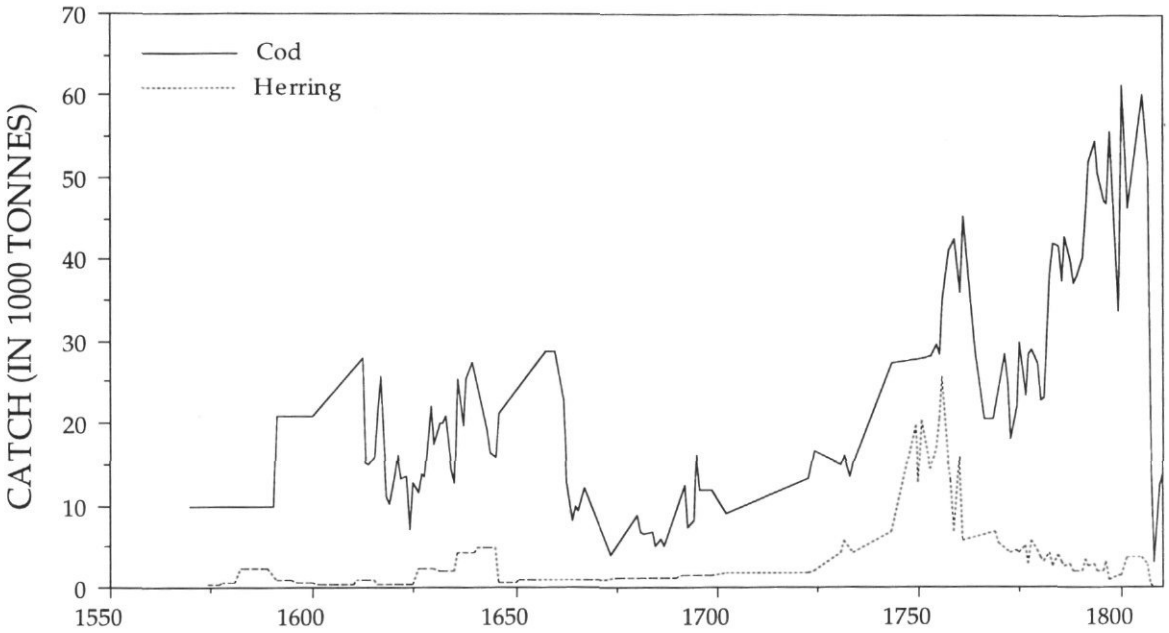


Figure 3. Landings in tonnes of NA cod (upper) and herring (lower; all types) along the west coast of Norway. The data are largely based on export records from Bergen, the main port of exportation. The cod data for 1610 to 1695 are based on tithe records from the Lofoten district adjusted to the level of export from Bergen in 1655. The cod records also include coastal cod catches and catches from the capelin-cod fishery (Dyrvik *et al.*, 1979; Fossen, 1979; Ertresvaag, 1982; Nedkvitne, 1988).

What was the size of the NA cod stock during the Little Ice Age? Did the fishery reflect its size? About 1590, a good fishery season could yield 1300 cod per fisherman, but the normal catch would be 600 to 700 cod, or about 30–40 våger, per fisherman (Dyrvik *et al.*, 1979; Nedkvitne, 1988). Similar mean values (500–1200 cod) were typical for the Lofoten region for centuries until 1925 (Rollefsen, 1954). Improved equipment and better fishing boats did not dramatically improve c.p.u.e. during this long period.[3]

Some of the annual variation was caused by weather conditions during the fishery season and also by the cod being mainly west or east of the Lofoten islands (Nedkvitne, 1988). However, these conditions would not bring about long-lasting trends in the catches; rather, they represented noise within periods of normal, above normal, or below normal catches.

Catches as low as 2–10 våger (40–200 kg) per fisherman after two to three months' effort, and with similar results for about 20 years throughout the Lofoten region, as reported during the 1680s and 1690s, might reflect a cod stock at an alarmingly low level (Nedkvitne, 1988).

The motivation for participation in the skrei fishery was very strong, as most fishermen needed the income to survive. Nevertheless, during prolonged periods of crisis in the fishery, participation would decline if alternative work existed or if the credit system was unwilling to risk further credit[4] (Lindbekk, 1974b; Nedkvitne, 1988). This might have been the case in the 1690s. Variations in the market might also have influenced the quantities caught.

The c.p.u.e. had a range of 1:7 within the timespan from 1864 to 1925, and this might indicate the range in abundance of skrei within that period (Rollefsen, 1954). C.p.u.e. information from the 1600s indicates a somewhat wider range during that century, perhaps about 1:10. The reported range of the tithes in the county of Nordland had values of 1:7 (Lofoten), 1:5 (Steigen), and 1:9 (Bodø), (Fig. 4). These values are within the same range as the abundance variation of NA cod after 1950, which has been about 1:7 (ICES, 1993). In the same timespan the spawning stock has had a range of 1:8, with a maximum of about 1.2 million tonnes in 1959 and a minimum of 150 000 t in 1988 (Nilssen *et al.*, 1994).

The variation in level of tithes at the Faroe Islands was 1:7 from 1584 to 1652 (a total of 39 annual tithe values preserved), if the mean values of the five smallest and largest tithes reported are compared (Zachariassen, 1959). Highest values were reported from 1613 to 1624, with very low values about 1630.

In conclusion, there is reason to believe that the main pattern of variation in catches reflected the true variations in the cod abundance.

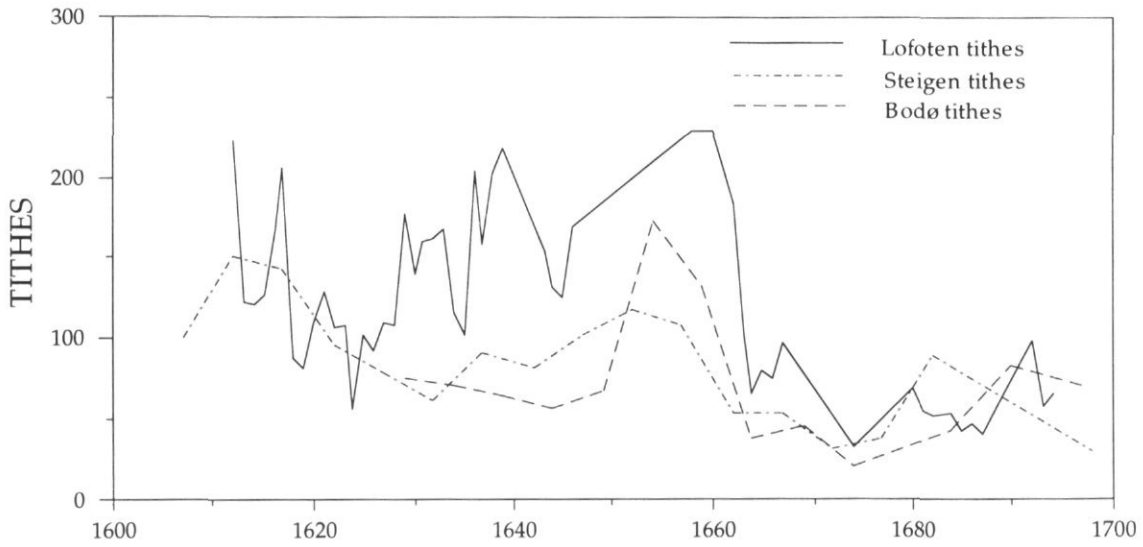


Figure 4. Relative tithe values from three locations in northern Norway to illustrate the common tendency in the fishery of low catches after the 1660s. The records from Lofoten have been divided by five (Aarsæther, 1981; Nedkvitne, 1988).

It is more difficult, however, to say anything about the *absolute* stock size around which these variations took place throughout these 300 years. The modest increase in c.p.u.e. from 1864 to 1925 might indicate that no significant increase in overall stock size took place in that timespan (Rollefsen, 1954). Furthermore, the similarity in c.p.u.e. between short periods during the 1600s, with typically high catch and c.p.u.e. values, and the late 1800s might suggest that the general level of the cod stock could have been similar for some hundred years. The huge increase in landings during the 1800s and 1900s thus being mainly a result of sharply increased fishing effort.

The pattern of participation in the fishery and demographic data

After the Great Plague, the increase in the Norwegian population was greatest in coastal areas with easy access to fishery resources (Aarsæther, 1980), while many former agricultural districts went into lasting decline. The reason for this preference could have been the high price paid for dried cod. Gradually, the price dropped; the turning-point came in about 1570, when the fish:grain price relationship became just as unfavourable as it was before the Great Plague, when 90 kg dry cod was needed to buy grain for one person's yearly need (Fig. 5c; Nedkvitne, 1988). At the same time, the population growth increased faster inland in agricultural districts, fishing villages in particular becoming depopulated (Fig. 5a; Lindbekk, 1974b; Aarsæther, 1980).

In many parts of northern Norway the population declined during the seventeenth century, partly due to periods of failed fishery, but also to repeated crop failure (Fig. 5a, c; Aarsæther, 1980). The combination of fishing and agriculture was the foundation for settlement along most of the Norwegian coast until recently (Lunden, 1976; Nedkvitne, 1988). In the northern district for skrei fishery, Senja, a new decline swept the area as people migrated inland or south (Fig. 5a; Lindbekk, 1974b). The severe living conditions are also reflected in the taxes in the seventeenth century, which declined in northern Norway relative to the rest of the country (Fig. 5b). The taxation per capita declined from 200% to 50% of the taxation level of farmers in Trøndelag from 1574 to 1647 (Lunden, 1976; Fladby, 1978).

Severe periods of famine, as in the 1690s and 1740s, might have led to the abnormal socio-economic reactions described by Petter Dass (1989)[5] (Fig. 5c; Olafsen, 1914). The long-lasting crisis in the cod fishery in the 1680s and 1690s resulted in a deterioration of the infrastructure supporting the fishery.

Recruitment in a colder ocean

The Little Ice Age was in general a lengthy period of low temperature, but also with more severe storms and more precipitation (Lamb, 1979). Its duration is still disputed, but 1550 to 1850 is a generally agreed estimate (Grove, 1988). The temperature record deduced for Iceland during the last 1000 years clearly emphasizes the Little Ice Age (Fig. 6b; Bergthórsson, 1969; Bryson, 1974). Glaciers advanced in the Alps, on Iceland, and in Norway (Grove, 1988). The cold conditions lasted to the

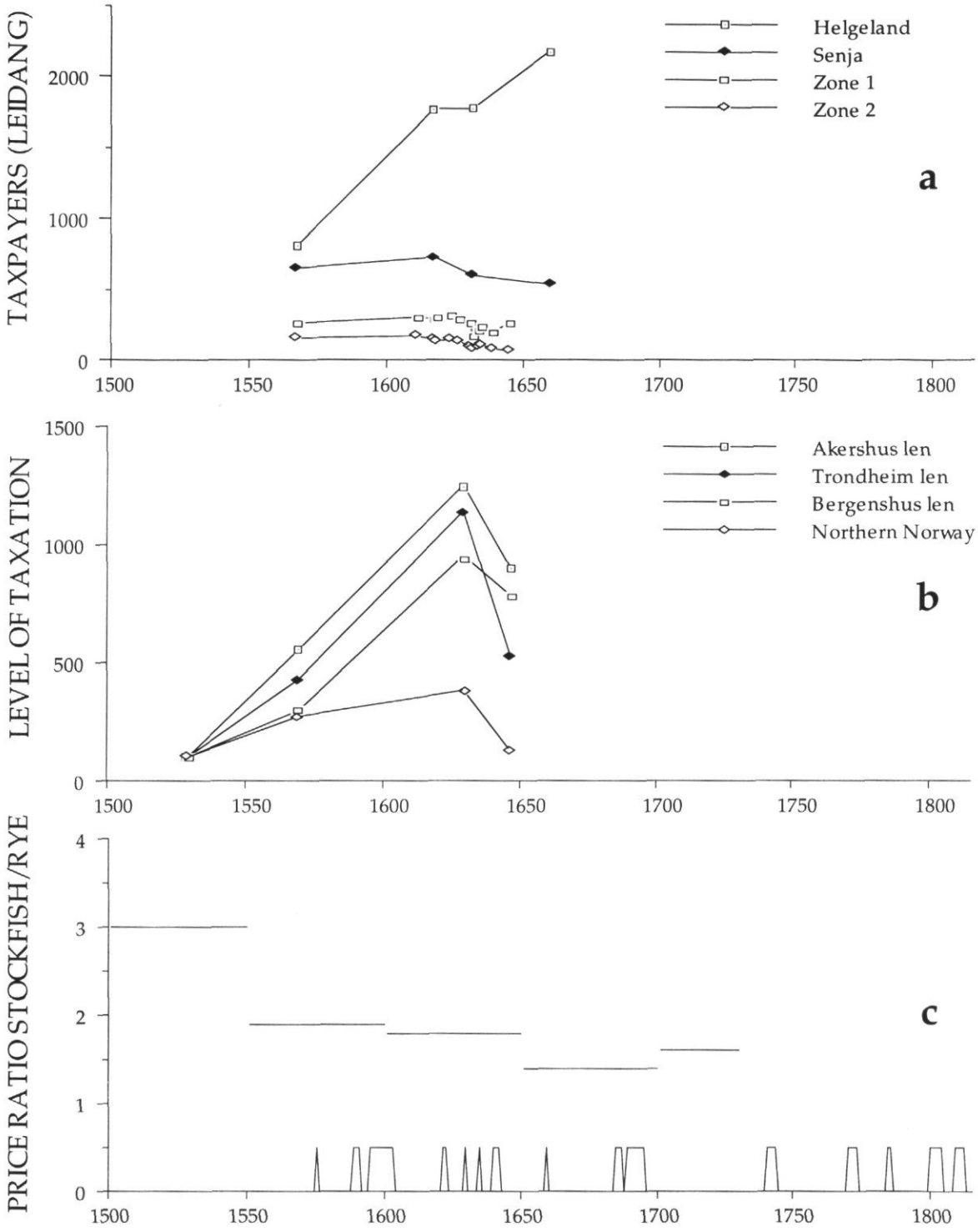


Figure 5. Comparison between a fishery district (Senja) and an agricultural district (Helgeland) to illustrate the changes in settlement preference during the 1600s. Within the Senja region there was a similar pattern recorded as that shown for zone 1 dominated by agriculture and zone 2 dominated by fishery (a; Kårstad, 1981); the shift in taxation level (set to 100 in 1530) in northern Norway during the 1500s and until the mid-1600s compared with the three regions in southern Norway; the depression in northern Norway is obvious (b; Lunden, 1976; Fladby, 1978); years with famine in Norway (c, indicated by peaks along the axis; Olafsen, 1914) and the relative mean price level between stockfish and rye (1 kg to 1 kg) during five time intervals (c, horizontal lines; Nedkvitne, 1988).

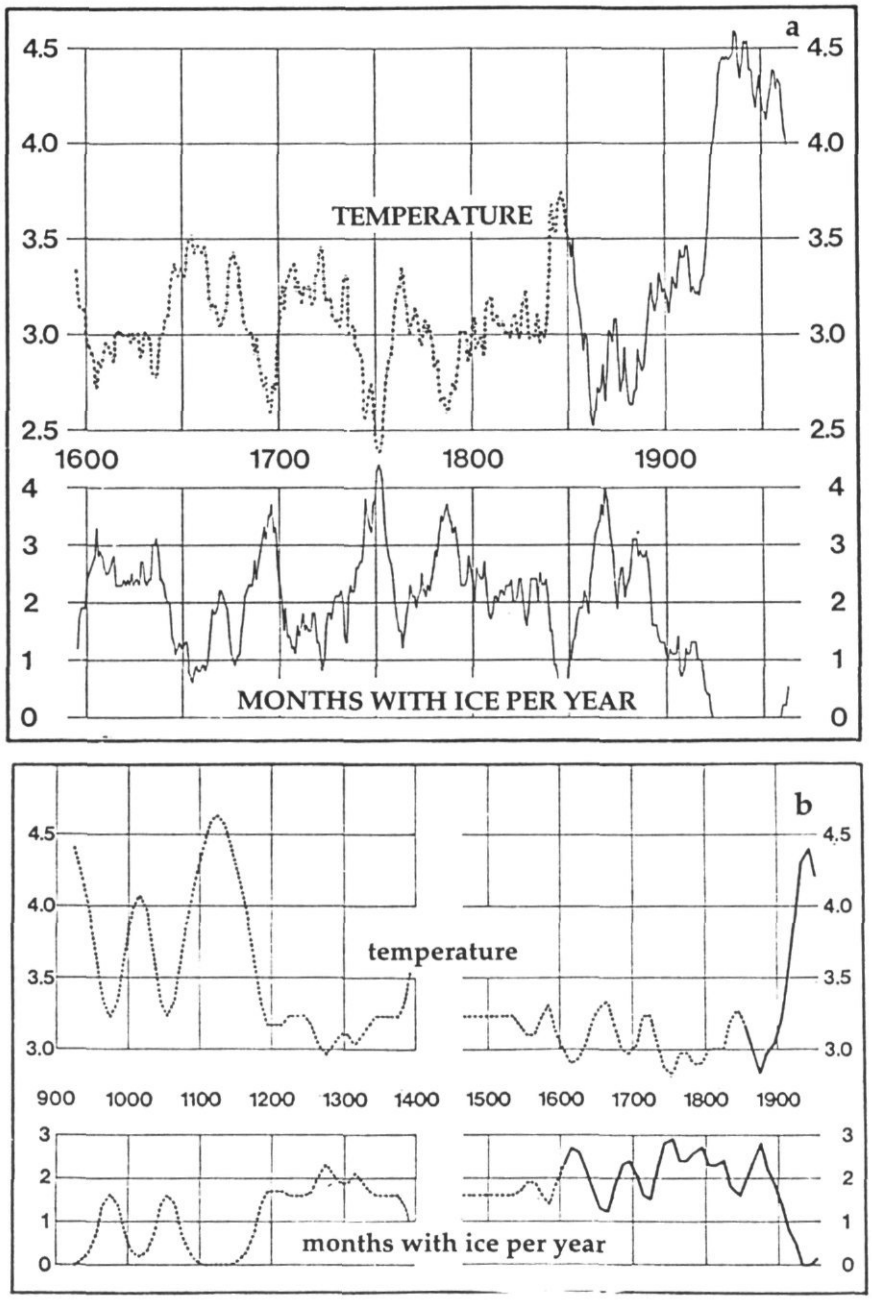


Figure 6. Decadal running means of temperature (top: a) and of ice incidence in months per year (bottom: a) from 1600 to 1950 and running 30-year means of temperature (top: b) and of ice incidence in months per year (bottom: b) from 900 to 1950. Estimated values are presented as dotted curves (Bergthórsson, 1969).

end of the nineteenth century, although episodes of warm summers and winters occurred (Lamb, 1979). The worst period was probably from 1675 to 1704, culminating in 1695, when the drift ice around Iceland reached the Faroes. During this period the sea temperature might have been 4–5°C below the normal for Faroe waters (Lamb, 1979).

There was almost no drift ice off the coast of Iceland from 1920 to 1965 (Fig. 6a; Bergthórsson, 1969; Grove, 1988). This period generally has temperatures above the

mean for 1900–1990 at the Kola section in the Barents Sea (Loeng, 1989). In the period there was a number of strong and medium-strong year classes of cod and herring, often with concurrently strong year classes for the two species (Sætersdal and Loeng, 1987). There seems to be a connection between climate in the Barents Sea and the Icelandic Sea due to the influence from the atmospheric pressure over the Arctic and the wind pattern dictated by the position of the anticyclonic centre (Hill and Jones, 1990; Jónsson, 1994).

In this century, strong year classes of NA cod have been produced only in years with above normal sea temperature in Lofoten and the Western Barents Sea (Ellertsen *et al.*, 1989; Ottersen *et al.*, 1994). Most of the Little Ice Age probably had temperatures below the normal for this century, thus probably resulting in predominantly weak or average strength year classes. Almost total failure might also have occurred, and might have caused the sharp stock decline in the 1680s. However, during the 1690s the capelin cod fishery in Finnmark was good, possibly indicative of a steady recruitment at that time. The relative importance of coastal cod increased during this period, and partly compensated for the decline in the skrei fishery, particularly off the Møre coast, through a coastal bank fishery for cod (Nedkvitne, 1988).

Based on the detailed information on ice around Iceland, there seems to have been a mild period from 1640 to 1670 (Fig. 6a) during which there was one of the best cod fisheries during the Little Ice Age. There was also a mild period from 1720 to 1740 and another from 1840 to 1865 (Grove, 1988) and in both these periods, too, cod recovered markedly. During the lasting mild period from 1920 to 1965, the fishery for NA cod increased from 150 000 t to 1.2 million tonnes (Bergstad *et al.*, 1987). Thus, cod recruitment may have improved during all these mild periods.[6]

The Norwegian herring fishery since 1520

The first fishery reported on spring-spawning herring started about 1520 (Nedkvitne, 1988) and came to an abrupt end in 1564. For about 100 years there was no spring-spawning herring fishery until the next started in 1656 and lasted for a few decades, contributing only very modest catches (Figs. 2b and 3).

A new recovery started in 1698 in the Bergen region, heralding the beginning of a significant fishery for spring-spawning herring in addition to a fat-herring fishery (Boeck, 1871). The best period was from 1749 to 1760 (Figs. 2b and 3). The fishery then declined sharply: from 1784 no spring-spawning herring were caught. Recovery started in 1808 when the spring-spawning herring suddenly showed up off the Norwegian coast and disappeared from Bohuslän (Fig. 7; Boeck, 1871). It culminated in 1872 with 130 000 t, but the contribution from spring-spawning herring that year was only 20 000 t; 1872 was the last year with more than 10 000 t of that herring type for 30 years (Solhaug, 1976).

The NSS herring fishery in Norway has been characterized by "herring periods". The herring fishery in Bohuslän normally evolves about the time the fishery terminates in Norway, and the former arose, according to Devold (1959), as a result of immigrants from the vanishing Norwegian population (Fig. 7; Ljungman, 1882; Pettersson, 1922).

The collapse of the herring population during the 1960s coincided with a severe decline in the production of phytoplankton and zooplankton in the traditional summer-feeding area for herring in the polar front northeast of Iceland, a decline caused by an expansion of polar water covering this area (Malmberg, 1988). A similar situation was observed in the same area at about the same time as the herring vanished in 1873; the

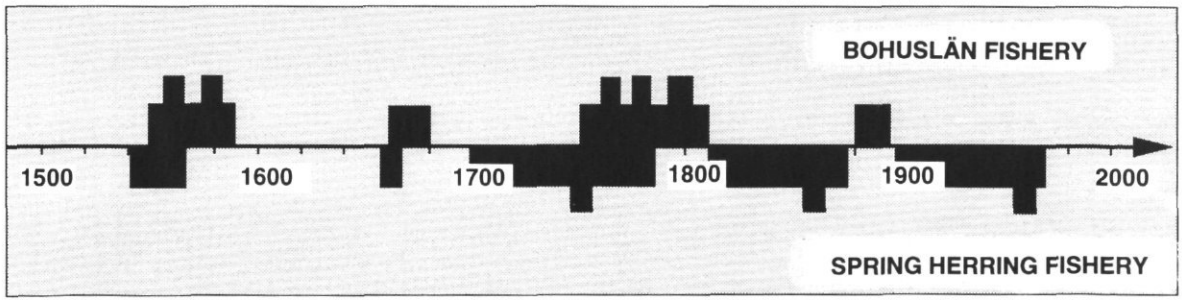


Figure 7. Herring periods off the coat of Bohuslän (above line) and the Norwegian coast; only periods with occurrence of Norwegian spring-spawning herring have been indicated. Culminations are indicated by peaks (Boeck, 1871; Ljungman, 1882; Pettersson, 1922).

Norwegian expedition northeast of Iceland in 1876 with RV "Vøringen" reported greenish water with no zooplankton, although Sars knew from numerous whaling reports that in these waters the ocean normally changed colour owing to the huge quantity of *Calanus finmarchicus* (Sars, 1879a). In general, the period from 1855 to 1902 was characterized by large quantities of drift ice (Fig. 6a; Lamb, 1979; Grove, 1988).

Although historic records from this summer-feeding area are fragmentary, there is strong reason to believe that this area was unsuitable for sustaining the feeding pressure from a large herring population during the very cold period from 1680 to 1710; during the 1780s with severe outbursts of polar water until 1820, and, from the early 1960s, when outbursts of polar water caused unfavourable conditions for production of food for the herring (Lamb, 1979; Malmberg, 1988). The situation back in the 1560s is more obscure, but in 1577 the Atlantic current had already shifted southward, initiating the Little Ice Age (Lamb, 1979).

The capelin cod fishery since the seventeenth century

The cod fishery along the coast of Finnmark has long traditions. It is known, for example, that the taxes paid by the fishermen in Finnmark in 1522 were twice those paid by farmers in Trøndelag (Dybdahl, 1971). In the late 1620s and lasting almost 20 years, this fishery went into crisis (ICES, 1890).

During the eighteenth century new collapses in the young-cod fishery took place, with the longest period said to have lasted for 15 years (ICES, 1890).

The next identifiable decline in the capelin–cod fishery is from about 1830, lasting for almost 15 years (ICES, 1890). The situation was similar off the Murman coast (Sars, 1879b).[7] Recovery started about 1840, but there was no significant fishery until after 1845; it then paralleled an improved fishery in Lofoten lasting until 1895 (Fig. 2a; Rollefsen, 1954; Solhaug, 1976).

Linking indices

The recent recovery of the NA cod stock has firmly demonstrated the tremendous ability of this species to expand in number and accelerate in growth when conditions are favourable. Similar shifts have been repeated over and over again, although none has been recorded in such detail as the one unfolding just now. The driving forces seem to be mainly three: a sharp decrease in fishing mortality since 1988 (Garrod and Schumacher, 1994); above-normal sea temperature since 1989, which may result in strong year classes (Sætersdal and Loeng, 1987; ICES, 1993); and an easy access to young herring as a surplus food supply. At present, about 4 million tonnes of young herring are distributed throughout the Barents Sea. These three factors may outweigh other forces, which then contribute only as minor adjustments.[8]

Higher temperatures are normally accompanied by a stronger flux of Atlantic water into the Barents Sea, leading to an expansion of the area occupied by cod (Jensen, 1939; Lee, 1949; Loeng, 1989; Øiestad, 1990). The higher inflow may also increase the supply of advected food resources, such as *C. finmarchicus* and krill species, especially *Meganyctiphanes norvegica*, and ensure a wider distribution of other food items such as shrimps (*Pandalus borealis*) and, most importantly, young-of-the-year herring (Ponomarenko, 1973; Berenboim and Lysy, 1987).

The cod–herring food web

In what way has the herring contributed as food for NA cod during the Little Ice Age?[9] The spring-herring fishery begun in 1697 reflects the increased availability of all types of herring as food for cod. This availability might have contributed to the recovery of the cod population, which must have been dramatically low during the 1680s and 1690s, when the c.p.u.e. dropped to 10–20% of the value for the best period of the seventeenth century. A strong recovery of the herring stock from the mid-1730s coincided with a strong build-up of the cod population.

In many respects, the fish resource situation in the 1700s had many parallels with this century, with an initial recovery of cod about 1710, stagnation until 1720, followed by a strengthened recovery during the 1720s and 1730s; a particularly good cod fishery in the 1750s and 1760s; decline during the 1770s and poor results in the 1780s. In parallel, the herring population was strong and increasing during the 1750s and 1760s, followed by a decline and final termination of spring-spawning activity along the Norwegian coast in 1784, although this had been negligible since the mid-1750s. During the 1790s there was a new and strong recovery of the cod fishery in the Lofoten region.

At the end of the eighteenth century, the Norwegian fishery in general was restricted to springtime and to the Lofoten region, as the cod fishing took place only in northern Norway with the herring fishery being insignificant everywhere.

The strong recovery of cod after 1845 was paralleled by a very stable capelin–cod fishery off the coast of Finnmark, indicating minor disturbance of the capelin stock by young herring in the Barents Sea. However, earlier, a report exists about herring in the Barents Sea in the 1830s, although no commercial herring fishery took place in northern Norway in that century before

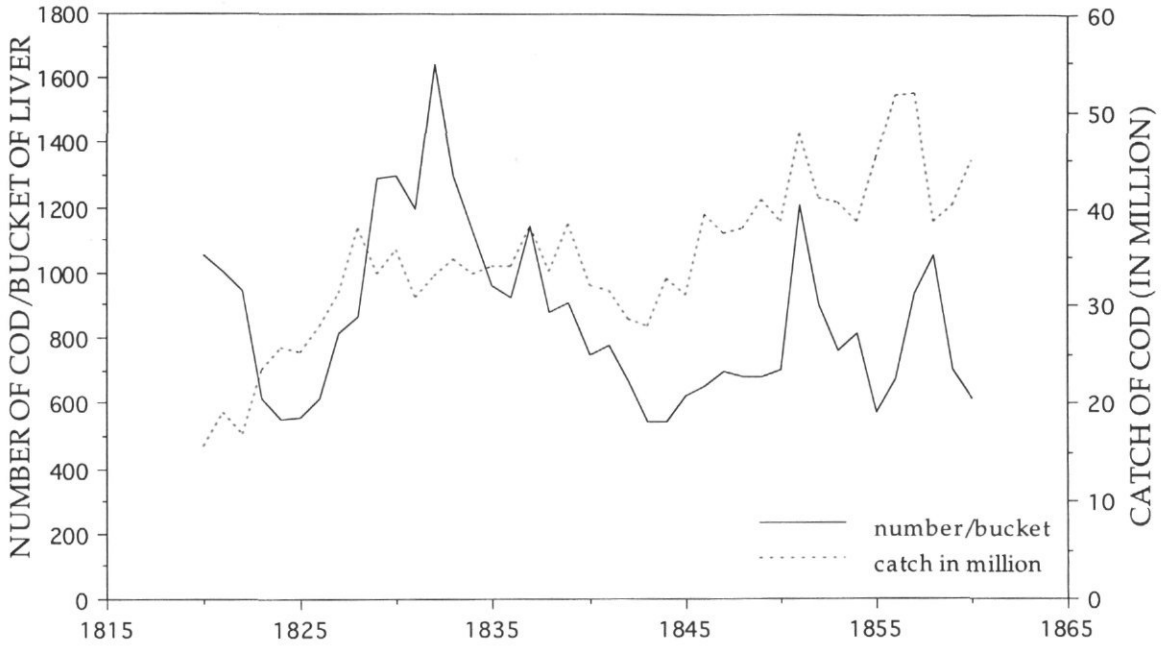


Figure 8. Liver index of the NA cod from 1820 to 1860 expressed as number of cod needed to fill one bucket. The number of cod caught in millions is indicated by a hatched line (Solhaug, 1976).

1850 (ICES, 1890). The strong recovery of the spring-spawning herring in the late 1820s, leading to a record fishery of herring in the 1830s, might have caused a collapse in the capelin population for more than ten years. The extremely small quantity of cod liver per cod from 1828 to 1842 indicates a prolonged food shortage in the Barents Sea (Fig. 8). The situation might have been similar to that observed in the Barents Sea from 1983 on: a single strong year class of young herring might have preyed heavily on the originally large population of capelin larvae in 1984 and 1985 drifting eastward through the area of distribution of young herring. Repeated lack of recruitment resulted in a collapse of the capelin population[10] (Hamre, 1991; Fossum, 1992). The 1983 year class of herring left the Barents Sea during early summer 1986, before it had contributed significantly as food for the cod (Røttingen, 1990a). The Barents Sea was left without any pelagic fish as food for the very numerous cod population (Nakken, 1994). Spawning cod "without roe and liver" was reported in the Lofoten in 1987 just as it was in 1832.[11] In the late 1820s and 1830s, a parallel to the 1983 situation might have occurred twice or even more often, causing the long-lasting decline in the stock of capelin, contributing to the low cod liver index, lasting from 1828 to 1842, and further contributing to a 20-year stagnation in cod catches (Figs. 2a, 7). A repetition of the 1983 situation is observed in 1993, but with a number of year classes of young herring staying in the Barents Sea, serving as food for a numerous and fast-growing cod population (ICES, 1993; Nilssen *et al.*, 1994).

The pulsing of the NA cod stock may be a delayed reflex of the pulsing in the herring population (Figs. 2a, b). This seems to be less clear during 1875 to 1890, a period with no known herring spawning in Norwegian waters, but with a very strong fat-herring fishery along the Norwegian coast. These immature herring most likely originated from spawning somewhere in the North Sea (Runnstrøm, 1935). The collapse of the Bohuslän herring fishery from 1896 was assumed to be the result of a change in current system in the North Sea (Pettersson, 1905, 1922). This change might have reduced the quantity of new recruits of herring being advected to Norwegian coastal waters, as the decline in the cod population was very sharp from 1895 to 1900: the number of spawning cod caught in the Lofoten district in 1900 was less than 25% of the number caught in 1895 (Helland-Hansen and Nansen, 1909).

The herring period initiated by the exceptionally strong 1904 herring year class may have contributed to a first modest recovery of the cod population. As no new strong year classes of herring occurred in the wake of the 1904 year class, the enhancement effect from that year class faded out about 1910, when all fat-herring had been recruited to the spawning stock, a stock with unknown summer-feeding areas and wintering locations, but with

a potential distribution out of range of the NA cod stock. Strong year classes of herring in the late 1910s provided a firm foundation for the observed recovery of the cod population after a new catastrophically low catch in 1920.

The impact on the NA cod stock from temperature and from availability of herring as food needs to be further elaborated. The interpretation given here may have given too much attention to the effect of herring on the NA cod stock, as capelin has been the dominating prey organism for decades (Nilssen *et al.*, 1994). Further examination with more data might highlight the modulating effects on both recruitment and growth from large-scale fluctuations in the two pelagic fish stocks and temperature.

The enormous increases in catches of herring, with typical values of 2000 t in the seventeenth century and 1 million tonnes in the twentieth century, might partly be due to lesser predation pressure from marine mammals. The parallel increase in the cod catches, from 10 000 t in 1590 to 1.2 million tonnes in 1965, might thus indirectly have been caused partly by the decline in carnivorous marine mammals. This trophic network needs further examination (Bax *et al.*, 1989).

Concluding remarks

Available information from the Little Ice Age has been scrutinized in relation to the four working hypotheses put forward in the Introduction. Severe declines of the NA cod stock took place in periods with particularly hostile climate (1) or when the food supply was deteriorating (2); declines in the capelin–cod fishery have occurred, but not necessarily in conjunction with strong recruitment of herring (3); there is strong support for the necessity of the summer-feeding area northeast of Iceland maintaining a strong NSS herring (4).

Most old records are only indicative in their support of the four hypotheses and not conclusive. Future work within this field should profit from the participation of a number of disciplines. This is not a new idea.

The collapse of the spring-spawning herring fishery in 1872 and the parallel recovery of the Bohuslän herring fishery gave rise to much speculation and led to international oceanographic studies in the Skagerrak–Kattegat. It also fostered a genuine interest in old records as a potential source of understanding this peculiar shift in herring fishery (Boeck, 1871; Ljungman, 1882). The Swedish fishery biologist Ljungman (1882) recommended close cooperation between historians and biologists, with historians going through old records under the supervision of biologists. Sars (1879a) suggested the same, but did not expect as much from historic studies as from new field studies.

Significant information on climate and fisheries may still be available from old books such as logbooks of British and Netherlands whaling vessels crossing the Northeast Atlantic from about 1620 to the end of the nineteenth century (Lamb, 1979). Records from Russian sources might soon be available from the same period. The close cooperation between historians and biologists suggested by Ljungman (1882) and Lamb (1979) might be more fruitful today than ever.

Notes

1. Dried cod had a weight of 24% of its round weight and a calorific content of 333 cal g^{-1} compared with 222 cal g^{-1} for salted herring, which had a higher water content (Nedkvitne, 1988).
2. The tithe was calculated when the fish were taken down from the drying rack; for that reason its value accurately reflects the total catch for each main centre of fishing. The method of calculation was stable for the fifteenth and sixteenth centuries, after which this source of information is almost lost because of changes in the taxation system (Nedkvitne, 1988).
3. Detailed information on c.p.u.e. is only available after 1864.
4. Most fishermen were dependent on a specific fishmonger who sold him the needed equipment and other supply on credit in advance of the fishing season. The fishermen were forced by law to sell their catches to the same fishmonger (Nedkvitne, 1988).
5. "The Sea withholds its wealth, before for a year, but now for ten; tumbledown sheds shivered in the cold rain; strong wind brought down the empty cod-drying racks; no vessels, no boats, no sails, no masts; as was the land all desolated", a poem from about 1695 describing the situation at the main fishing harbour, Vågan, in the Lofoten region (first published in 1739; translated for this report by Øiestad).
6. During the warm period in the 1930s, eggs and larvae of cod and haddock were registered on the Bear Island Bank, indicating that some spawning had taken place that far north (Iversen, 1933).
7. Sars got this information from Nordvie, who got it from a Russian publication by Danilewsky on the Murman fishery.
8. Helland-Hansen and Nansen (1909) postulated better recruitment in years with *below*-normal temperature, but they had a short time series from 1899 to 1906 and based their postulate on the quantities of roe and liver: lesser quantities in years with higher temperature.
9. The Norwegian scientist G. O. Sars (1879a) commented on the cod–herring food web in his report to the government, saying: "If the Norwegian Sea did not have the enormous quantities of herring, it would probably not be able to support the huge stock of cod embodying these waters. The richness of carnivorous fish species is dependent upon the abundance of the oceanic herring."
10. Strong year classes of herring might have caused repeated declines in the capelin population following the 1937, 1950, and 1959 year classes (Olsen, 1968). Better described is the decline of the capelin stock following the 1983 outburst of herring and the recent decline of the capelin stock following the 1991, 1992, and 1993 year classes of herring (Røttingen, 1990a, 1990b; Fossum, 1992). Perhaps we will ex-

perience a long-lasting decline of the capelin stock, like the one observed from 1826 to 1840, unless considerably spawning takes place east of the main young herring distribution in the southeast Barents Sea (Olsen, 1968; Hamre, 1991).

11. Also the quantity of roe was exceptionally low in 1832 (Solhaug, 1976). A similar situation was also observed in 1903 when the index for both liver and roe dropped dramatically from a high level in 1900 (Helland-Hansen and Nansen, 1909).

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Bioarchaeology and cod fisheries: a new source of evidence

Thomas Amorosi, Thomas H. McGovern, and Sophia Perdikaris

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Archaeological excavations in the North Atlantic basin over the past two decades have recovered large amounts of fishbones from datable deposits extending back over 8000 years in some areas. Coverage of the last 1000 years (with particular emphasis on the climatic cooling of the "Little Ice Age") is increasingly complete. Recent research makes it possible to reconstruct live lengths from commonly recovered fishbone elements. Preliminary findings indicate that cod of 1 to 1.5 m were being regularly taken in the eleventh to nineteenth centuries throughout the North Atlantic. Changes in fish size and mix of species taken probably reflect technological as well as biological variables. The development of commercial fisheries and the interaction of climate are major research concerns of the North Atlantic Biocultural Organization (NABO), and recent NABO data from Iceland, Greenland, and northern Norway are reported here. Both archaeology and fisheries science may benefit from more active collaboration towards a better integration of a growing body of bioarchaeological evidence with existing documentary and statistical records.

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Introduction

This study is a preliminary and somewhat limited attempt to communicate across major disciplinary barriers. It is preliminary in that it cannot present a complete review of bioarchaeological evidence for medieval and early modern fisheries in any portion of this wide study area, because ongoing research on major collections now under way will surely modify any specific statements made here within the next few years.

It is limited in that we do not pretend that this small research group adequately represents the many workers active in the field of maritime zooarchaeology. Closely comparable work is now being carried out with materials from the Shetland Islands (Bigelow, 1984), Caithness, and Orkney (Barrett, 1993), and by a wide range of scholars active in the International Congress of Archaeozoologists (ICAZ – Brinkhuizen and Clason, 1986). The ICAZ fish working group is acting to coordinate fishbone research world-wide (IOAN, 1992), and will certainly play the leading role in any comprehensively systematic attempt to integrate bioarchaeology with fisheries biology. Several useful reviews of fishbone bioarchaeology summarize current research trends and review the literature (Casteel, 1976; Colley, 1983, 1990; Wheeler and Jones, 1989; Jones, 1991; Rojo, 1991) and we do not attempt to duplicate this coverage here.

This article is also inevitably unsatisfactory, as the need to address a wide range of topics is best treated in a monograph format that is comprehensible to a well-educated but non-specialist audience. But, the necessarily limited space of a short paper runs the risk of simultaneous oversimplification and obfuscation by intradisciplinary jargon. This paper is thus not a theoretical statement, not a literature review, and not a fully developed presentation of basic data. What then do we hope to accomplish by presenting it in such a distinguished collection of international fisheries research?

Our presentation has three major objectives:

(1) To alert the fisheries science community to the existence of a previously unused body of data of potential significance in their efforts to develop long-term models of changing fish populations in different parts of the North Atlantic. Climatologists (Bryson and Murray, 1977; Wigley *et al.*, 1981; Ogilvie, 1991), agricultural historians (Biddick, 1984), historical ecologists (Cronon, 1983; Crosby, 1986; Crumley, 1994), and biogeographers (Dugmore, 1987; Buckland, 1988) have begun to make extensive use of bioarchaeological data in

integrative modeling. Fisheries biologists have not yet made similar use of these increasingly abundant data. Our own experience suggests that this is the result of disciplinary divisions that discourage communication rather than a reasoned rejection. Informing the fisheries science community of the existence of these data is a necessary first step.

(2) To stimulate a dialog with fisheries scientists on the appropriate and more effective use of archaeological fishbone evidence for the mutual benefit of maritime archaeology and marine biology. Such dialog has proven highly productive with a wide range of terrestrial natural scientists during the past two decades. Holocene paleoecologists, in close cooperation with bioarchaeologists and historians, are now producing a dramatic new picture of a wide range of terrestrial ecosystems significantly shaped and directed by pre-industrial societies world-wide (for review see Butzer, 1981; Roberts, 1989; Crumley, 1994). The old view of a pristine pre-human landscape has been banished along with the expectation of a wholly "natural" baseline suitable for starting management models (Cronon, 1983; Crosby, 1986). With the active cooperation of specialists in diverse fields, multi-authored and genuinely multidisciplinary syntheses have generally replaced unsophisticated "data raids" by one discipline upon another in such dryland investigations of human–landscape interaction. The complementary interdisciplinary links that will allow comparable sophistication in maritime human–seascape interaction are only weakly developed at present. We hope that this article will be a small step towards such integration, if only by provoking fisheries scientists to educate maritime bioarchaeologists about the complexity of the marine ecosystems they know so well.

(3) To underline a clear trend in widely separated archaeological fishbone collections that may be of immediate relevance to current fisheries science and management debates. A growing number of substantial, well-excavated bioarchaeological collections suggest that some stocks of cod and other commercial species regularly taken by past North Atlantic fishers were substantially larger and older than most current landings in the same area. These patterns are strongly evident in substantial animal bone collections dating back to the ninth century (AD), and are unlikely to be the result of archaeological sampling error. While these patterns may eventually be demonstrated to be artifacts of preservation, chance, or past fishing practices, we feel that the existence of this widespread pattern urgently needs to be brought to the attention of the professional fisheries community.

Data limitations

However, it is important to emphasize the limitations of zooarchaeology as well as its proven potential. Zooarchaeology cannot provide a direct count of living animals in some ancient sea, nor does this subdiscipline provide a menu for particular meals or reliable estimates of caloric intake of any past human population. Most of the zooarchaeological evidence we now have has been subjected to a daunting range of transformations by ancient humans, scavengers, decay, and archaeological recovery techniques. Much recent research has sought to identify and quantify these taphonomic[1] agents of attrition and sources of statistical "noise". We certainly understand the limits of inherent precision of resolution and the critical issues of sample size and adequacy far better today than a decade ago (Rackham, 1983; Grayson, 1984; Bonnichsen and Sorg, 1989), but more work is still needed in these areas.

Figure 1 presents a simplified model of the degree of attrition suffered by bioarchaeological samples in their transformation from a portion of a living organism in a living population to a preserved and recovered bone

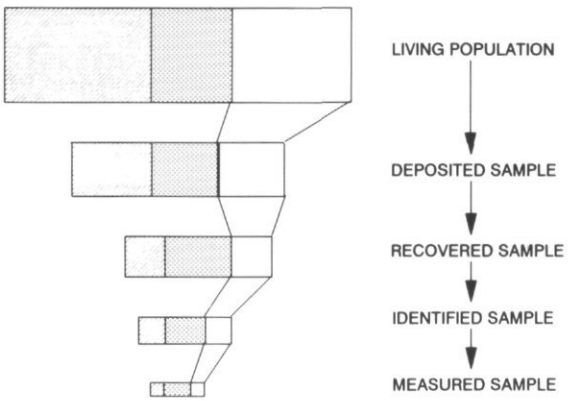


Figure 1. Attrition of archaeological samples. Any archaeological collection is a small fraction of the material originally deposited. This figure illustrates the effect of non-random reduction of the original sample of bones by the effects of decay and differential recovery. The horizontal bar is divided into three major taxa, the clear bar representing cod. Note the changes in relative proportion resulting from different forces of attrition, and the tiny fraction of the original sample that can be measured. Archaeofauna are thus proxy measures of past living populations.

[1]Taphonomy is the study of all the processes of deposition, decay, and destruction that intervene between the death of an ancient organism and its study in the modern laboratory. This is a major subfield of both paleontology and zooarchaeology.

sample. As the figure suggests, only a small percentage of the excavated sample that can be identified to species level can be used for an osteometric study such as employed in this article. The over 30 000 bone fragments thus far identified to species level from the Icelandic site of Stóraborg (Snæsdóttir, 1991a,b) produce only 186 cod premaxillae and 254 dentaries that can be used to reconstruct cod length, despite favorable conditions of preservation and careful excavation.

Most of the bones of most of the animals that died to feed the human occupants of an ancient site never reach the zooarchaeologist – representation is far less than one bone per animal. Except in exceptional circumstances of catastrophic deposition of whole skeleta (as in a bison drive or similar mass kill) (Speth, 1983), bones are usually so scattered that it is unlikely more than a very few were derived from the same individual. Archaeological bone collections (archaeofauna) are thus samples of a far larger ancient population. Zooarchaeological collections are proxy, not direct, measures of past economy and land-use. We are normally comparing patterns in highly transformed samples, not counting whole skeletons.

Trends in such proxy data sets need to be carefully investigated to determine whether they are wholly the result of post-depositional attrition, or if they reflect some surviving patterning in the original economy. Are patterns in individual archaeofauna effectively random? Are clearly non-random patterns primarily structured by the differential preservation and recovery of the basic data? Such proxy data gain their strength and utility through systematic comparison of large samples from well-controlled contexts. Both comparisons of different evidence from the same archaeological site and intersite comparisons of similar materials dated within a narrow temporal framework are now becoming increasingly possible in our region.

One site is a curiosity, two produce controversy, but fifty produce quantifiable patterns with interesting outliers. North Atlantic archaeologists now rarely need to argue the merits of a single site in isolation, but instead are honing their skills in pattern recognition. Such intersite comparisons often demonstrate multiple indicators with the same overall patterning that allows workers to better identify the stochastic "noise" of taphonomy and the preserved outlines of past behavior. Subtle, small-scale shifts in species abundance or morphology tend to disappear in the random noise of archaeological excavation and taphonomic attrition. When a zooarchaeological pattern appears that crosscuts multiple site collections and is recognized by multiple workers in different research centers, it tends to be neither local nor subtle.

This paper reports some selected patterns observed by many workers in a growing number of North Atlantic archaeofauna which we feel are neither random nor shaped entirely by post-depositional taphonomy. However, the satisfactory *explanation* of these patterns is by no means clear-cut. Are persistently repeated patterns in archaeofauna that differ from modern fauna in the same area the result of local or regional biological changes in the prey population, technological changes by the human predators, or archaeological sampling problems? Such explanations will surely require prolonged interdisciplinary cooperation to develop. Before we turn to such specific interpretive issues, some general cultural background may be helpful.

Historic background and research history

North Atlantic Region

Viking-age Scandinavian populations expanded into the North Atlantic between 800 and 1000 AD, probably colonizing the eastern island groups of the Shetlands, Faroe, Orkney, northern Hebrides, and Scottish mainland by 825. The more distant western islands, Iceland, Greenland, and Vinland, were settled within the next three generations – Iceland (traditionally) by 874, Greenland by 985, and Vinland sometime around 1000. This wave of seaborne migration carried an initially homogeneous culture, technology, and economy into the western hemisphere. The first settlers shared a hierarchical, chiefly political organization, a well-developed seafaring tradition, a subsistence economy based primarily on domestic animals and some cereal cultivation and an opportunistic readiness to exploit available wild resources of both sea and land.

Subsequently, during the Medieval period, the various island communities became less homogeneous in subsistence and trading economies, while at the same time undergoing political integration into a Norwegian (and later Danish) Atlantic realm. The increasing diversification of economic strategy in the later Middle Ages partly reflected local adaptation to significantly different local environments, but also seems tied to the relative distance from continental market centers. Archaeological research in some eastern North Atlantic Norse settlements has revealed an eleventh to twelfth century transition from Viking period (ca. AD 800–1100) architecture and artifact assemblages to a Late Norse pattern that persisted through the Middle Ages (Bigelow, 1985, 1992; Batey, 1987). This transition reflects increased importation of durable goods from urban centers, expansion and elaboration of fishing technology, adoption of domestic pottery-making and some less well-understood changes in butchery practice and settlement layout. A Late Norse transition in Iceland is less evident, and it now seems doubtful that the somewhat isolated Greenland colony ever underwent

same sort of transition as can be documented in the eastern island communities. All of these Scandinavian Atlantic communities had significant impact on local flora, fauna, and landforms. By the later Middle Ages, soil erosion and declining fertility were growing problems in Iceland and Greenland (McGovern *et al.*, 1988; Christensen, 1991; Fredskild and Humle, 1991; Hansen, 1991; Jakobsen, 1991).

Beginning around 1300, the climatic cooling known as the "Little Ice Age" began to have a varied but significant impact on local subsistence economies all across the North Atlantic (Ogilvie, 1981, 1991; McGovern, 1990; GISP2, 1992). While the coldest portion of the Little Ice Age seems to have occurred at the end of the seventeenth century, most of the Scandinavian North Atlantic communities felt major effects by the early fourteenth century. The entire region is marginal to submarginal for cereal agriculture and many other components of the transported continental agricultural system were at the edges of their climatic tolerance limits. The region as a whole is thus particularly vulnerable to relatively small-scale shifts in northern hemisphere climate.

The later Middle Ages and Early Modern period saw the complete extinction of the Greenlandic colony (ca. 1450–1500) and major loss of population in Iceland, while the eastern settlements in Shetland and Orkney apparently experienced modest prosperity and population stability or increase. The available evidence thus far suggests that the eastern island communities were more successful in their long-term adaptation to changes in their natural and social environments.

What role did the expansion of commercial fisheries in the later Middle Ages have in the different histories of the eastern and western North Atlantic? How did local elites and commoners respond to the different options provided them by changing natural and commercial environments after initial settlement? How did the existing patterns of exploitation of marine and terrestrial resources affect local decisions to adopt or forego a transition to full-scale commercial fishing? Did pre-industrial fishers have the capacity to affect local fish stocks? The answers to these questions may suggest the complexity of the social dimension of the spread of large-scale fishing in our region.

Fish allometry

Methodology

The estimation of the size of fish from archaeological remains is not new. There are many studies in which various cranial elements have been used to estimate the size (either length or weight) of the animal (summarized in Casteel, 1976; Bigelow, 1984; Rojo, 1986; Amorosi, 1989; Wheeler and Jones, 1989; Colley, 1990; Jones, 1991; Barrett, 1992). Studies simply comparing the archaeological bone with a modern bone (where the size, weight, and age were known for modern comparative specimens; see Casteel, 1976) have given way to more refined statistical analyses (for review see Colley, 1983; Jones, 1984, 1991).

Such comparative approaches are most effective if a large number of modern specimens are available for comparison with the excavated specimens. Modern examples should be close to the size of archaeological fish recovered, and should also include a wide range of variability sufficient to account for the natural variation of bone size in the species (Desse, 1984). Wheeler and Jones (1976) have carried out such an analysis for the Atlantic cod (*Gadus morhua*) using two bone elements in the skull – the premaxillary and dentary (see also Morales and Rosenlund, 1979; Rojo, 1986).

Measurements taken on the dentary and premaxillary follow Wheeler and Jones (1976) and are illustrated in Figure 2. They were taken with a digimatic caliper (Mitutoyo, Model Series 500), reading to the nearest 0.01 mm. The dentary measurement described as "D1" by Jones (1991) is the dentary depth taken at the mental foramen (Rojo, 1991). The measurement taken on the premaxillary is the length of the constricting neck of the anterior portion (or symphyseal margin, Rojo, 1991) of the ascending and articular processes.

The regression formulae as developed by Wheeler and Jones (1976) are:

$$\text{Dentary "A" or "D1": } Y = (80.14 \times X) + 102.3$$

and

$$\text{Premaxillary "A" or "P1": } Y = (60.83 \times X) + 10.35.$$

The "A" notation follows Wheeler and Jones's (1976) original paper. Jones, in his 1991 thesis, describes the same measurement but gives a different notation, "D1". Similarly, Jones later assigns the notation "P1" in his 1991 study for the premaxillary measurement. We suggest that Jones's 1991 terminology be accepted as standard to avoid confusion.

Limits of precision

Both Härkönen (1986) and Jones (1991) have argued that these regression formulae do not provide a statistically calculated confidence or prediction interval. Both these authors have extensively demonstrated that the relationship of bone element size to estimated fish length for small to medium-sized individuals is fairly regular. However, in large-sized animals this relationship has been described by Jones (1991, pp. 115–116) as more variable.

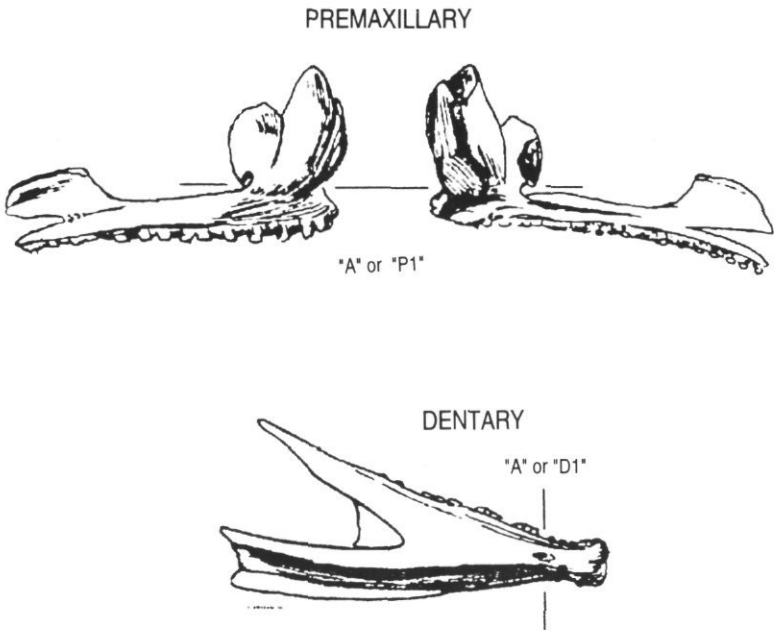


Figure 2. Osteological measurement points. The premaxillary and dentary are two skeletal elements which regularly survive in measurable condition in archaeological collections. Standard measurement points follow Wheeler and Jones (1989). "A" or "P1" = premaxillary width; "A" or "D1" = dentary depth.

The true importance of Jones's careful study is not that it flags yet another area of statistical imprecision in fuzzy archaeological data sets, but that Jones's method and results establish a practical limit to cod length reconstruction regression formulae. Jones (1991, pp. 116–165) further investigated this problem by examining bone measurements of the cleithra, dentaries, premaxillae, and otoliths of modern cod, saithe (*Pollachius virens*), pollack (*P. pollachius*), haddock (*Melanogrammus aeglefinus*), and ling (*Molva molva*). His meticulously gathered findings demonstrate three important points:

1. Selected fishbone and otolith size parameters were indeed strongly correlated with fish total length (many of Jones's graphs show an r value of >0.95.
2. Large fish produce bones and otoliths which are more generally irregular in their proportions relative to fish length than those of small fish. Older fish appear to have more variable growth rates.
3. Most bone elements show a size relationship that is curvilinear. Growth slows with age.

Of particular interest for this study is Jones's second result, namely, that large fish produce a more variable length size than those of smaller individuals. Our reconstructions of cod length from archaeological specimens are thus most accurate for smaller fish, but the precision of the reconstruction decreases with the larger individuals. Jones's data indicate that the regressed reconstructed cod estimated at 140 cm show a ± variation just under 20 cm (Jones, 1991, Figs. 43 and 44). For larger specimens, our data might be better presented as a probability range rather than as a point estimate (e.g. 120–160 cm rather than 140 cm). While single-point estimate figures will be used in this preliminary presentation, users should be aware of the variability inherent in the reconstructions.

As noted above, a practical response to inherent fuzziness in archaeological (or any other) data is to expand the number of data points and increase their geographical and temporal range. If distributions prove consistent, or at least present logical patterns of variability, we may have some basis for separating signal from noise. This article adopts this comparative approach, presenting data from three different parts of the medieval–early modern North Atlantic, where three distinct (but related) human populations interacted with at least three distinct "cod stocks".

Greenlandic data

A substantial number of quantifiable archaeofauna have been recovered from both the Eastern Settlement (modern Qaqortoq and Narsaq districts in the extreme south) and the smaller Western Settlement (modern Nuuk district in the southwest) during nearly one hun-

dred years of professional archaeological research (see McGovern, 1985b for summary, also Nyegaard, 1992). None of the nearly 30 excavated archaeofauna have contained more than a tiny number of fish bones, despite extensive sieving efforts since 1976 and generally excellent conditions of organic preservation. While Norse Greenlanders undoubtedly exploited fish more than the bone collections document, it also seems clear that they did not participate in a commercial fishery comparable to those documented historically and by zooarchaeology from Iceland, Shetlands, and North Norway.

Most of these Greenlandic animal bone collections are from the later phases of the Norse occupation, when Greenlandic cod stocks were probably adversely affected by cooling climate (see Jónsson, 1993; Buch *et al.*, 1994; Dickson *et al.*, 1994). However, three stratified collections from Greenland are now radiocarbon-dated to the settlement period (ca. 985–1100), one from the Eastern Settlement at Narsaq (Ø 17a, Vebæk, 1993) and two (V51 Sandnes, V48) from the Ameralla region of the Western Settlement (McGovern *et al.*, 1983; McGovern and Bigelow, 1984; McGovern, 1985a; Arneborg, 1991; Vebæk, 1993). These collections provide a view of economic organization in the Medieval Warm Period (MWP) prior to impacts of the Little Ice Age (Table 1).

As Table 1 indicates, Greenlandic settlers of the Medieval Warm Period did not exploit fish any more heavily than their descendants living at the beginning of the Little Ice Age. Some changes between the early and final phases (only the top and bottom of the deep middens at V51 and V48 are presented here) are evident, but these economic changes are evolutionary, not revolutionary – cod fishing did not boom and then bust (Fig. 3). From the beginning, Norse Greenlanders apparently adopted a very different approach to marine resource extraction and transatlantic commercial contact, emphasizing seal hunting and long-distance hunts for walrus ivory and other high arctic products (McGovern, 1985a, 1992). If cod fish were indeed plentiful in southeast Greenland during the settlement period, the Norse Greenlanders did not choose to exploit them intensively. Norse Greenlanders of the eleventh and twelfth centuries (like their descendants in the fourteenth and fifteenth centuries) apparently centered their marine hunting effort on seals, not cod.

As emphasized elsewhere (Keller, 1991; McGovern, 1991), Norse Greenland may serve as a classic example not of implacable climate impact on humans, but of the effect of human politics and social organization on resource use. The Greenlandic case also underlines the need to examine all the evidence for a past economy – zooarchaeological, locational, paleoecological, and historical – in attempting to assess climate impact on a particular economic component. Fluctuations in the cod catch that stressed Icelandic settlements in the later Middle Ages may not have bothered the Greenlanders at all.

Table 1. Animal bone collections from eleventh century and fourteen–fifteenth-century sites in Greenland. Three stratified sites from the extinct Norse colony in West Greenland provide a comparison of economic organization in the settlement period (ca. AD 985–1100) and the end of the Norse occupation (ca. AD 1350–1450). Only large collections are included (NISP = number of identified specimens). Note that even during the Medieval Warm Period of the eleventh century fishbones make up only a trace element in the bone collections. Seals and walrus apparently provided subsistence and market products. Data from McGovern (1985) and the NABO Zooarchaeology Database.

Settlement	Eastern		Western		Western	
Sieved?	n	n	y	y	y	y
Site status	Middle		High		Low	
Site locality	Narssaq	Narssaq	Ameralla	Ameralla	Ameralla	Ameralla
Sample size (NISP)	1,073	505	503	1,832	1,159	3,679
Site name	Ø 17a	Ø 17a	V 51	V 51	V 48	V 48
Phase	Lower	Upper	Phase 1	Phase 5	Phase 1	Phase 4
Approx. dates (AD)	ca. 4000	? terminal	ca. 1000–1175	ca. 1250–1325	ca. 1000–1100	ca. 1300–1350
Total % NISP						
Total domestic	35.51	37.5	16.9	15.87	15.01	9.84
Caribou	8.01	4.37	7.95	16.09	4.4	4.54
Birds	2.89	1.19	4.37	11.15	6.04	3.46
Cetaceans	3.17	4.17	4.57	3.19	0.09	0.42
Seals	46.97	50.2	32.01	20.76	68.51	81.26
Walrus	2.33	0.6	17.69	32.02	0.6	0.18
Fish	0	0.2	0.2	0.05	0	0.22
Molluscs	0	0	15.31	0.82	4.83	0

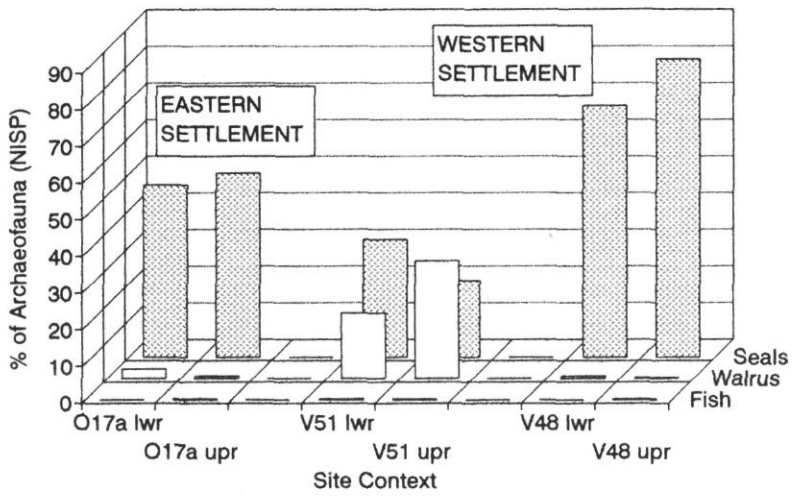


Figure 3. Major marine taxa exploited in Norse Greenland. The lowest (eleventh century–Medieval Warm Period) levels of three Norse sites in Greenland compared to upper levels (fourteenth–early fifteenth century–Little Ice Age). Even during the Medieval Warm Period prior to AD 1300, fish were not extensively exploited in either the modern Nuuk district (V 51, V 48) or the modern Narsaq District (Ø17a). See also Table 1.

Icelandic data

The Icelandic data collected for this article represent a varied set of samples (Tables 2, 3) from stratified, multicomponent sites of Viðey (Hallgrímsdóttir, 1987a, b, 1989, 1991a, b, 1992; Amorosi and McGovern, 1993) and Bessastaðir (Smith, 1987; Baldursson, 1990; Amorosi, 1991; Ólafsson 1991, Amorosi *et al.*, 1992) located in the greater Reykjavík vicinity, the abandoned farmstead of Miðbær (Amorosi and McGovern, 1989), located on the island of Flatey in Breiðafjorð, western Iceland, the church farms of Svalbarð in the northeast (Amorosi, 1989, 1991, 1992), and Stóraborg located on Iceland's south coast (Snæsdóttir, 1987, 1991a,b; Amorosi, 1989, 1991). Historically, these sites functioned as "elite" farmsteads. The sites of both Bessastaðir and Viðey served in the medieval period as the chieftain's manor; Viðey also served as the site of a cloister. In the more recent past, both sites served as quasi-Danish colonial residences in the 1700–1800s. The sites of Svalbarð and Stóraborg were church farms throughout much of their history, and it is surmised that the site of Miðbær served in a similar capacity. Animal bone data from these farms provide interesting evidence of access to an apparently wide range of resources.

Table 2. Animal bone collections from ninth to thirteenth century sites in Iceland. Five sites dating to the Icelandic Settlement Period (traditionally ca. AD 870–930) and the Commonwealth Period (AD 930–1264) provide a sampling of economic strategies in different parts of Iceland in the two periods. Note the highly variable role of fishing in the early Middle Ages in these samples. Only larger collections are included in this table. Data from Amorosi (1991) and the NABO Zooarchaeology Database.

Sieved?	n	n	y	y	n	y
Site status	?	?	Middle	High	High	High
Site locality	Reykjavík	Westman Is.	Eyjafjord	Þistilsfjörð	Hrafnkelsdal	Þistilsfjörð
Site territory	SW coastal	S coastal	N inland	NE coastal	E far inland	NE coastal
Sample size (NISP)	517	1,860	1,656	1,502	1,492	1,594
Site name	Tjarnargata 4	Herjólfsdalur	Granastaðir	Svalbarð-2	Aðaibol	Svalbarð-4
Phase	Settlement	Settlement	Commonwealth	Commonwealth	Commonwealth	Commonwealth
Approximate dates (AD)	9th century	9th century?	ca. AD 950	AD 1050–1150	before AD 1158	AD 1150–1250
Total % NISP						
Total domestic	33.75	22.7	86.15	37.22	97.86	15.31
Birds	62.87	74.8	0.81	8.52	1.81	37.89
Cetaceans	0.42	0.23	0	2	0	3.01
Seals	0.21	0.55	0	6.06	0	3.01
Other mammals	0.63	0	0	0	0.07	0
Fish	2.32	1.72	12.55	42.74	0.27	34.76
Molluscs	0	0	0.49	3.46	0	6.02

Table 3. Animal bone collections from later Medieval to Early Modern sites in Iceland. Six sites from different parts of Iceland that span the later Medieval (ca. 1264–1550) to Early Modern (ca. 1550–1800) periods provide a sample of later economic strategies. Note the increasing relative percentages of fish in collections from Breiðafjorð (Miðbær) and Reykjavík area (Nesstofa, Viðey, Bessastaðir) and the consistently high relative percentages of fish in the collections from the south coast (Stóraborg) and the northeast (Svalbarð). Only larger collections are included. Data from Amorosi (1991) and the NABO Zooarchaeology Database.

Sieved	y	y	y	y	y	n	n	
Site status	?			High		High		
Site locality	Breiðafjorð			Þistilsfjörð		Reykjavík		
Site territory	NW coastal			NE coastal		SWcoastal		
Sample size (NISP)	701	5,232	2,770	1,058	3,668	2,784	3,218	
Site name	MIDBÆR			SVALBARD		VIDEY		
Phase	Lower	Middle	Upper	AU5	AU7/8	Medieval	Early modern	
Approx. dates (AD)	ca. 1250–1400	ca.1500–1600	ca. 1600–1700	ca. 1250–1400	ca. 1636–1800	L. Medieval	18th–19th century	
Total % NISP								
Total domestic	2.28	0.97	0.42	27.32	10.2	41.56	18.46	
Birds	40.94	33.21	12.27	6.81	1.28	21.3	20.73	
Cetaceans	0	0	0	6.81	0.83	0.18	0.34	
Seals	6.13	2.82	0.46	2.17	17.58	1.44	0.09	
Other mammals	0	0	0	0	0.09	0.11	0	
Fish	34.66	52.24	75.60	55.58	57.7	34.12	56.06	
Molluscs	15.98	10.76	11.16	1.32	12.255	1.29	4.32	

Sieved?	y	y	y	y	y	y	y	y
Site status	High			High		Medium		
Site locality	Reykjavík			Reykjavík area		South coast		
Site territory	SW coastal			SW coastal		S coastal		
Sample size (NISP)	2,187	1,171	5,894	95	11,096	19,189	2,450	10,686
Site name	NESSTOFA			BESSASTAÐIR		STÓRABORG		
Phase	Early	Middle	Late	L. Med.	Early Modern	Early	Middle	Late
Approx. dates (AD)			17th–19th	14th–15th	17th–19th	ca. 1450–1600	1600–1700	1700–1800
Total % NISP								
Total domestic	1.83	5.38	0.78	95.79	8.12	13.01	18.61	16.1
Birds	0.1	0.09	0.41	1.05	1.21	1.9	0.49	0.3
Cetaceans	0	0	0	0	0.03	0.04	0.04	0.02
Seals	0	0	0.02	0	0.03	0.15	0.04	0.03
Other mammals	0	0	0	1.05	0.31	0	0	0.01
Fish	46.41	87.45	93.62	2.11	87.02	84.23	79.96	81.8
Molluscs	51.35	7.09	5.48	0	3.28	0.68	0.86	1.75

There are numerous archaeological patterns that can be observed in the Icelandic archaeofauna (cf. Amorosi, 1989, 1991). Those pertinent to this article include:

(1) Icelandic sites have had a variable percentage of fish from settlement times onwards (Table 2), with local geography and possibly status playing a major role (contrast inland sites like Granastaðir with Svalbarð). Unlike in Greenland, in Iceland there is clear evidence of locally significant subsistence fishing back to the tenth century (see discussion in Amorosi, 1989, 1991).

(2) Cross-cutting all local variation there is a clear trend towards a greater relative percentage of fish in later sites (Table 3). The increase becomes particularly marked during later medieval times (ca. 1250–1500). By early modern times (ca. 1500–1800) fish bones dominate all recovered bone collections, comprising between 60 and 90% of the total archaeofauna of existing early modern sites. While preservation and recovery factors certainly affect these numbers, the order-of-magnitude differences in overall pattern are clear cut. Zooarchaeology confirms the existing documentary evidence for the development of commercial fishing in Iceland, and should allow greater detailed reconstruction in the future.

(3) While some other species have been identified, the Icelandic archaeofauna is dominated by Atlantic cod. This seems to be the case for all time periods now documented. This is not the case in other North Atlantic archaeofauna, where other species are almost as common (Colley, 1983, 1990; Bigelow 1984; Jones, 1991; Barrett, 1992).

(4) Application of the osteometric techniques discussed above to these excavated collections has indicated a fairly consistent patterning in reconstructed cod lengths (Figs. 4, 5). Both the dentary and premaxillary specimens measured produce similar normal distributions, with a mean around 90–100 cm (except at Miðbær, where the mean is ca. 60 cm). The data are internally consistent and are unlikely to be the product of recovery or preservation alone. There is no significant variation in

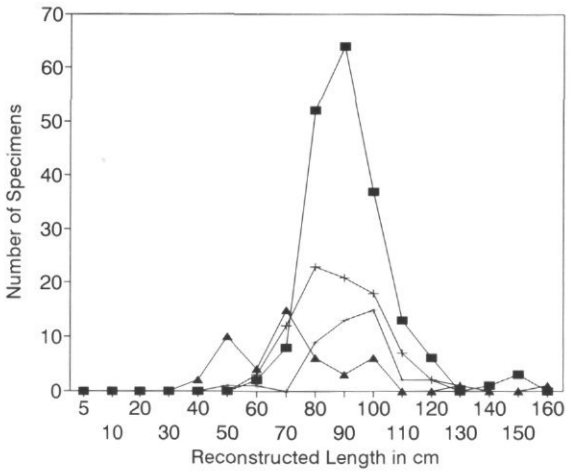


Figure 4. Distribution of reconstructed cod length based on premaxillary. Reconstructed cod lengths from Miðbær (Breiðafjörð), Viðey (Reykjavík), Svalbarð (Þistilsfjörð), and Stóraborg (south coast). While the mean reconstructed length on the premaxillary samples for Viðey (Reykjavík), Svalbarð (Þistilsfjörð), and Stóraborg (south coast) appears strongly unimodal with mean around 90–100 cm, the Miðbær premaxillaries suggest a less unimodal distribution of somewhat smaller individuals. ■ = Stóraborg; ∗ = Viðey; ▲ = Miðbær; + = Svalbarð.

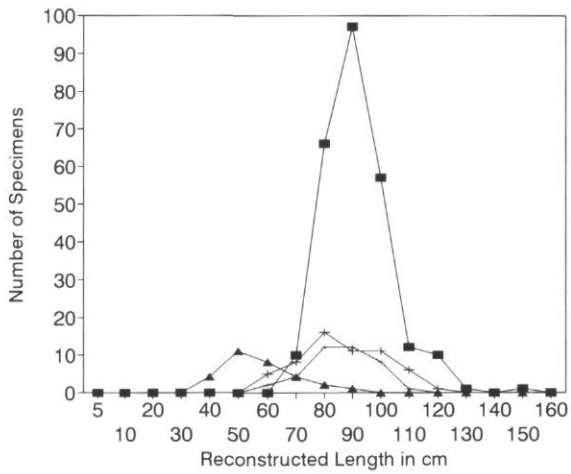


Figure 5. Distribution of reconstructed cod length based on dentaries. Reconstructed cod lengths from Miðbær (Breiðafjörð), Viðey (Reykjavík), Svalbarð (Þistilsfjörð), and Stóraborg (south coast). While the mean reconstructed length on dentaries for Viðey, Svalbarð, and Stóraborg again appears strongly unimodal with a mean around 90–100 cm, the Miðbær premaxillaries again suggest a different distribution of smaller individuals. ■ = Stóraborg; ∗ = Viðey; ▲ = Miðbær; + = Svalbarð.

this distribution pattern through time at any site from ca. AD 1050–1800 (Table 4). Present data thus indicate remarkable stability in the recovered cod sample over a 400–800-year time period in the northeast, south, and southwest coastal regions. Internal consistency of data within sites and in intersite comparison is impressive, and probably reflects real trends rather than taphonomic noise.

Northern Norwegian data

There has been much archaeological research in northern Norway that has provided paleofisheries information (see Johansen, 1979, 1982; Holm-Olsen, 1981, 1986; Bertelsen, 1979) and has demonstrated that fishing has been an important economic adaptation in the region for thousands of years.

More specific forms of information about medieval and post-medieval fisheries have emerged at an increasing rate from excavations in the Lofoten and Vesterålen Islands, as well as the Karlsøy commune, Helgøy project in the past 15 years. These rugged island groups extend westward from North Norway's arctic coast. Although located well above the Arctic Circle, the islands enjoy a temperate to boreal climate, and they may have supported a range of possible economic adaptations, including pastoral agriculture (Bertelsen, 1991, p. 23).

Late Medieval and Early Modern archaeofaunas from sites in the Karlsøy commune include high percentages of fishbones (Table 5). In common with Icelandic fishbone samples, the studied North Norwegian collections include a full range of domestic fauna largely comprising cod remains, although on some sites the bones of saithe, ling, cod, haddock, and flatfish species have been recovered in greater than trace quantities (Fig. 6). Fish length data for these collections have not been published.

Excavations at the site of Vågan, near the center of the modern Lofoten fishing industry, have also produced large fishbone collections that will eventually yield vital information on medieval and post-medieval commercial fishing. Investigations at Vågan have documented the evolution of a proto-urban center, a process which began ca. AD 1200 (Bertelsen, 1979, 1991; Bertelsen *et al.*, 1987). "Storvågan" developed into an important node in the growing Norwegian codfish trade of the Middle Ages, sending dried fish south to Bergen, and ultimately to the Hanseatic trade network during the fourteenth and seventeenth centuries (Urbańczyk, 1992). While extensive studies of stratigraphy, site architecture, and artifacts have been undertaken, zooarchaeological analyses are just beginning. The Storvågan archaeofauna now number approximately 60 000 identified fragments (Perdikaris, 1993), and the sample will increase while excavations continue.

Table 4. Distribution of reconstructed cod length at Stóraborg. These data are aggregated by period (AD 1450–1600, 1600–1700, 1700–1800) and serve to indicate the stability of the distribution of reconstructed cod length over the ca. 350-year time period documented. Other Icelandic fishbone collections show similar stability in reconstructed fish length from ca. AD 1050–1800. Data from McGovern *et al.* (1985).

Length group (in cm)	Early phase ca. 1450–1600		Middle phase ca. 1600–1700		Later phase ca. 1700–1800		Total 15th–18th centuries	
	no.	%	no.	%	no.	%	no.	%
5–9	0	0.00	0	0.00	0	0.00	0	0.00
10–19	0	0.00	0	0.00	0	0.00	0	0.00
20–29	0	0.00	0	0.00	0	0.00	0	0.00
30–39	0	0.00	0	0.00	0	0.00	0	0.00
40–49	0	0.00	0	0.00	0	0.00	0	0.00
50–59	0	0.00	0	0.00	0	0.00	0	0.00
60–69	0	0.00	0	0.00	0	0.00	0	0.00
70–79	2	1.60	3	10.00	5	5.05	10	3.94
80–89	25	20.00	5	16.67	36	36.36	66	25.98
90–99	43	34.40	13	43.33	41	41.41	97	38.19
100–109	35	28.00	9	30.00	13	13.13	57	22.44
110–119	10	8.00	0	0.00	2	2.02	12	4.72
120–129	8	6.40	0	0.00	2	2.02	10	3.94
130–139	1	0.80	0	0.00	0	0.00	1	0.39
140–149	0	0.00	0	0.00	0	0.00	0	0.00
150–163	1	0.80	0	0.00	0	0.00	1	0.39
Total	125	100	30	100	99	100	254	100
Mean	89.56		83.29		91.86			
SD	3.53		2.96		2.97			
Range maximum	146.47		98.38		122.43			
Range minimum	65.53		64.73		78.35			

Measurement A (x) regression (after Bigelow, 1984) $y = 80.14x + 102.3$.

Although analyses are ongoing, some clear zooarchaeological trends are already apparent in the Storvågan collections (Fig. 7). The great variability in cod size in the early and late phases could reflect the influence of several ecological, technological, and consumption variables. The analysis is too preliminary to distinguish the particular variable accounting for the diverse cod size present at Storvågan at different times. More concrete

Table 5. Animal bone collections from later Medieval to Early Modern sites in northern Norway. Four sites from the Karlsøy region in Arctic Norway that have produced substantial animal bone collections. The Helgøy farm mound collection indicates a major increase in relative percentage of fishbones between the mid-fourteenth and mid-fifteenth centuries. Ongoing research should help clarify the changing mix of subsistence and commercial resource exploitation strategies in this important fishing region. Data from the NABO Zooarchaeology Database, courtesy of Reidar Bertelsen and Inger-Marie Holm-Olsen.

Sieved?	y	y	y	y	y	y
Site locality	Karlsøy	Karlsøy	Karlsøy	Karlsøy	Karlsøy	Karlsøy
Sample size (NISP)	2,308	3,618	3,608	32,982	11,396	20,177
Site name	Helgøy	Helgøy	Rodgamme	Nordskar	Helgøy	Grunnfjord
Phase	14th century	15th century	16th century		17th century	
Approx. dates (AD)	1350	1450	1505	1530	1600	1600
Total % NISP						
Dometic	46.14	9.73	6.57	1.2	10.5	2.89
Caribou	0.04	0.25	0	0.04	0.09	0.03
Birds	3.12	0.88	0.36	0.29	1.41	67.00
Cetaceans	0	0	0.03	0.12	0	0
Seals	8.67	2.21	0	0.05	0.15	0.03
Fish	42.05	86.93	92.93	93.27	87.85	30.04
Molluscs	0	0	0	0	0	0

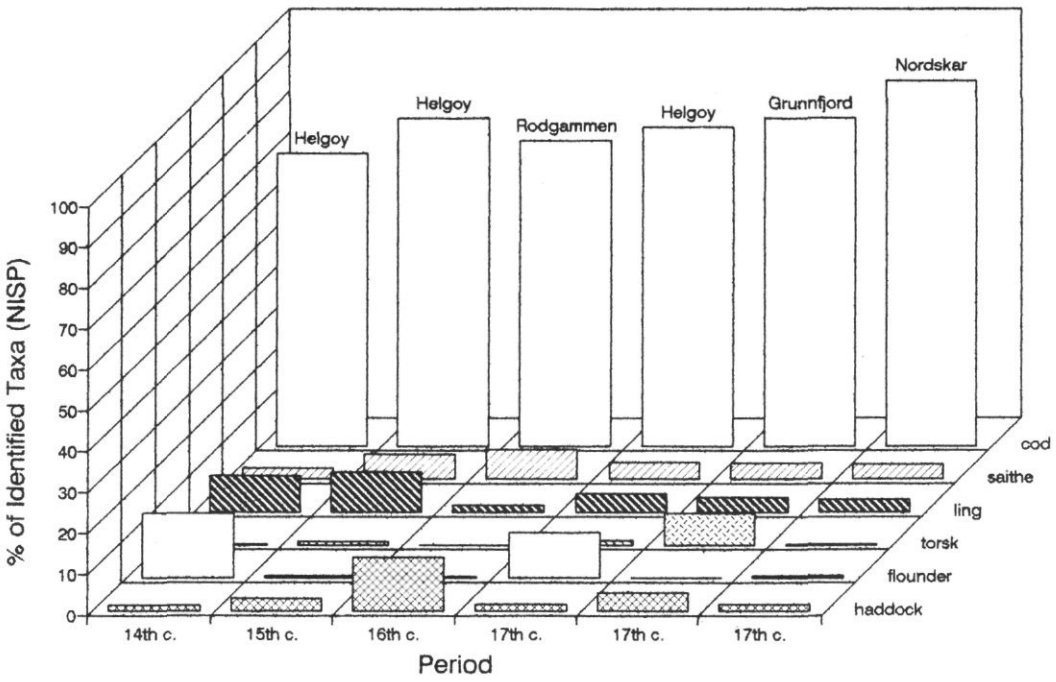


Figure 6. Fish species composition in North Norwegian archaeofauna. While several fish species have been identified from North Norwegian sites, the majority in all periods were cod (data courtesy Reidar Bertelsen and Inger-Marie Holm-Olsen).

indicators may possibly be identified when the site's faunal analysis is completed. The data cited here are from the 1985–1987 excavations, and are dated to the tenth to nineteenth centuries. The most important trend discernible at this time is that the relative mean lengths of cod whose bones were deposited at Storvaagan over its long occupation largely ranged from 650 to 900 mm (Fig. 7). This size range compares well in its upper limits with the larger fish caught in Iceland (Amorosi, 1989) and Shetland (Bigelow, 1984) during the various pre-modern periods discussed above.

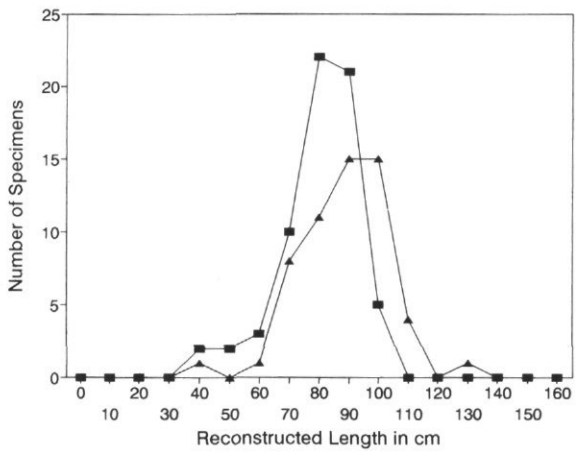


Figure 7. Distribution of reconstructed cod length from Storvågan, Northern Norway. Both dentary and premaxillary reconstructions indicate medieval cod slightly smaller than those from medieval Icelandic sites. ■ = Dentary; ▲ = premaxillary.

Modern and archaeological cod length

It will be apparent that the archaeologically reconstructed lengths of cod described in this article form distributions different from those observed in most modern cod stocks. Other workers (Colley, 1983, 1990; Bigelow, 1984; Jones, 1991; Barrett, 1993) describe similar archaeological samples with mean reconstructed cod length around 90–100 cm from the Shetland Islands, Orkney, and Caithness. These distributions appear to extend back beyond the Norse period into the Pictish Iron Age in Orkney and Caithness (Colley 1983, 1990; Jones 1991). While sample sizes and conditions of preservation vary, it is apparent from both published data and anecdotal communication with a wide range of other researchers that this pattern of large (presumably old) cod is extremely widespread in the growing bioarchaeological record. The existence of this distribution is not controversial, and appears to constitute one of those robust archaeological patterns that is neither local nor subtle.

Figure 8 illustrates the difference in distribution of reconstructed archaeological cod from the south coast site of Stóraborg (near modern Skogar) and measured modern cod from southern and southwest Iceland. Modern data are drawn from four years of research trawls (1976–1979) reported by Pálsson (1983, Table 4), and are based on a total sample of 10 476 fish. Table 6 presents the raw data for the 1976–1979 research trawls (first column) and the reconstructed archaeological cod length distributions for what are presently the four largest fish archaeofauna from Iceland: Stóraborg (south coast), Viðey (Reykjavík), Miðbær (Flatey in Breiðafjorð in the northwest), and Svalbarð (Þistilfjorð in the northeast). The archaeological data are represented by 745 measured fish premaxillae and dentaries drawn from archaeofauna totaling 80 820 fragments identified to species level. When these sites are temporally disaggregated by phase, they show no significant change in distribution pattern in either measurable element (Table 4). Additional sites are now under analysis.

Table 6 reveals that the distributional pattern of Figure 8 is somewhat deceptive, as the archaeological collections simply lack any cod smaller than 40 cm reconstructed length, and these make up 48% of the research trawls. This clearly does not imply that cod smaller than ca. 40 cm were absent from waters about Iceland in medieval or early modern times. Instead, it seems likely that premodern fishing technology and perhaps seasonality of fishing effort selected for large fish and missed the smaller and younger animals taken by the modern research trawls. Thus, comparison of the lower tails of the archaeological and modern fish size distributions is meaningless.

However, inspection of Table 6 suggests that there is something odd about the upper tail of the modern and archaeological fish length distributions. Given the different overall distributions, percentage comparisons of modern and medieval–early modern cod length is fruitless, but the raw numbers continue to raise questions. Figure 9 compares the raw numbers of cod of 100

Table 6. Modern and Medieval cod length distribution in Iceland. Cod measured during systematic fisheries trawls during 1976–1979 (north, northeast, east and south coasts) are compared to reconstructed cod length distributions from Stóraborg (south coast), Viðey (Reykjavík), Miðbær (Breiðafjorð, northwest coast) and Svalbarð (Þistilsfjörð, northeast coast). Note the absence of cod reconstructed as less than 40 cm in length, except at Miðbær on the island of Flatey. Medieval fishing gear, unlike modern fisheries trawls, seems to have selected against smaller fish. Note however, the substantial number of fragments (both dentaries and premaxillaries) from the archaeological sites which derive from fish 100 cm and longer (bottom rows).

	Measured fish	Archaeological reconstructions							
Length groups (in cm)	Icelandic trawl fisheries 1976–1979 total	Stóraborg 15th–18th c. total Premax.	Stóraborg 15th–18th c. total Dentaries	Viðey 13th–18th c. total Premax.	Viðey 13th–18th c. total Dentaries	Miðbær 13th–18th c. total Premax.	Miðbær 13th–18th c. total Dentaries	Svalbarð 11th–18th c. total Premax.	Svalbarð 11th–18th c. total Dentaries
5–9	83	0	0	0	0	0	0	0	0
10–19	632	0	0	0	0	0	0	0	0
20–29	1220	0	0	0	0	0	0	0	0
30–39	1489	0	0	0	0	0	0	0	0
40–49	1622	0	0	0	0	2	4	0	0
50–59	1765	0	0	1	0	10	11	0	0
60–69	1669	2	0	1	2	4	8	3	5
70–79	1133	8	10	0	4	15	4	12	8
80–89	538	52	66	9	12	6	2	23	16
90–99	223	64	97	13	12	3	1	21	11
100–109	62	37	57	15	8	6	0	18	11
110–119	28	13	12	2	1	0	0	7	6
120–129	4	6	10	2	0	0	0	2	1
130–139	8	0	1	0	0	1	0	1	0
140–149	0	1	0	0	0	0	0	0	0
150–159	0	3	1	0	0	0	0	0	0
160–169	0	0	0	0	0	1	0	0	0
Total	10476	186	254	43	39	48	30	87	58
Number >= 100 cm	102	60	81	19	9	8	0	28	18
Number >= 120 cm	12	10	12	2	0	2	0	3	1
Number >= 140 cm	0	4	1	0	0	1	0	0	0

*Source**: Olafur K. Pálsson (1983) Feeding habits of demersal fish species in Icelandic waters. Rit Fiskideildar 7(1) Marine Fisheries Inst. Reykjavik, Iceland.

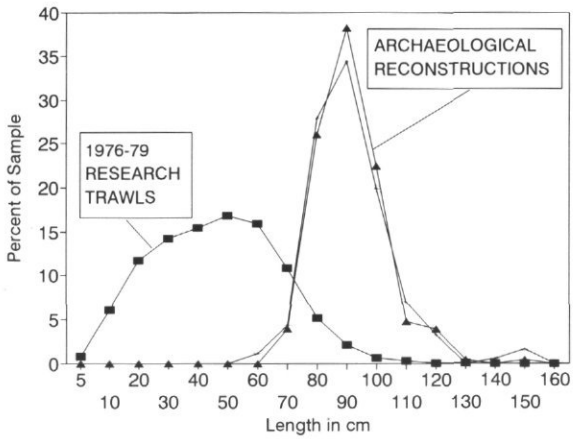


Figure 8. Comparison of modern and archaeological cod length distributions. Distribution of reconstructed cod length from Storaborg (south coast) compared to modern fisheries trawls from NE, NW, E, and S Iceland 1976–1979 (Pálsson, 1983). The archaeological collections lack cod smaller than 40 cm, and contain many specimens 100 cm and longer. This pattern is strongly shaped by the medieval fishing methods (mainly hand lines) and does not directly reflect the actual distribution of medieval cod populations. See Table 6 for the comparative numerical data. ■ = Modern; * = premaxilla; ▲ = dentary.

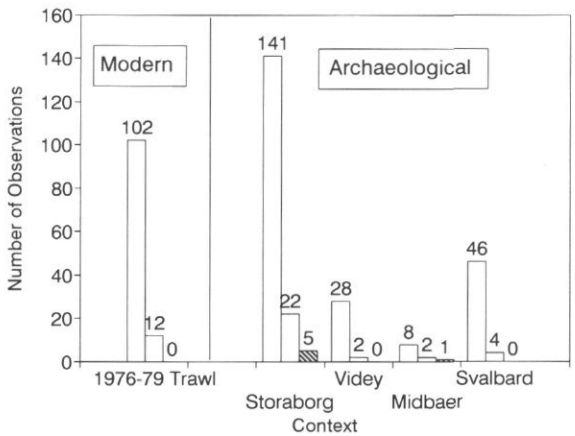


Figure 9. Comparison of counts of modern and archaeological cod larger than 100 cm. While differences in collection method make direct comparison of modern and medieval length distributions questionable (Fig. 7) the absolute number of modern cod recovered in research trawls from 1976–1979 show the 100 cm or larger size class, is smaller than the absolute number of similarly large sized cod bones recovered from archaeological sites. Cod 100 cm and larger are now comparatively rare in the waters around Iceland. It appears that such large cod were not uncommon in medieval–early modern times. Also see Table 6 for data. □ = >100 cm; □ = >120 cm; ▨ = >140 cm.

cm length and larger taken in the 1976–1979 trawls with the raw counts of measured bones recovered from the sites. Note that while the four-year research trawl effort turned up only 102 fish longer than 100 cm (of a total landing of over 10 000 fish) the site of Stóraborg alone generated 141 bones allowing reconstruction of length over 100 cm. The 1976–1979 fisheries trawl recovered only 12 cod longer than 120 cm: Stóraborg produced 22 bones indicating length over 120 cm. Even allowing for imprecision of measurement, these raw figures suggest that substantial numbers of cod 100 cm long and longer were being landed in the past at many locations around Iceland.

Note again that these archaeological data are not counts of individual fish, but samples of a distribution of a far larger number of individuals. Fishers operating out of Stóraborg between ca. AD 1450 and 1840 landed not just 254 cod, but many thousands of fish, 254 dentaries of which have survived. While level of fishing effort by individual farms is difficult to calculate for even the nineteenth century, it is instructive to realize that if we conservatively estimate a landing of 500 cod per year at Stóraborg, the zooarchaeological distribution data suggest that around 30% would be 100 cm or longer, yielding a figure of around 150 cod longer than one meter (700 cod per year would produce around 200 such cod, 200 per year would produce 60 one meter or greater cod). While such estimates are highly speculative, they may serve to illustrate how many landed fish might stand behind the archaeological samples. Both the fisheries data in Pálsson (1983) and anecdotal reports by modern fishermen suggest that even the lowest estimated landing rate of cod 100 cm and above would be difficult to duplicate today, even with modern gear.

How can these patterns be explained? Three major approaches to explanation are open to us:

(1) On all sites now known to North Atlantic zooarchaeologists, forces of attrition and archaeological recovery have systematically skewed the sample reaching the laboratory. Small individuals have been systematically destroyed or rendered un-identifiable, and larger animals are disproportionately represented. The bioarchaeological data are thus mainly noise, and reflect little or nothing about past fishing or fish stocks.

(2) Past fishing methods (in most cases some form of hand line with baited hook), fishing locations, and preferred fishing seasons have all differentially selected for large individuals. Small cod only rarely entered the archaeological record and thus are not often reflected in the excavated samples. The bioarchaeological data thus mainly reflect selective exploitation of fish stocks by past fishers and reflect little or nothing about the actual characteristics of any past cod stock.

(3) While forces of attrition and recovery and the technology and culture of past fishers have certainly skewed the archaeological sample distribution, the root cause of the differences between modern (post AD 1900) and archaeological cod measurements lies in significant differences between age/size structures of the different cod populations sampled. Cod greater than 100 cm long were regularly landed by pre-industrial fishers all across the North Atlantic from ca. AD 800 to 1840, and cod greater than 120 cm were common enough to be landed often enough to appear regularly in the archaeological record. Several cod stocks in the North Atlantic thus held substantially higher proportions of large, old cod than do modern cod stocks in the same area.

These three avenues of explanation are of course not entirely mutually exclusive, and further research will be needed to better understand which most accurately explains the observed distribution of archaeological data. However, we feel that even with the present data some explanations are more likely than others.

As better controlled archaeological data enter the record, the first explanation (the "null hypothesis" of overwhelming taphonomic noise) seems increasingly less persuasive. Archaeofauna derived from sieved excavations and laboratory flotated whole-soil column samples in Iceland do not produce reconstructed cod size distributions markedly different from less intensively sieved contexts. Some species (especially herring and most salmonids), have overall a much poorer chance of preservation and recovery than Atlantic cod, and all otoliths are particularly sensitive to soil acidity. However, there is little measurable difference in bone density between premaxillae and dentaries of cod ca. 40–80 cm long and those of cod 90–120 cm long. In practice, the smaller mouth parts of the smaller individuals are less subject to breakage than the larger bones of very large cod, and thus are *more* likely to survive in measurable state. As Table 6 indicates, some cod bones in the 50–80 cm reconstructed range are present in virtually all the reported archaeofauna. While attrition and recovery problems will always remain significant, they do not appear to account for the patterns observed.

The second explanation of different fishing gear and strategies by premodern fishers certainly has considerable merit. Archaeofaunas are not random samples of any biological distribution. Culturally patterned selective filters are at work even in simple human economies, regularly collecting some individuals of some species, and failing to secure others. As many maritime social scientists working with modern fishing populations have pointed out, we still know too little about the interaction of local fishers and local fish stocks. As Table 6 suggests, there is some interesting variability between sites in different parts of Iceland which demands more intensive investigation of local factors affecting fishing and fish stocks. Pre-industrial fishers tended to be exploiters of local ecosystems, not whole biospheres (McGoodwin, 1990), and we need to be careful to select appropriate geographical and temporal scales for our analyses. There would appear to be fruitful ground for cooperation between maritime archaeologists, ethnologists, historians, active fishers, and fisheries scientists in improving our understanding of long-term local level interactions in the past.

The third explanation implying a substantially different distribution of age/size classes in several premodern cod stocks in the North Atlantic region cannot be proven on the basis of current bioarchaeological data, but it cannot be dismissed either. The existing archaeological data (both as distributions and as raw counts) from Iceland would be difficult to generate from what we know of modern cod stocks in the area. Archaeological data from other parts of the North Atlantic suggest similar unexpected abundance of large cod in several other stocks. More extensive comparison of landing records and research trawls with bioarchaeological samples and closer and more systematic integration of bioarchaeological data and fisheries records would seem to be indicated.

Concluding points

Virtually all these data are in some respect preliminary, and we clearly have a good deal of work to do to refine and expand this bioarchaeological evidence for past fisheries. We are only getting to the position where a useful contribution can be made to the ongoing debates concerning fish population dynamics and management strategies. More excavated archaeofauna, integrative modeling, and cooperative work with other archaeologists, historians, and natural scientists will be required before the full potential of these data sets can be realized.

While these data are only beginning to be tapped for fisheries science, they by no means represent a small or closed set incapable of rapid expansion. New excavations underway throughout the region and continued analyses of already excavated samples promise major improvement in our ability to contribute more fully in the near future. To mention only a few important localities: major fish-rich collections from Strandasýsla in northeast Iceland include a matched home farm at Gjögur and a multi-phase fishing station at Akurvík now urgently await analysis (Amorosi and McGovern, 1992), substantial archaeofauna from Sandwick (Bigelow, in progress) Shetland and Freswick in Caithness (Morris, Batey, Rackham *et al.* in press) and major fishing station collections from Roberts Haven in northern Scotland are nearing completion (Barrett, 1992). This very brief

and preliminary presentation can only suggest the full potential of this approach, the near future will see far more useful tools offered to North Atlantic natural scientists by historical ecologists using archaeological evidence.

Three points may serve to close this preliminary, limited, and ultimately incomplete presentation.

1. Environmental baseline estimates used for a wide range of urgent management questions regularly lack time depth beyond the limits of the instrumental record. Archaeological and historical data can help to fill these gaps, both by providing basic data (such as cod length ca. AD 1300) and by improving integrative models of long-term human–resource interaction.

2. Coastal sites rich in fish remains are lost or damaged each year through marine erosion and human action. Proposed global warming, sea-level rise, and accelerated coastal development indicate rapidly accelerated threat in the near future. While capable of rapid expansion with existing techniques, this long-term bioarchaeological record is fragile and in urgent need of recovery.

3. Human subsistence and commercial economies are (and have been) complex and multi-stranded. Marine and terrestrial components of past economies are strongly inter-related and attempts to use bioarchaeological data for environmental reconstruction must take a wide range of social and ideological factors into account. As the example of Norse Greenland suggests, humans are not simply random samplers of past environments. Effective use of bioarchaeological data requires active cooperation of trained bioarchaeologists with fisheries biologists and maritime anthropologists. We cannot simply extract fishbone percentages from bone reports and relate these to climate curves or landing data without significant potential for error. Genuine, active interdisciplinary cooperation is required if we are all to make full use of these new (if ancient) data.

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Deterministic signals in Norwegian cod records

T. Wyatt, R. G. Currie, and F. Saborido-Rey

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The nodal tide (M_n) of 18.613 year period, and the solar cycle (S_c) of 10-11 year period, introduce important signals into many geophysical, meteorological, and biological time series. These signals are non-stationary with variable amplitude and phase, features which give rise to complex temporal and geographical patterns. Historical records of Norwegian cod catches were taken from Aarsberetning Vedkommende Norges Fiskerier (1885 to 1931) and from Sætersdal and Hylen (1964) for 1872 to 1951. We present results of maximum entropy spectral analysis (MESA), and describe the contributions of the M_n and S_c signals to these records through an examination of their time domain wavetrains. The main results are as follows. Data from northern Norwegian recording districts (except Finnmark) reveal a strong M_n signal, but no sign of S_c. Data from southern districts show both signals, and, in addition, the M_n signal here provides evidence of a phase shift following maximum lunar declination in 1917. A weak third signal has the same period as the 8.85 year tide dependent on the longitude of perigee of the lunar orbit. The lunar waves in extreme northern and southern districts are in phase during the years dealt with here, but approximately 180° out of phase or of mixed phase in the intermediate region.

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Introduction

There is general agreement that the relevant time scales for examining changes in fish stock abundance are of the order of decades to centuries (Cushing, 1982; Kawasaki, 1991). The most remarkable study of periodicity in Norwegian cod catches is that of Ottestad (1942), who identified four periodic signals of 11, 17.5, 23, and 57 years in the time series. Ording (1941) had just then published an analysis of tree ring growth periodicity in pine and spruce at Sørfold, near the area where the Lofoten fishery is prosecuted, and identified the same four signals (as well as three others of 2.75, 8.5, and 35 years). With Ording's phase data, Ottestad combined his four periods, as sine functions of equal amplitude, to simulate the yield of cod in the Lofoten fishery from 1885 to 1940. We comment on Ottestad's study later. Signals of approximately 11 and 19 years, identified with the solar (S_c) cycle and nodal tide (M_n) respectively, are almost ubiquitous in a variety of geophysical (sea level, rainfall, drought indices, air temperatures) and biological (tree rings, dates of wine harvests) time series worldwide, including fish stock records (Currie, 1991; Wyatt *et al.*, 1992; Currie *et al.*, 1993). The 19-year nodal cycle has previously been identified in Norwegian cod records using a fast Fourier transform technique (Wyatt, 1984; Wyatt and Vazquez, 1988). Here the analysis is repeated using maximum entropy spectral analysis (MESA).

Methods

Historical records of Norwegian cod catches were taken from Aarsberetning Vedkommende Norges Fiskerier (1885 to 1931) and from Sætersdal and Hylen (1964) for 1872 to 1951. Catches are given as numbers of fish, and as tonnes, respectively.

Analytical procedures are described by Currie *et al.* (1993) and in earlier papers cited there. Briefly, we used two $(2N + 1)$ high-pass digital filters with $n = 6$ and $n = 4$ for weights w_k ($k = 1$ to n), where $w_k = w_{-k}$ and w_o is the centre weight. The same techniques were used to design the $n = 30$ weight bandpass filters centred at 18.6 and 10.5 years. The responses of the filters were calculated for frequencies $f_i = i/400$, $i = 1$ to 200 cycles per year

(cpy). Each time series of yearly fish catches was convolved with the n = 6 filter by the equation:

$$y_n = \sum_{k=-6}^{k=6} w_k x_{n-k} \quad (1)$$

where x_n is the original record and y_n is the filtered time series whose spectrum is to be computed. Note that six annual values off each end of the original data are lost by this operation. The unwanted mean and any ultra low frequencies, such as secular trends or other signals whose periods are comparable in length to the record, have been eliminated.

In MESA, the power spectrum gives the power as a function of frequency f in terms of the filter coefficients α_j as:

$$P(f) = 2P_L \Big/ \left| \sum_{j=0}^{L} \alpha_j \exp(-2\pi i f j) \right|^2 \quad (2)$$

where the sequence of coefficients $\alpha_o, \ldots, \alpha_L$ in Equation (2) is called a prediction error filter of order L. For j = 0, a zero order spectrum, the equation yields $P(f) = 2P_0$ where P_0 is the zero lag variance of the data. In this case the spectrum is a constant, appropriate to white noise.

The denominator in Equation (2) is the power transfer function of the filter as a function of frequency f. For higher order filters one avoids computing lagged autocorrelation functions and constructs directly from the data by a recursive technique, using all data in each recursion from j = 1 to j = L. The algorithm for doing this is mathematical and lengthy, so we refer the reader to Marple (1987). Once the filter coefficients are obtained, one can calculate any number of spectral estimates desired. Here, power estimates $P(f_i)$ for frequencies f_i = i/400 cycles per year, i = 1 to 50 were computed, then divided by the amplitude squared response of the n = 6 high-pass filter to restore proper power.

The order L of the filter in Equation (2) was determined empirically, as suggested by Marple (1987), because the criteria available to determine it are based on the arguable assumption that time series are generated by an autoregressive process driven by white noise; that is to say, time series arising in meteorology, geophysics, and biology are not supposed to contain deterministic signals (except for the seasonal term), but are to be described by low order time domain models which may or may not be correct.

Each fish catch series was reduced to unit variance, convolved with the n = 6 filter using Equation (1), MESA power spectrum computed using Equation (2), and each spectrum finally divided by the power response of the high-pass filter. Discussion of the value of L is given by Currie *et al.* (1993).

Results

Power spectra for the Northern and Southern District (data from Sætersdal and Hylen, 1964) for the period 1872 to 1951 are shown in Figures 1a and b, and for the sum of the recording districts from Finnmark to Stavanger (data from Aarsberetning Vedkommende Norges Fiskerier) for the period 1885 to 1930 in Figure 1c. We deem the nodal signal, M_n, to be detected when a peak lies between 16.0 and 22.2 years, and the solar signal, S_c, when a peak lies between 9.5 and 11.4 years. A way to assess the statistical significance of these peaks is described by Currie (1993). At values of $f_i < 0.03$, the spectra in Figure 1 rise rapidly due to the power response of the high-pass filter used. At values of $f_i > 0.03$, and using a white noise model, it can be shown using Student's *t*-test that the peaks are significantly non-random at the 99.9% level. All three spectra are dominated by a peak near 19 years. What may be the S_c signal is prominent only in Southern District series, but the period (12.1 years) lies outside the accepted range. Power spectra for individual recording districts show that S_c is just visible in Bergen and Stavanger data, at 11.1 and 11.4 years respectively. Thus S_c is not convincingly detected by our procedures in these time series, but may be present as a weak signal in the southern part of the cod's range in Western Norway.

In contrast, the M_n signal is very strong in all districts except Finnmark, and accounts for about 50% of the total variance in numbers of fish caught over the time period considered, and a surprising maximum of 71% in the case of Sogn-og-Fjordane (Table 1). For shorter segments of the time series, these figures vary considerably, as can be seen from inspection of the time domain wavetrains (Fig. 2).

Table 1. Correlation coefficients between cod catches and nodal wavetrains for recording districts. M_n signal was not detected in Finnmark and S-Trøndelag.

District	r	r^2
Finnmark	(0.10)	(0.01)
Troms	0.60	0.36
Nordland	0.56	0.32
N-Trøndelag	0.55	0.30
S-Trøndelag	(0.12)	(0.01)
Romsdal	0.33	0.11
Sogn-og-Fjordane	0.71	0.51
Bergen (Hordaland)	0.49	0.24
Stavanger (Rogaland)	0.54	0.29

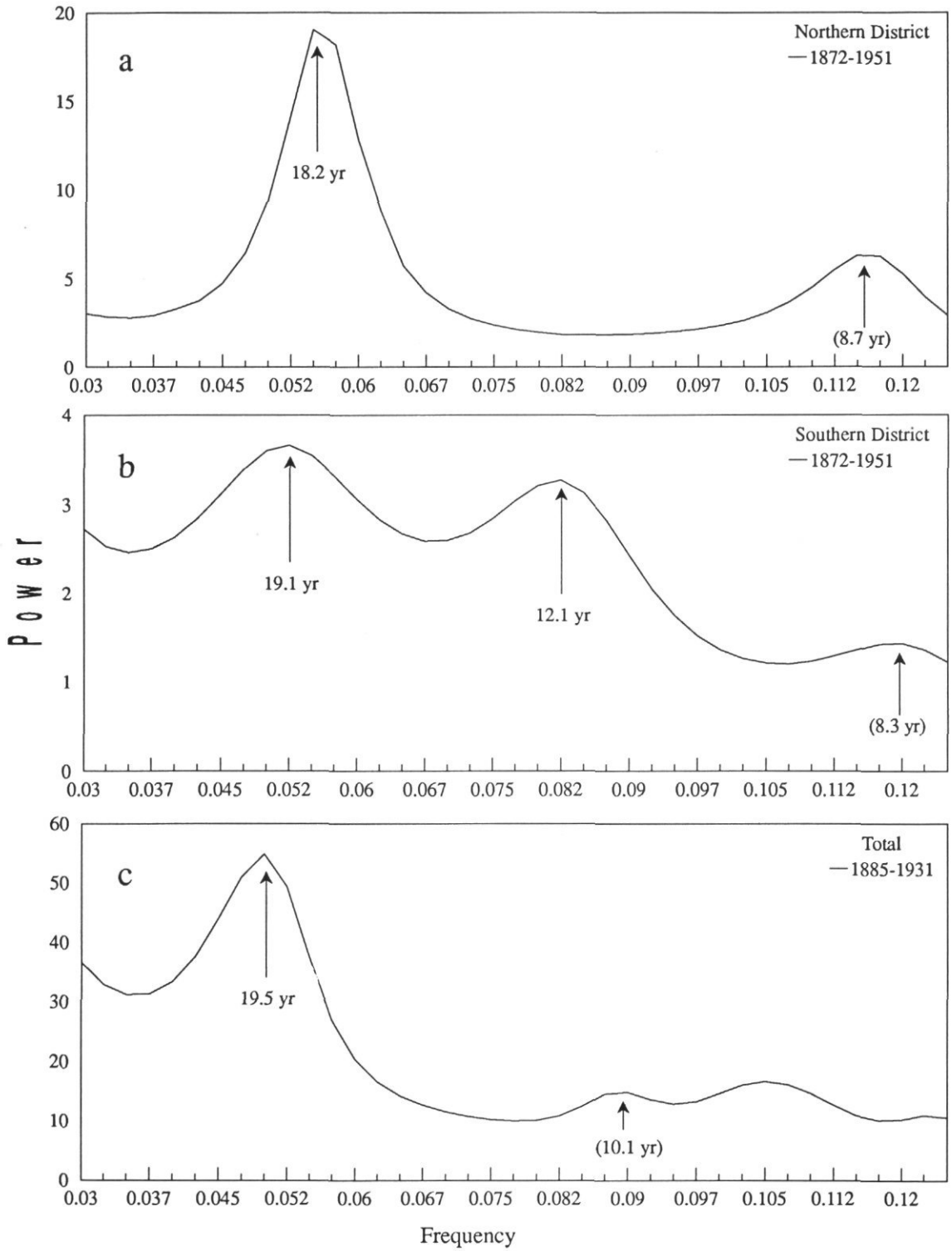


Figure 1. Power spectra for Northern and Southern districts, 1872 to 1951 (a and b), and for sum of recording districts, 1885 to 1931 (c). Units: a and b = 10^3 tonnes, c = 10^3 fish.

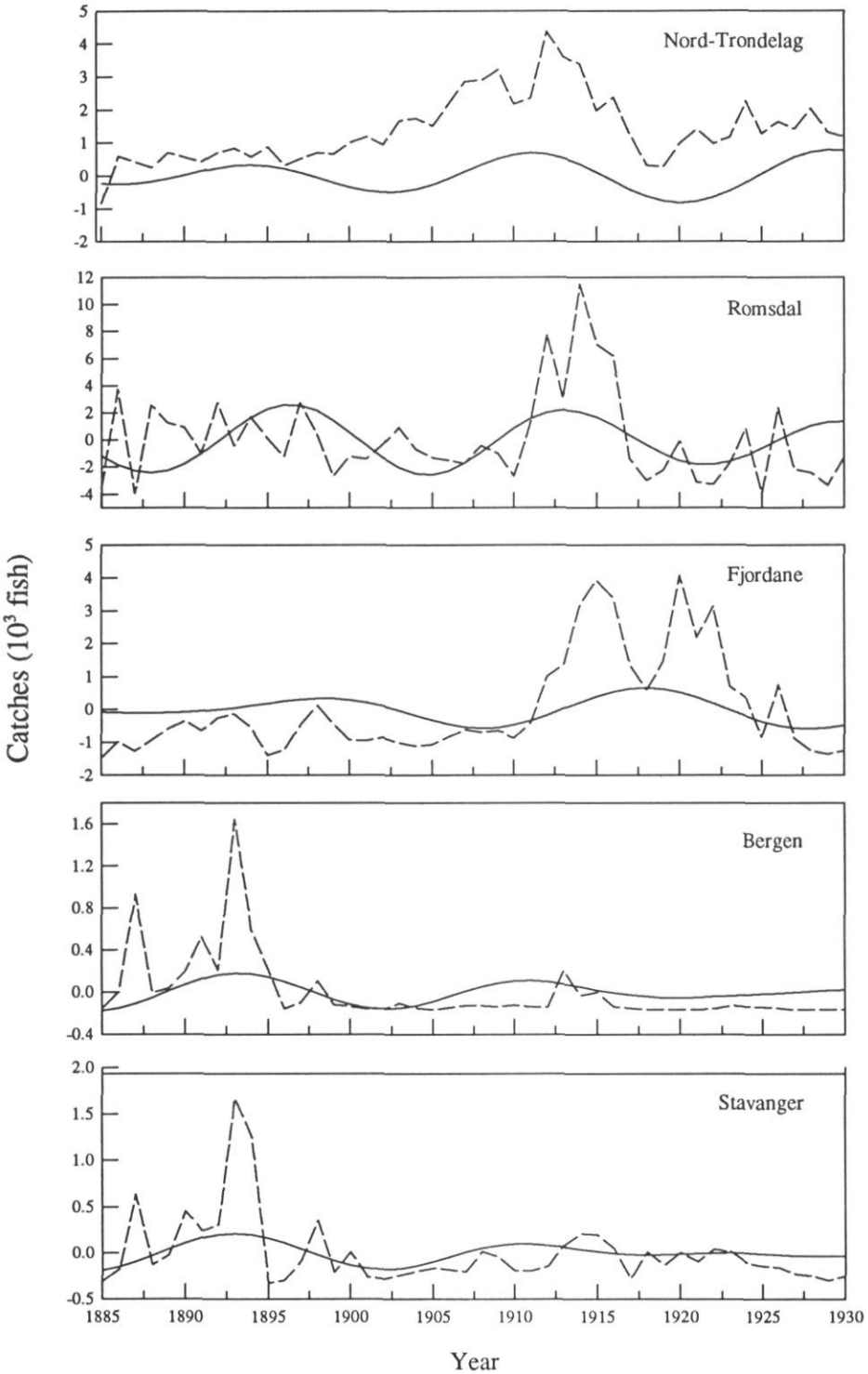


Figure 2. Nodal wavetrains for five Norwegian recording districts with years of maxima and minima indicated, and catches (broken line) for 1885 to 1931. Catches in thousands of fish.

Figure 2 shows the M_n wavetrains for five districts, together with the original data. Several features are apparent:

(i) It can be seen that in the south (Stavanger, Bergen) the fit of the wavetrain is good until 1902 and poor subsequently, when catches in any case fell to almost nothing in these districts. In the more northerly districts, the fit of the wavetrain is best after 1900. It should be noted that the increments and deficits in cod catches do not of course occur in the smooth way shown by the nodal wavetrains, since the smoothness is an artefact of the bandpass filter used. But the increments and deficits are clustered over 5- to 6-year intervals. So it is the persistence of the amplitude modulation over such time intervals which lies behind the catch fluctuations.

(ii) The wavetrains for Bergen and Stavanger clearly entered a period of changing phase after 1918–1919. It looks likely that the wavetrain for Sogn-og-Fjordane had just emerged from such a phase change at the beginning of the series. This series too has a phase difference of 4–5 years compared with the other districts, and the phase of Romsdal is approximately intermediate between it and Nor-Trondelag. Phase changes of 180° were originally identified in Patagonian tree ring data (Currie, 1983), and subsequently in many other biological and geophysical time series, including cod landings extracted from French archives for the period 1662 to 1792 (de la Villemarqué, 1991; Wyatt *et al.*, 1992), and flood levels of the St Lawrence (Currie and O'Brien, 1989) which may influence the ecology of some cod stocks in the western Atlantic (Koslow and Thompson, 1987).

(iii) For the time period shown in Figure 2, maximum tidal forcing due to M_n occurred in 1899, 1917, and 1936. Inspection of the wavetrain for the Stavanger series shows that the early peak in catches in 1893 took place about six years before epoch 1899, or four years after mid-epoch in 1890. The same pattern can be recognized in other wavetrains where the phase is not mixed, and suggests that maxima and minima of the nodal tide have their impacts several years before cod recruit to the coastal fisheries, presumably during the larval or juvenile phase.

(iv) The amplitudes of the nodal wavetrains are variable. In time series previously reported, amplitudes decrease as phase changes are approached, and increase again after phase changes are completed. This appears to be the pattern here too, but these time series are too short to unambiguously reveal such a pattern.

Discussion

The amplitude of the nodal tide is twelfth largest in equilibrium theory. If, as in Proudman's (1960) analysis, it follows the equilibrium law, then the amplitudes at different latitudes are as given in Table 2. But we lack sufficient data firmly to establish the geographical trend. Godin (1972) provides information on the extent to which the nodal tide modulates the more familiar M_2, O_1, and K_1 tides. The figures are +3.7% for M_2, +19% for O_1, and 11% for K_1. These figures are based on Newton's equilibrium theory, which neglects inertial forces. Modulation of M_2 is 180° out of phase with that of O_1 and K_1, so that the impact of the nodal tide varies in accordance with the semidiurnal, mixed, or diurnal character of the local tidal regime. Tides along the Norwegian coast between Stavanger in 58°59′N and Hammersfest in 70°40′N are strongly diurnal, with values of $K_1 + O_1/M_2 + S_2$ ranging between 0.08 and 0.16. This modulation gives rise to variations in the average speed of tidal currents (u) and, as Loder and Garrett (1978) explain, must affect vertical diffusion coefficients (A_z). Further, since A_z depends on the density stratification, and increases in u decrease stratification, there is positive feedback, and signal (SST in their study) amplification occurs (Loder and Garrett, 1978). In Norwegian coastal waters, and if the nodal tide were not modulated on longer time scales, maximum values of A_z should be in phase with the epochs of nodal forcing. This is one mechanism from below whereby the mixing depth, a key component of production models, can change systematically with a period of 18.6 years.

Table 2. Amplitudes of the nodal tide at different latitudes.

Latitude (degrees)	Height (mm)
90	−44
80	−41
70	−36
60	−27
50	−17
40	−5
30	5
20	14
10	20
0	22

Calculated by Maximov; see Lisitzin (1977), p. 41.

A second way in which mixing depth can change is through the effect of nodal forcing in the atmosphere. Since this forcing leads to changes in rainfall and runoff, changes in stabilization will be induced from above. Rainfall patterns are also responsible for variations in crop yields and tree ring growth (Currie, 1987), so that we have here a rather clear reason for the success of Ottestad's (1942) result referred to earlier.

If Newton's second law is written in rotating coordinates, the Earth's rotation rate is found to accelerate and decelerate by 18.6 years periods (O'Brien and Currie,

1993). This pattern can be recognized in the length-of-day (LOD) data summarized by Barnes *et al.* (1983) from AD~1800 to the present, but not from 1600 to 1800 when the data is less reliable. The amplitude of this term in rotation rate is the largest tidal constituent (Yoder *et al.*, 1981), and changes over this interval are of the order of 10^{-3} s yr^{-1}. Conservation of momentum requires that these changes in the Earth's mantle be compensated. Short-term changes (months) are compensated by the atmosphere (Barnes *et al.*, 1983) and longer-term changes (centuries) by the Earth's core. Mörner (1988), in a search for the "missing excitation" of Lambeck and Casenove (1976), argues that changes in mantle momentum on decadal time scales must be compensated by the hydrosphere, and lead to intensification and relaxation of the ocean circulation similar to those envisaged by Iselin (1940). The evidence which can be mustered in support of this hypothesis in the Atlantic is not very strong, but Tameishi *et al.* (1991) demonstrate a rather convincing parallel between LOD and the intermittent meander of the Kuroshio Current off Enshu-nada, Japan.

Thus there are several potential mechanisms which can lead to changes in productivity following Sverdrup's (1953) model, hence to changes in the survival of fish larvae following Hjort's (1914) hypothesis. In view of the values of correlation coefficients between cod catches in Norway and the nodal wavetrains (Table 1), which are generally higher than in meteorological records, systematic changes in mixing depth caused by internal tides may provide the basis for a more attractive hypothesis than similar changes caused by atmospheric phenomena. But if Norwegian river discharge rates should also yield strong M_n signals, then mixing depths and productivity might change over the 19-year period in response to runoff as well, lending support to several studies which link fishing success to freshwater runoff (Helland-Hansen and Nansen, 1909; Sutcliffe, 1972; Skreslet, 1986).

As already seen (Fig. 2), the nodal wavetrains in this study provide some evidence that phase reversals occur, as in our earlier analysis of French cod records (Wyatt *et al.*, 1992). Thus the nodal signal has the appearance of a carrier, although we cannot determine the wavelength of the modulation. Ottestad's (1942) identification of a 57-year signal may be an echo of this modulation, and is close to the longer period sunspot and Northern light cycles, now known as the Gleissberg cycle. The existence of these phase changes may be one reason why statistical comparisons of fishing records and environmental parameters break down as time series are extended.

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French cod fisheries from the sixteenth to the middle of the twentieth century

Jacqueline Hersart de La Villemarqué

Hersart de La Villemarqué, J. 1994. French cod fisheries from the sixteenth to the middle of the twentieth century. – ICES mar. Sci. Symp., 198: 56–58.

French cod fishing began in the sixteenth century and was very important economically. The abundance of cod brought about tremendous development in the cod fishery, especially around Newfoundland. Many factors – some negative, some positive – including wars and natural fluctuations in climate have had an impact on the fishery. Using records and published works, an attempt is made to estimate the fishing effort of France between 1500 and 1950.

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Since its discovery toward the end of the ninth century by the Vikings and its rediscovery by Basque people in the fourteenth century, Newfoundland has been considered as an exceptional fishing ground for cod, so it was first known as "Terra Bacalaos".

Development of the cod fishery in the Northwest Atlantic

For about five centuries the quantities of fish found around Newfoundland by fishermen from all parts of France caused a rush towards the Northwest Atlantic Ocean which lasted until the twentieth century. France was not the only country which harvested this resource, large numbers of fishermen sailed from Portugal, Spain, and England to Newfoundland very often engaging in long struggles to protect their own fishing rights.

Since the sixteenth century, cod fisheries have been considered a major factor in the French economy. The "bankers", ships fishing for cod on the Newfoundland "Banks", were registered in about fifty harbours. In the seventeenth century more than a hundred ports were engaged in this cod fishing. The economic growth of ports such as Dunkerque, Granville, Saint-Malo, La Rochelle, Bordeaux, and Bayonne was the result of the cod fisheries expansion. Later, most of them were to be greatly affected by the decline in this activity.

The ships which crossed the Atlantic Ocean to Newfoundland and the Banks in the sixteenth and seventeenth centuries were either very heavily built ships of 200 or 300 GRT, such as "dogres" and "roberges" which stayed for one or two months near the coast, or lightweight ships of 40 or 70 GRT, such as "caravelles" and "brigantins", which fished on the Banks and returned to France when loaded. In the eighteenth and nineteenth centuries, the schooners became the best "bankers", lightweight and fast-sailing, sailing sometimes to Newfoundland for two fishing periods per year. In the twentieth century, trawlers powered by steam engines were able to bring back to France twice as much cod as a sailing ship and to have two fishing periods per year.

In order to supply the market with a good product, the fish was prepared ungutted and salted or dried on beaches after being heavily salted. They were known as "green cod" and "dry cod", respectively.

At the beginning of the cod fisheries little was known about fish physiology and behaviour, fishing being carried out in summer when sailing conditions were at their most favourable. With the increasing seaworthiness of vessels, however, the best fishing season was in early spring. This became clear as more became known about the overall hydrology in the Northwest Atlantic Ocean and of the life cycle of cod, which guided the fishermen to the best grounds and season for fishing.

Climatic conditions

Cod is reputed to require fairly optimal conditions in terms of water temperature and salinity. So, climate changes have (and have had) a dramatic influence on its distribution over time. For four and a half centuries, climate has fluctuated, some periods with a better climate than others. Since 1150, four periods have been identified:

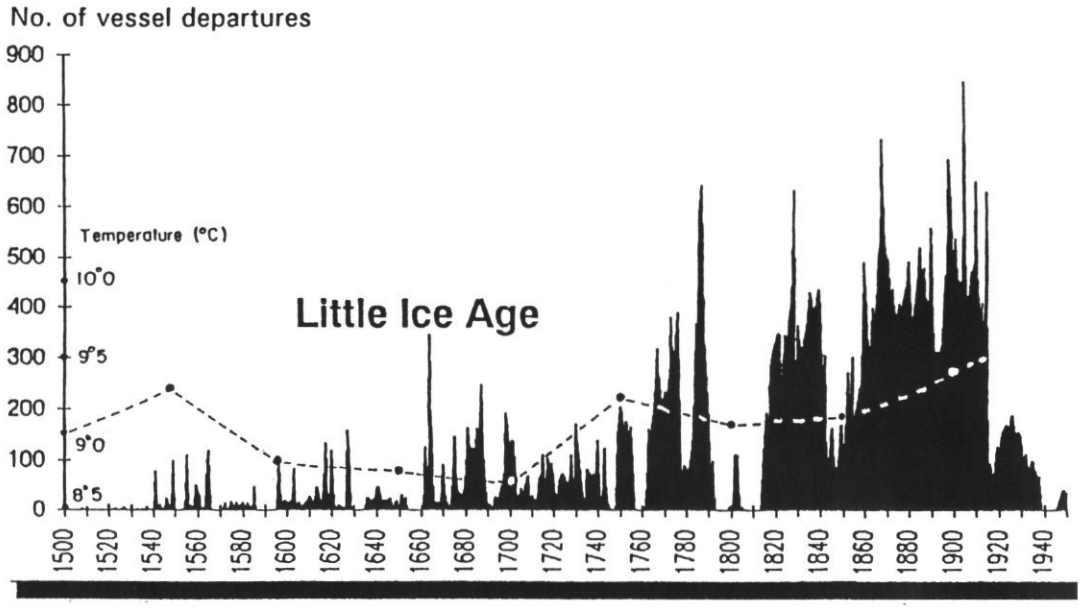


Figure 1. Number of vessel departures in the French cod fishery from 1500 to 1950; and temperatures in central England (50-year averages, from Lamb, 1965).

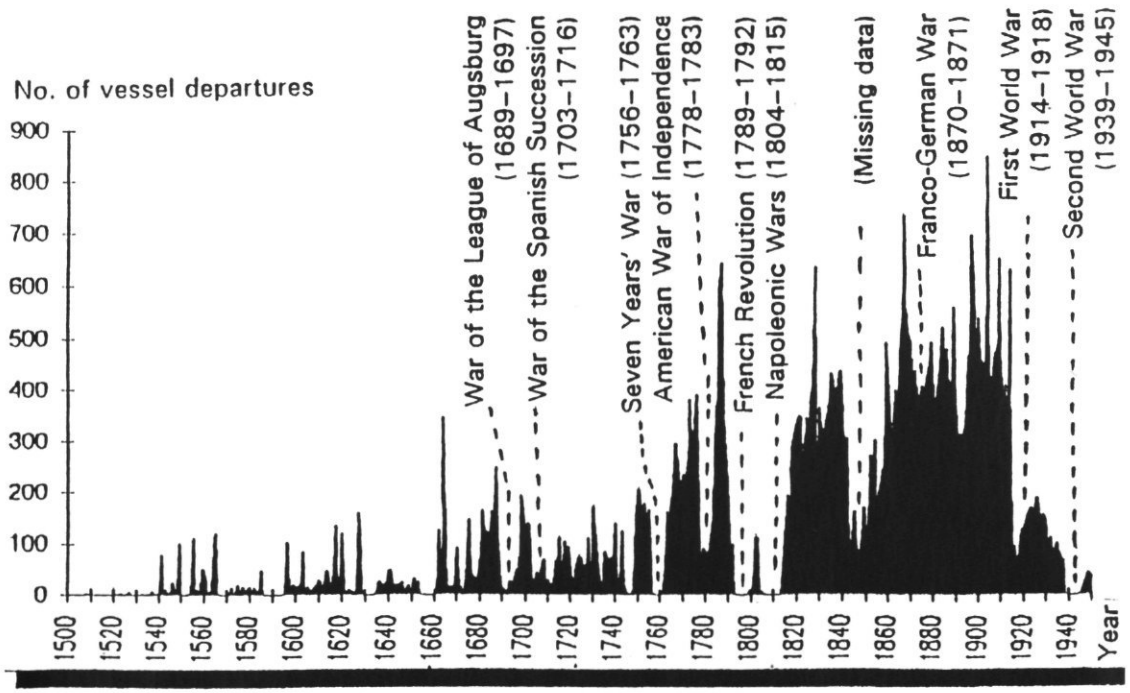


Figure 2. Number of vessel departures in the French cod fishery from 1500 to 1950 and wars from 1689 to 1945.

- the Little Optimum from 1150 to 1300
- a cooler and unsettled period between 1300 and 1550
- the Little Ice Age between 1550 and 1700 (even perhaps 1800)
- a warmer period from 1800 to the present

During the Little Optimum the climate over Europe was fairly warm, similar to the present climate. The following period was cool and wet, the rediscovery of Newfoundland taking place around 1540. A period of cool weather began in 1550, with storms and expansion of ice and snow in Europe as well as in a great part of the world: this was the "Little Ice Age" (Fig. 1). At the end of the seventeenth century, ice around Iceland sometimes remained for up to four to six months of the year. There were also strong northerly winds prevailing in Scandinavia, the British Isles, and France. Near Newfoundland, ice and pack-ice remained over long periods, sometimes until June. This type of climate is supposed to be more favourable for cod resources than a warm period with increased sea temperatures, but so difficult for fishermen that fishing was seriously curtailed.

The "human impact"

In addition to these climatic events, numerous wars added major difficulties, especially during the eighteenth century. In the Little Ice Age, six wars between 1689 and 1815 induced many sea battles and the blockade of numerous ports. During these confused periods French fishing vessels experienced great difficulties reaching their fishing grounds and the fishermen were put on navy ships (Fig. 2). In addition, the consequences of treaties have often meant the loss of good fishing rights and/or areas like Newfoundland and the Canadian coasts. All this resulted in the failure of the cod fishing activity.

Conclusion

With the help of records and published works, I have been able to restore chronological lists of data documenting the cod fishing of France in four-and-a-half centuries, and have attempted to explain the influence of each factor upon this fishery. In my view there are five negative factors:

- numerous wars over several centuries
- poor climatic conditions for work and accessibility at sea during the Little Ice Age
- lack of understanding of the hydrology and climatic conditions (end of spring and summer were the fishing seasons)
- taxes on salted cod in several ports
- much greater profit from trade with the West Indies in the eighteenth and nineteenth centuries

Nonetheless, there are also four positive factors which contributed to the growth of the cod fishery in France:

- good climatic conditions for cod resources during the Little Ice Age
- improvements in ships throughout the centuries
- financial initiatives to promote cod fishery
- usefulness of the fishery for training sailors for the navy

All these factors are to some extent interdependent, but it is not possible at present to rank them in order of importance or to appreciate whether the climate has been the major factor conducive to cod fishing.

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North Atlantic cod: the broad canvas

D. J. Garrod and A. Schumacher

Garrod, D. J., and Schumacher, A. 1994. North Atlantic cod: the broad canvas. – ICES mar. Sci. Symp., 198: 59–76.

The catches of North Atlantic cod in the twentieth century are reviewed, with emphasis on the period since 1950 when landings statistics are considered to have been highly reliable. Time series of landings data are used to describe the historic development of the fisheries and the main events affecting catches. These are coupled with a comparison of trends among stocks to distinguish environmental and climatic effects from fishery-induced changes. An overview of North Atlantic cod landings indicated that, following a highly productive period 1950–1965, the cod fisheries have subsequently suffered a protracted decline. Concomitant environmental changes would not be expected to cause a consistent decline in all cod stocks throughout their north–south climatic range; if some might have improved, others might not. Comparison of landings trends between various stocks provide some evidence of climatic effects; however, the very widespread decline in landings in nearly all stocks speaks in favour of increased fishing mortality as the dominant factor in recent years. The potential benefits of a precautionary management approach to rebuilding cod stocks is discussed and recommended.

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Foreword

Fishery statistics were originally introduced in the context of national and regional economic issues as the main source of information on the catch and effect of fishing rather than for research purposes. When the scientific evaluation of fishery resources began it required a more complete reporting system of catches taken by all participants in a fishery and, owing to the international character of most fisheries, this, in turn, required international cooperation. It was the International Council for the Exploration of the Sea (ICES) which, at the beginning of this century, started to organize the collection and publication of the information required for stock evaluation purposes.

Obviously, such an undertaking could not immediately be successful. A certain period of learning and adaptation was required and improvements in the reliability of the fishery statistics have mainly been associated with the progress made by ICES and other international fisheries organizations (i.e., the International Commission for North Atlantic Fisheries (ICNAF); North Atlantic Fisheries Organization (NAFO); and the United Nations Food and Agriculture Organization (FAO)) to obtain appropriate and complete data from all countries. Nonetheless, there have been periods when the accuracy of this information has not been as precise as desired. Within the ICES area, the uncertainty of the statistics lasted into the 1920s, and for the ICNAF area (judging from the ICNAF *Statistical Bulletin*) not before 1959 from many stocks. From then until the mid-1970s the information could be regarded as being fairly complete and reliable. There were difficulties with catch allocation for some of the smaller stocks, but aggregate landings statistics for broad stock areas were generally satisfactory. However, with the beginning of the 1970s, when the discussion on management by catch limitation and the introduction of Exclusive Economic Zones (EEZs) started, misreporting began to introduce a new element of uncertainty.

Inaccuracy began to occur owing to: (i) over-reporting of catches to support claims in negotiations about fishing opportunities or shares of TACs (quotas), and (ii) concealing overfishing of quotas, mis-reporting catches of quota species from another fishing area, or as different species, or perhaps not at all. These deficiencies have to be kept in mind when drawing conclusions from fishery

statistics alone. However, the present article considers the development of the cod fishery in the North Atlantic in a wider context, and therefore the less reliable data are not expected seriously to affect the conclusions.

Introduction

The historic development of individual Atlantic cod fisheries is dealt with in the area reviews presented later in this Symposium. Our purpose is to present the evolution of the fisheries in the Atlantic-wide context, drawing on the similarities and differences between stocks to illustrate common trends and key events in management. The factors which have contributed to this history inevitably lead back to the persistent issues of fisheries science, namely the relative importance of environmentally and fishery-induced changes in determining the productivity of fish stocks. We hope that the comparisons between stocks will add to conclusions that will emerge from consideration of individual stocks.

Our information is drawn from the reports of ICES and NAFO working groups, coupled with advice from the scientists concerned with each stock. **All such catch series involve a measure of interpretation by the scientists best placed to do so, and these have been accepted as of 1992, without detailed annotation of each data set in the knowledge that discrepancies are minor in relation to the broad features referred to in this review. The statistics have NOT been updated to conform exactly to the data in other papers presented at this Symposium and it is those which should be regarded as the authorized record. In the interests of brevity the various sequences are presented as figures rather than tabulations.**

North Atlantic cod catches – the twentieth century (Table 1) (Data sources listed in the References)

Total Atlantic

The major cod fisheries of the Northeast Atlantic were developed in earlier centuries. The early history of the Northwest Atlantic (Newfoundland) fisheries has recently been reconstructed from historical archives (Cushing, 1988). The present review begins with the earliest year of this century, but is primarily concerned with the period since 1930.

The development of cod landings from the Atlantic since 1930 is shown in Figure 1. The steady increase to about 3 million tonnes in 1956 was only interrupted during the war period 1939–1945. In 1968, maximum landings of about 3.9 million tonnes were reached, followed by a continuous decline to the lowest level of the past 60 years. Three main areas, i.e., the Northeast Atlantic, Northwest Atlantic, and the European Shelf region, contribute to the development of the total yield, but in different ways.

Northeast Atlantic (Fig. 2)

Total catch

A strong component of the total Atlantic cod fishery has always comprised the yields from the cod stocks in the boreal Northeast Atlantic (especially Northeast Arctic, Iceland, and Greenland). Fishery statistics for these stocks have been available since the turn of the century and are thought to be of sufficient accuracy to describe the historical development of the fisheries in broad terms.

Apart from the interruption of two war periods, there has been a steady increase in total landings from the Northeast Atlantic from a level of about 400 000 t at the beginning of this century to a maximum of more than 2.2 million tonnes in 1956. The following period, with a generally declining trend, showed some high peaks as a result of a few good year classes available for exploitation in the Northeast Arctic cod stock. Catches from this stock have dominated the total yield from the Northeast Atlantic since the mid-1930s.

Northeast Arctic and Iceland cod

The Northeast Arctic and Iceland stocks have amongst the longest recorded histories of any of the North Atlantic cod stocks and many ecological similarities within their own geographical and seasonal ranges. Both fisheries have the distinctive elements of a traditional fishery on spawning cod of great antiquity which, with the advent of powered trawlers, was then extended on to often less accessible feeding grounds. The fisheries were then further developed in the 1920s by trawler fleets of northwest Europe. The development of the fisheries through the 1930s was followed by the interruption of the war years, when the landings from the Northeast Arctic cod must be in some doubt, but renewed post-war expansion led to a peak in landings during the mid-1950s. This was followed by a protracted decline to the present day. Northeast Arctic cod stocks show a high level of short-term variability throughout the time series. This is less marked in the Icelandic fishery, where catches reached an all-time peak of over 500 000 t during 1930–1933. This may reflect the first benefit at Iceland of immigrant spawning cod from the expanding cod stocks at west Greenland.

The proportions of Icelandic and distant water fisheries at Iceland became almost equal from 1920. There was a decline from the 1933 peak due to economic reasons, and in the war years, but this was followed by redevelopment reaching a level of 300 000–400 000 t

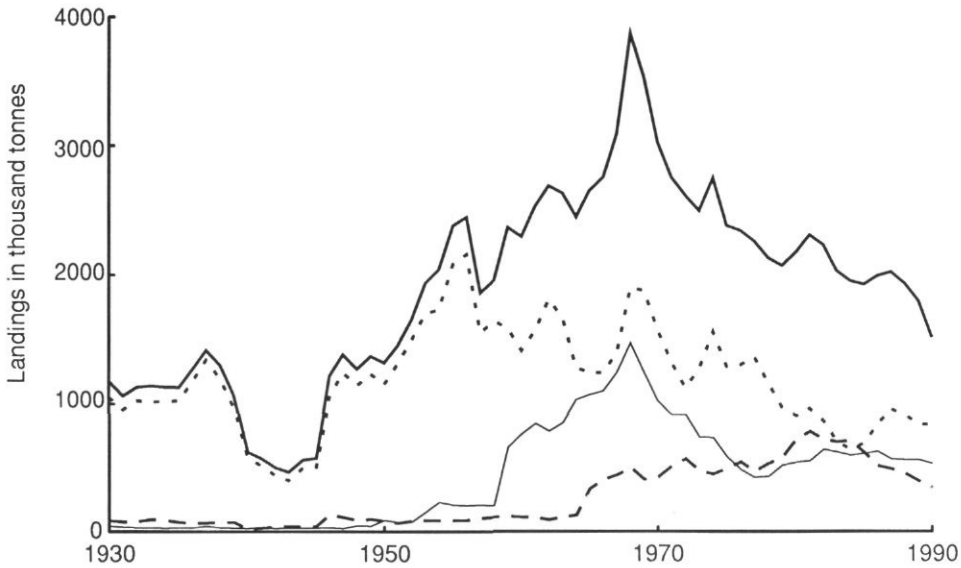


Figure 1. Total landings in the North Atlantic cod fisheries 1930–1990. —— Total; – – – European Shelf; - - - - NE Atlantic (excl. European Shelf, inc. Greenland); —— Northwest Atlantic.

which was maintained (with fluctuations) until around 1970 and then followed, despite the termination of the traditional distant water fisheries, by a more persistent, gradual decline, but with occasional better periods.

Data on mean fishing mortality are illustrated in Figure 3 and show, for Icelandic cod, a continuous increase from 0.3 in 1955 to about 0.8 in 1976. There was a reduction in 1977, when EEZs were introduced. How-

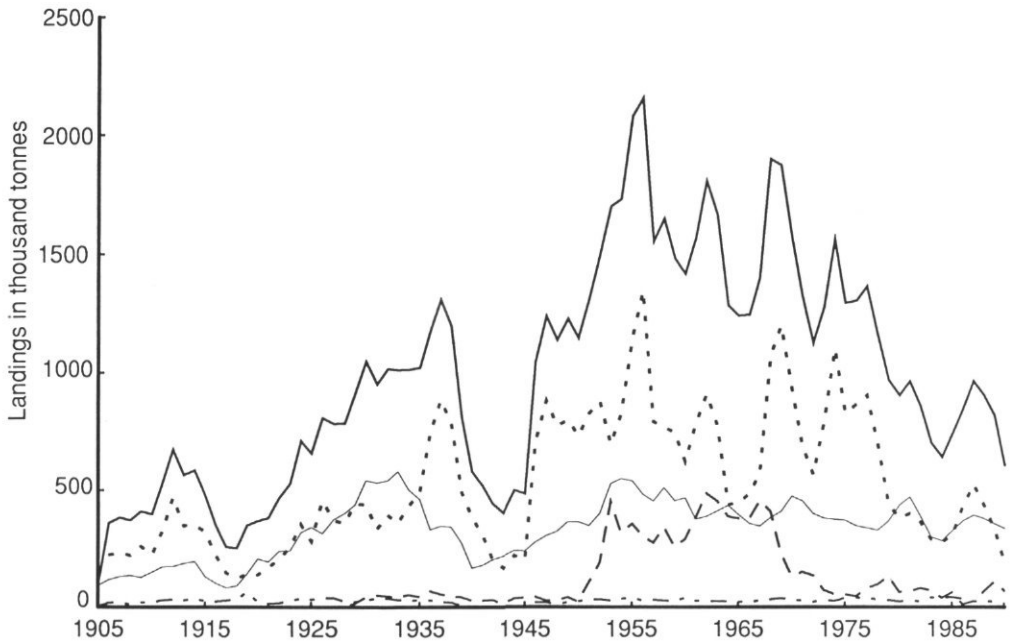


Figure 2. Total landings in the Northeast Atlantic cod fisheries 1905–1990. —— Total; - - - - - - NE Arctic; ——— Iceland; - - - - Faroe Is; — — — — — Greenland.

Table 1. Total cod catch (t) (rounded to the nearest thousand)

	Overall stock totals									Aggregated stocks			
			European Shelf										
	NE Arctic & Iceland	Faroes	North Sea Kattegat and Skagerrak	Other: incl. Baltic	E. W Greenland	2G–3NO	3M	Nova Scotia.Sth Newfoundland 3Ps-4X Newfoundland	S.A.5&6	Total of regional totals	NE Atlantic excl. European Shelf incl. Greenland	European Shelf	NW Atlantic excl. Greenland
1905	92	4	–	–	–	–	–	–	36	132	96	–	36
1906	341	19	89	–	–	–	–	–	62	510	360	89	62
1907	362	20	85	–	–	–	–	–	57	524	382	85	57
1908	358	12	94	–	–	–	–	–	40	504	370	94	40
1909	387	20	115	–	–	–	–	–	40	562	407	115	40
1910	376	19	115	–	–	–	–	–	35	545	395	115	35
1911	497	30	119	–	–	–	–	–	26	672	527	119	26
1912	641	32	130	–	–	–	–	–	28	830	673	130	28
1913	535	29	129	–	–	–	–	–	24	718	565	129	24
1914	546	38	161	–	–	–	–	–	33	778	584	161	33
1915	452	25	107	–	–	–	–	–	18	602	477	107	18
1916	326	26	82	–	–	–	–	–	19	452	351	82	19
1917	230	27	59	–	–	–	–	–	21	337	257	59	21
1918	216	36	65	–	–	–	–	–	30	347	252	65	30
1919	285	64	110	–	–	–	–	–	30	489	349	110	30
1920	344	23	156	–	–	–	–	–	27	550	367	156	27
1921	367	14	143	–	–	–	–	–	32	555	381	143	32
1922	445	19	131	–	–	–	–	–	31	626	464	131	31
1923	501	26	86	–	–	–	–	–	30	643	526	86	30
1924	672	45	82	–	–	–	–	–	33	832	717	82	33
1925	623	38	85	–	–	–	–	–	34	781	662	85	34
1926	767	44	99	–	3	–	–	–	40	953	814	99	40
1927	742	45	97	–	3	–	–	–	39	926	790	97	39
1928	757	30	79	–	2	–	–	–	35	903	790	79	35
1929	874	27	75	–	14	–	–	–	37	1026	915	75	37
1930	977	33	84	–	43	–	–	–	41	1179	1053	84	41
1931	862	45	74	–	51	–	–	–	33	1066	959	74	33
1932	932	45	78	–	47	–	–	–	31	1134	1024	78	31
1933	938	38	93	–	42	–	–	–	32	1143	1018	93	32
1934	930	35	87	–	53	–	–	–	28	1133	1019	87	28
1935	949	32	74	–	45	–	–	–	31	1131	1026	74	31
1936	1078	35	64	–	68	–	–	–	31	1275	1180	64	31
1937	1230	27	67	–	55	–	–	–	40	1418	1311	67	40
1938	1132	24	71	–	46	–	–	–	32	1304	1201	71	32
1939	924	6	70	–	43	–	–	–	28	1072	974	70	28
1940	551	–	23	–	27	–	–	–	24	626	579	23	24
1941	490	–	25	–	28	–	–	–	32	575	518	25	32
1942	408	–	38	–	31	–	–	–	25	502	439	38	25
1943	388	–	39	–	14	–	–	–	27	467	401	39	27
1944	462	–	35	–	36	–	–	–	28	561	498	35	28
1945	469	–	39	–	41	–	–	–	29	577	509	39	29
1946	983	30	131	–	44	–	–	–	30	1219	1057	131	30
1947	1188	31	112	–	29	–	–	–	23	1383	1247	112	23

Table 1. Continued

	Overall stock totals									Aggregated stocks			
			European Shelf										
	NE Arctic & Iceland	Faroes	North Sea Kattegat and Skagerrak	Other: incl. Baltic	E, W Greenland	2G–3NO	3M	Nova Scotia.Sth Newfoundland 3Ps-4X Newfoundland	S.A.5&6	Total of regional totals	NE Atlantic excl. European Shelf incl. Greenland	European Shelf	NW Atlantic excl. Greenland
1948	1098	21	85	–	27	–	–	20	25	1276	1146	85	45
1949	1164	28	97	–	43	–	–	16	25	1372	1235	97	41
1950	1096	36	81	–	24	–	–	65	20	1322	1156	81	85
1951	1174	35	65	–	107	–	–	53	18	1453	1316	65	71
1952	1277	30	82	–	190	–	–	60	14	1653	1497	82	74
1953	1221	27	87	–	449	66	–	73	11	1935	1698	87	151
1954	1374	36	86	–	319	135	–	81	12	2042	1728	86	228
1955	1686	38	87	–	355	114	–	80	12	2374	2080	87	207
1956	1824	28	86	–	303	65	–	121	13	2440	2155	86	199
1957	1246	31	100	–	276	90	–	104	13	1862	1554	100	207
1958	1273	28	111	–	341	48	–	137	16	1955	1642	111	202
1959	1297	26	116	–	259	427	7	211	16	2358	1582	116	661
1960	1087	39	110	–	290	547	1	203	14	2291	1416	110	765
1961	1158	27	108	–	381	581	20	229	18	2523	1566	108	849
1962	1296	24	91	–	485	543	16	200	27	2681	1805	91	785
1963	1186	24	110	–	452	583	33	208	30	2626	1662	110	854
1964	871	25	125	–	385	676	39	290	28	2440	1282	125	1033
1965	839	26	186	147	378	694	54	282	42	2648	1243	333	1072
1966	841	23	230	177	379	728	29	286	58	2751	1243	408	1100
1967	918	27	250	195	454	894	37	270	43	3088	1399	445	1244
1968	1456	34	283	216	409	1058	34	331	50	3870	1899	499	1472
1969	1604	38	196	212	232	917	22	266	46	3534	1875	408	1251
1970	1405	32	226	198	134	649	18	327	34	3023	1571	424	1027
1971	1143	28	346	165	153	578	25	279	36	2752	1323	511	917
1972	964	24	375	193	137	575	57	252	32	2609	1125	568	916
1973	1173	27	264	212	75	435	23	245	35	2490	1275	476	739
1974	1477	27	242	207	54	450	25	227	35	2744	1559	449	737
1975	1200	39	218	275	54	339	22	192	34	2373	1293	493	587
1976	1216	42	251	294	46	244	22	189	30	2335	1304	545	485
1977	1245	37	225	244	82	194	27	161	40	2255	1364	469	422
1978	1027	35	300	232	99	158	33	193	48	2125	1161	533	432
1979	809	29	267	315	133	197	30	241	50	2070	971	582	517
1980	815	24	292	431	66	198	10	270	62	2169	906	723	541
1981	868	27	342	442	69	199	14	287	55	2302	964	783	554
1982	752	25	310	413	83	275	13	286	71	2227	860	723	644
1983	590	41	280	425	71	264	10	287	63	2030	701	705	624
1984	562	39	230	484	41	261	13	274	49	1954	642	714	597
1985	633	44	220	400	17	269	14	281	48	1925	694	620	611
1986	799	36	189	327	11	303	15	276	36	1991	846	516	629
1987	915	28	200	291	19	277	11	241	38	2020	962	491	567
1988	813	28	167	288	72	312	2	202	47	1931	913	455	563
1989	689	24	140	255	126	287	40	192	43	1796	840	394	562
1990	522	14	130	214	101	248	32	196	58	1516	638	345	533

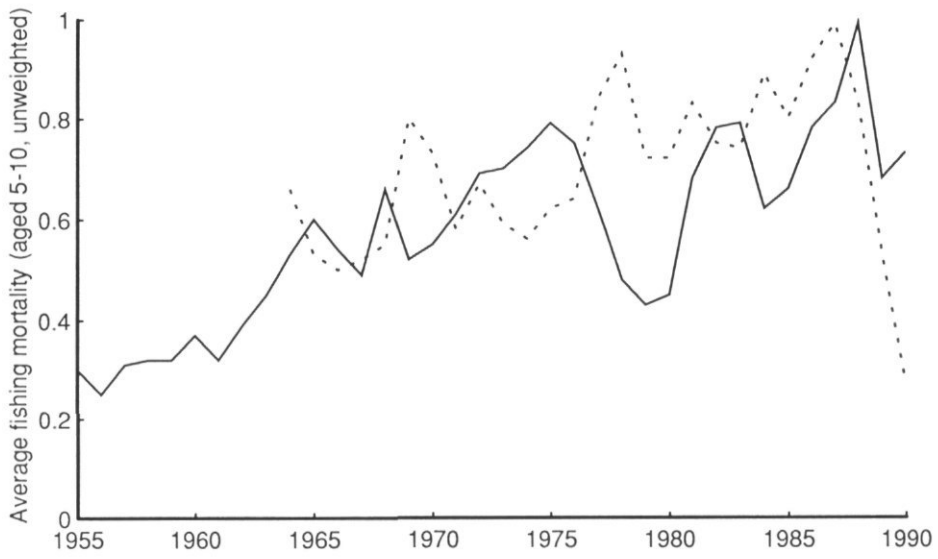


Figure 3. Fishing mortality in the Northeast Arctic and Iceland cod stocks 1955–1990. - - - - NE Arctic–Norwegian; —— Iceland.

ever, it appears that this lower level was only maintained over a short period, and by 1982 fishing mortality had returned to the previous relatively high level. The reduction in fishing effort following the exclusion of distant water fisheries was soon compensated for by the coastal state fishery.

An increasing trend in fishing mortality over the last 25 years is evident for the Northeast Arctic cod. There was, however, no significant drop in fishing mortality after introduction of the EEZs, since the two coastal states have always taken the largest proportion of the total yield.

Greenland

The time series for the Greenland fisheries are also shown in Figure 2 and are taken here to complete the overview of all the "Arctic" stocks (other than Labrador), which are subject to the low winter temperatures defining the northern limit of the range of the species in the Atlantic. The east Greenland fishery had always been relatively small in tonnage terms and somewhat intermittent, depending on ice conditions as much as on availability of cod. As noted above to emphasize the potential importance of the link with Iceland, the west Greenland fishery was redeveloped in the early 1930s. However, the main expansion took place after 1950. Landings peaked at 485 000 t in 1962 (from Table 1) but declined to less than 15 000 t during 1985–1987.

The high catch level in this period is almost exclusively the result of distant-water fishing activity, fishing on a much increased level of the cod stock (Dickson, 1994; Buch, 1994). The beginning of the "cod period" in the early 1950s cannot be explained by a sudden increase in fishing effort alone. Even before the start of this period there had been a continuous cod fishery at West Greenland by various distant-water fleets. The area was kept under continuous observation, and the first signs of increased fishing opportunities would have been detected and triggered a rapid expansion similar to the 1950s. The numbers of cod at West Greenland appear to have increased throughout the 1940s and attracted increasing fishing at the turn of the decade into the 1950s. This relatively sudden increase in yield at West Greenland is accepted as having been the result of an increase in biomass due to favourable environmental conditions.

Faroes

Although not subject to the Arctic extremes of winter temperatures, the cod in the Faroe area share many affinities with those at Iceland and in the Northeast Arctic. As can be seen in Figure 2, the stock is relatively small (catches ca. 30 000 t), but is of considerable interest because, having been one of the first to be developed in the early years of the century, catches have varied relatively little over the past 70 years compared to most other cod stocks (see also Fig. 11). It has, however, suffered a decline in the most recent five years, which must reflect a severe failure in recruitment.

Northwest Atlantic

Total catch

It has been possible to obtain some landings figures for the Northwest Atlantic as a whole, starting in 1930, but a more detailed area breakdown could only be presented from the beginning of the 1950s onwards (Fig. 4).

Yields from stocks in the Northwest Atlantic increased, with minor fluctuations, almost continuously to a maximum of 1.3 million tonnes in 1968, followed by a steady decline to a low of 344 000 t in 1977. They have since stabilized at about a level of 500 000 t.

Labrador to Newfoundland

The dominating component in the Northwest Atlantic has always been the cod stock from the Labrador and northern Grand Bank region (NAFO Areas 2J+3KL). Yields from this stock peaked at 810 000 t in 1968, but thereafter declined to 138 000 t in 1978. Landings ranged between 167 000 and 269 000 t during 1979–1990. Owing to marked declines in stock abundance, a fisheries moratorium was introduced in 1992.

The catches at Flemish Cap (NAFO Area 3M) are less certain than most because of the location and the different pattern of exploitation by various countries in recent years. The record since 1959 shows a peak catch of 60 000 t in 1965 followed by an almost uninterrupted decline (Table 1).

The development of yield from the Southern Grand Bank cod stock (NAFO area 3NO) and the St Pierre Bank cod stock (NAFO area 3PS) show trends similar to those of the Northern cod stock (Fig. 4).

Trends in exploitable biomass and fishing mortality for the Northern cod stock (NAFO 2J3KL) are shown in Figure 5 as percentages of the mean 1963 to 1984. The decreasing trend in exploitable biomass from the early 1960s to the mid-1970s is obvious as well as the increasing trend in fishing mortality during that period. As can be seen from Figure 6 this development was caused by the increase in distant water fishing activity since the late 1950s. The total cod yield from the distant water fisheries in all Northwest Atlantic regions reached a maximum of slightly below 1 million tonnes in 1968 and in every year over the period 1964–1974 the distant water fisheries took over 70% of the total landing, whilst the yield of the coastal state fisheries showed a somewhat declining trend. This pattern can also be found in the data for cod in NAFO 3NO and 3Ps. The mean fishing mortality for these three Northwest Atlantic stocks increased almost simultaneously – with the usual fluctuations – peaking suddenly at extremely high levels in 1974–1976 at a time when the catch of the distant water fisheries actually declined. Some of the lowest catches on record must therefore have been taken by a level of effort comparable to those preceding years.

A sharp reduction in mean fishing mortality from the high 1976 level and a stabilization or reversal of the declining trend in exploitable biomass (as well as grow-

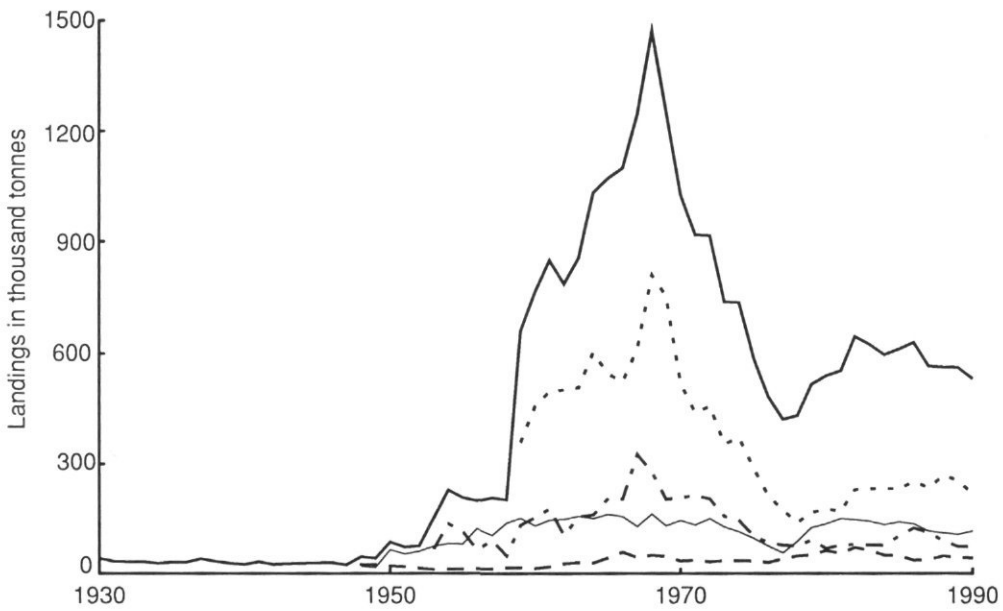


Figure 4. Total landings in the Northwest Atlantic cod fisheries 1930–1990. —— Total; - - - - 3M, 3NO & 3Ps; — — — — SA5 & 6; - - - - 2J 3KL; —— SA4.



Figure 5. Exploitable biomass and fishing mortality; Northern cod (NAFO 2J + 3KL) 1963–1984. —— Exploitable biomass; - - - - - - Fishing mortality.

ing yield of the coastal states fishery) can be seen following the introduction of EEZs in 1977. A new increase in fishing mortality has been observed since the minimum in 1980, but it would be premature to comment on the most recent development, since it seems that some questions associated with environmental phenomena have to be clarified before final conclusions can be drawn.

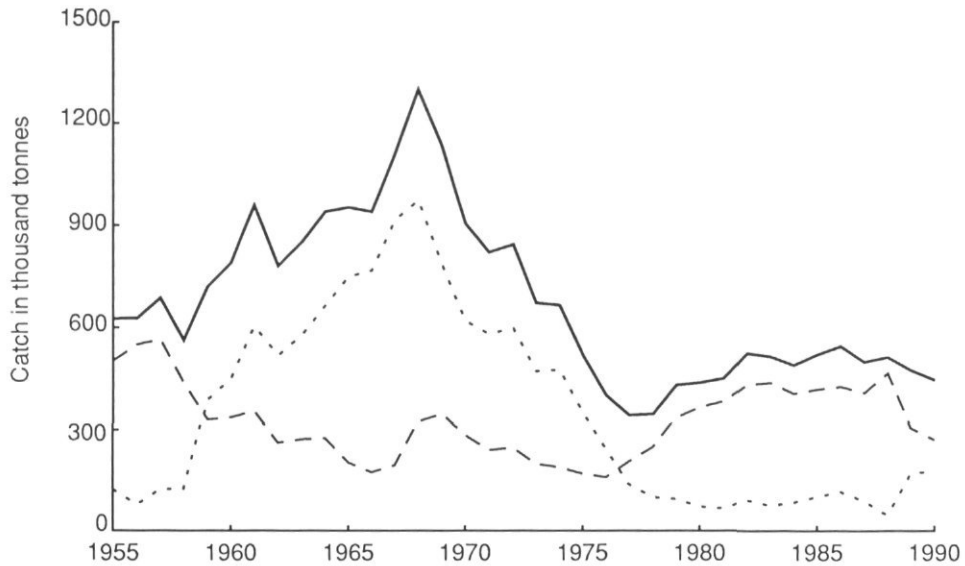


Figure 6. Comparison of landings in the distant water and coastal cod fisheries of the Northwest Atlantic 1955–1990. —— Total; - - - - - - Distant water fisheries; – – – Coastal states.

South from Newfoundland

Similar considerations and conclusions can be applied to the group of cod stocks lying off the eastern seaboard of North America south from Newfoundland. The time series of aggregate catches shows a maximum in the late 1960s followed by a secondary maximum in the 1980s. The secondary maximum is most evident in the New England series (SA 5&6), together with the cod fisheries off Nova Scotia (4x, 4VsW). Stocks more influenced by the Gulf of St Lawrence show complex intermediate variations. The purpose of summarizing the cod catches in this way has been to draw attention to significant correlations between some of the series of cod catches which are discussed later.

European shelf waters

The Northwest European shelf complex of stocks is as difficult to summarize as the stocks in the vicinity of the Scotian Shelf in the Northwest Atlantic, because the boundaries between some of them, and especially the fisheries, are not very distinct. Figure 7 gives catches from:

North Sea
  West of Scotland (ICES VIa)
  English Channel (ICES VIId–e)
Baltic (Areas 22–32)
  West of Scotland (ICES VIb)
  Bristol Channel (ICES VIIf, g)
Kattegat and Skagerrak
  Irish Sea (ICES VIIa)
  Celtic Sea (ICES VIIb–c, h–k)

The time series of catches which can be *reliably* ascribed to each particular stock area is relatively short for all except the Baltic and North Sea cod. The series for the Kattegat and Skaggerak begins in 1970 and these, taken together, show the same pattern of variation in catches as the North Sea fishery. For the present broad purposes they have therefore been combined into the larger, adjacent North Sea stock in Table 1. Together, the Baltic and North Sea catches represent a steady expansion in landings from a level recorded as less than 200 000 t in the first half of the century to a peak in the early 1980s.

The time series for the North Sea is long, and, in fact,

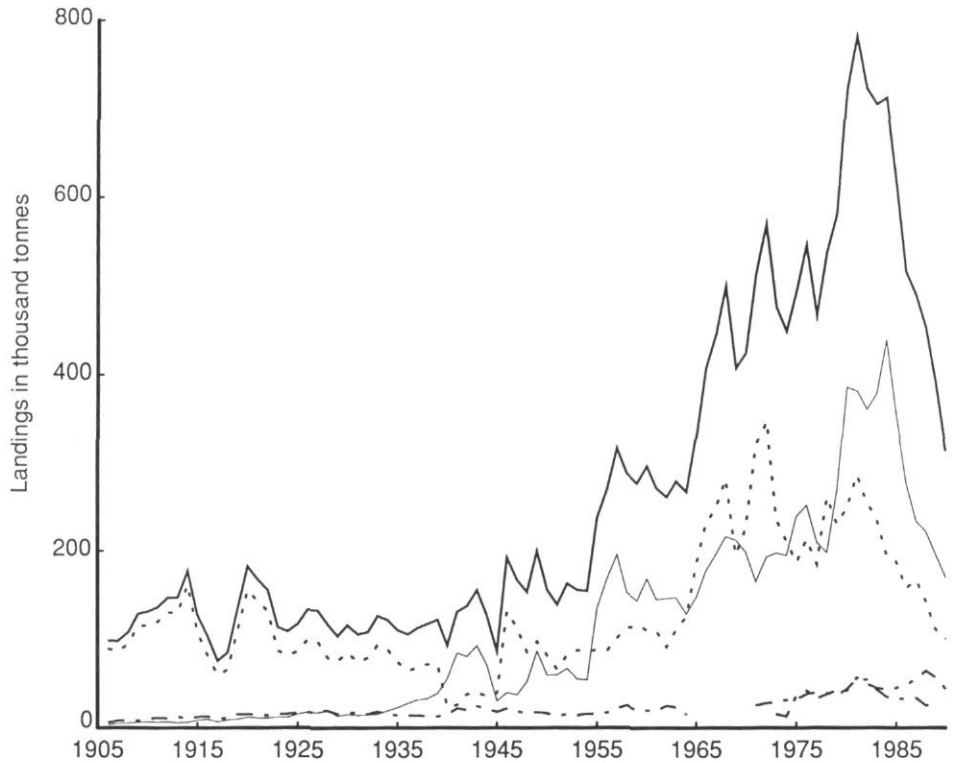


Figure 7. Total landings in European shelf cod stocks 1905–1990. —— European Shelf; —— Baltic; - - - - - Skagerrak and Kattegat; - - - - - - North Sea; – – – Channel and west of British Isles.

excluding war years, catches were surprisingly stable over the half century 1906–1963. There then followed what has come to be referred to as the "gadoid outburst" represented, in cod, by the very good year classes in 1969, 1970, 1976, and 1979. It is not really clear what is meant by an "outburst", nor whether the increase in catches in the late 1960s was associated with more favourable environmental circumstances. Although catch records are available, the detailed age composition of the North Sea cod stock is only very sparsely documented before 1963. Careful reconstructions confirm that even on alternative assumptions on the level of exploitation in the 1930s, the recruitment and stock size of North Sea cod increased to record higher levels in the 1960s and 1970s (Daan and Heessen, 1994, Fig. 8d). The improvements in catches in the late 1960s and 1970s reflect the more recent and well-documented increase in exploitation, coupled with the effect of an improved recruitment. Catches have since fallen back to the 1960s level in a decline which is still continuing.

The other catches from the southwestern area, ICES Subarea VII, cod fisheries are much smaller. They are not illustrated because the landings from some of them, and the distinctions between them, are generally poorly determined, particularly in earlier years, and they are especially sensitive to the occasional stronger year class. Although crucial details of the 1950–1960 period remain uncertain because of the lack of detailed data on stock structure, the catches of all these stocks have declined since 1980s, with the onset of the decline in the Baltic being slightly later.

Fishing mortality for North Sea and Baltic cod is shown in Figure 8. Landings from both these stocks increased in the 1965–1990 period. This development in the stocks on the European shelf, and in particular the great extent of it, is hard to explain solely by the drastic changes in fishing effort during the same period. It seems more to have been a case where the influence of environmental factors may also have played a major role.

Overall trends

Since 1950, it has been clear that similar trends are apparent in each of the major sectors we have considered – the Northeast Atlantic "Arctic", Northwest Atlantic fisheries, and the European shelf fisheries. The fisheries and catches expanded through to the mid-1960s, driven largely by the expansion of the so-called distant-water trawl fisheries on both sides of the Atlantic. The peak was followed by a sharp decline as the declining catch was associated with high levels of exploitation. One might conclude that the peak catches could not be sustained. Certainly the change contributed to the extension of fishery limits which, in turn, led to the demise of the distant-water fisheries, some more rapidly than others! This reduction in effort, however, was quite rapidly offset by the expansion of coastal fisheries, and fishing mortality has reverted to its former levels almost

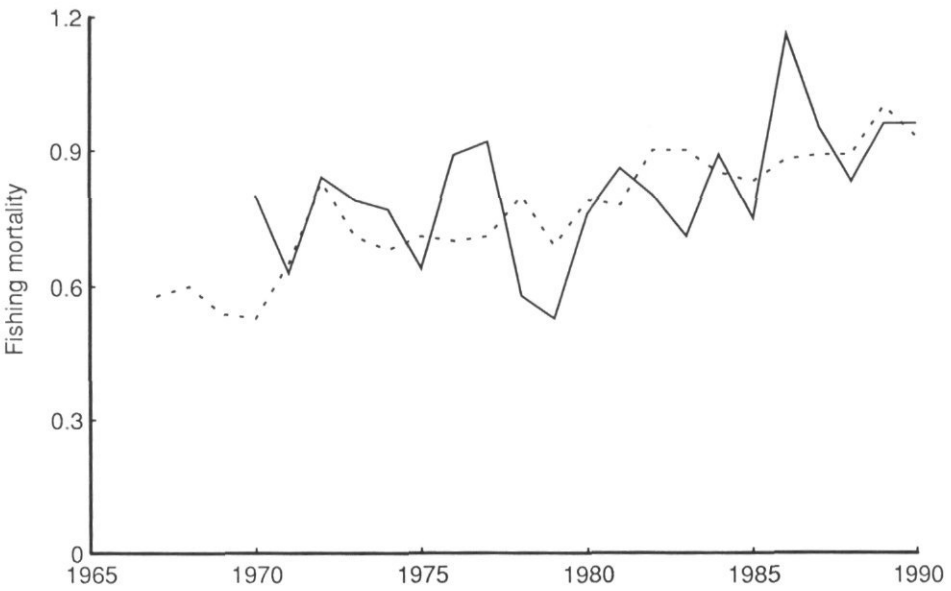


Figure 8. Fishing mortality in the North Sea and Eastern Baltic cod stocks 1965–1990. - - - - North Sea; —— Eastern Baltic (22–32).

everywhere (see below). More severe management measures were introduced in some areas, but these have not been effective in reducing fishing mortality or in promoting stock rebuilding. The one exception is the Northeast Arctic cod stock, where Fs have declined since the late 1980s and stock recovery is taking place.

Although the record for the early years is incomplete, there is no reason to doubt the gradual expansion to the peak of around 3.5 million tonnes in the late 1960s shown in Figure 1. This has been followed by a steady decline to the current level of around 1.5 million tonnes. This MUST be a matter for serious concern, and could be presented as a classic illustration of the consequences of overexploitation that corresponds very closely with theoretical expectations.

But is that the "whole story"?

The underlying trends in exploitation referred to earlier have been brought together in Figure 9 in "stock pairs", viz.

Northeast Arctic/Iceland
Labrador/Grand Bank (NAFO 3NO)
North Sea/Baltic
St Pierre Bank 3Ps/4x

For convenience, the annual F values for individual stocks have been calculated relative to their individual internal means 1970–1978 and then combined as the arithmetic mean of the named pairs. The pairings are based on geographical and ecological proximity in order to represent broad areas of the cod distribution. Statistical analysis indicates that there were no significant differences within the four pairs. More extended analysis showed a statistically significant linear trend in mortality with time in each pair. There was also a difference between the slopes, but all are positive. It is clear that although the rate has varied, there has been a gradual and systematic increase in exploitation throughout the North Atlantic stocks and the introduction of extended fishery limits failed to achieve more than a temporary hiatus before coastal states replaced the distant water fisheries and the anticipated fishery management benefits were lost. Transfers or exclusion of effort between one location and another did no more than temporarily delay a seemingly inevitable process. Indeed, even at Labrador and Grand Bank, where the sudden surge of exploitation was rapidly and dramatically restricted to the mid-1970s, the increase in F was almost immediately resumed.

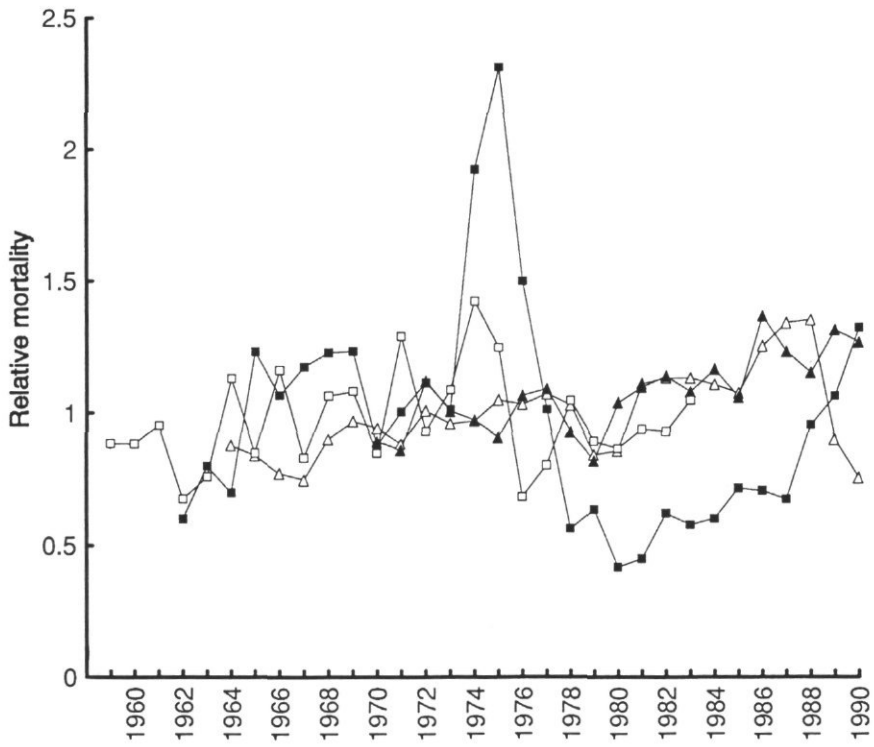


Figure 9. Trends in relative fishing mortality in selected cod stocks. △ Northeast Arctic and Iceland; ■ Labrador and Grand Banks; ▲ North Sea and Eastern Baltic; □ 3Ps and 4X.

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It is perhaps a little difficult to reconcile the steady increase in exploitation at broadly similar levels in all these stocks with the difference in timing of the increase, peak and then the decline in yield in all major sea areas, as summarized in Figure 1. The differences are more what one might expect where yield is influenced by environmentally induced trends in recruitment occurring at different times in the different sectors.

These second thoughts on the influences determining overall yield are reinforced by the scale of the changes. Figure 10 shows the relative yield from a stock with constant recruitment fished at progressively higher levels of exploitation (similar to the levels that have been recorded) showing the transitional yield as it is "fished up" by increasing levels of exploitation. The increase in exploitation has been distributed throughout the period in one case (Fig. 10a) and compressed into the early years of the series in the other case (Fig. 10b). The net benefit in yield from the fishing up of the "surplus" biomass by a progressive increase in exploitation is only in the order of 15%. This is far less than the scale of increase recorded in the fisheries themselves, and the larger transitional yield achieved by a rapid increase in exploitation would be restricted to only a very short period. The sustained improvement in catches from many of the Atlantic cod stocks is what could be expected from an increase in biomass and yield over and above what could be achieved from a stock where the recruitment was fluctuating without trend. It also suggests that the increase could not be achieved by an increase in catchability of the stocks as a result of some environmentally induced distribution change, because that is already reflected in the recorded increases in the fishing mortality.

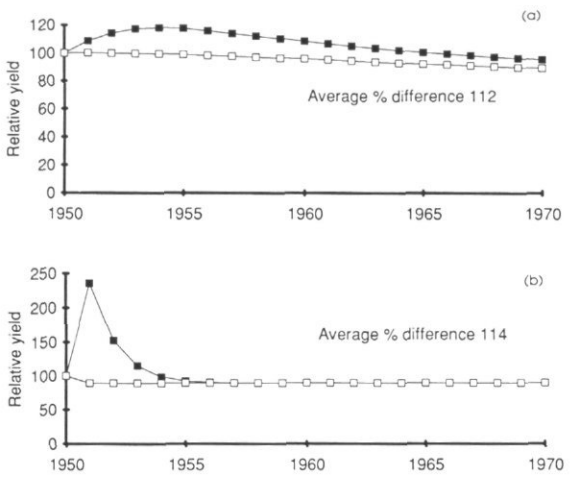


Figure 10. Comparison of transitional yield (as defined) and equilibrium yield at F = transitional F, (a) transitional fishing mortality increased from 0.3 to 0.9 over 20 years, i.e. 0.03 per year; (b) transitional fishing mortality increased 0.3 to 0.9 in 1951. ■ Total transitional; □ Total equilibrium.

The environmental evidence

The search for correlation between environmental variables and fish catches and, more specifically, variation in year-class strength, has a long and distinguished history but, except in the context of the El Niño and its effect on Peruvian anchoveta, the proposed relationships have had very little predictive capability. The difficulty should not surprise us. There are problems with the biological estimates, and the choice of environmental variable is invariably limited by the time series of data available. The environmental variables used most have been sea-surface temperature and atmospheric pressure, at spatial scales which are not necessarily closely related to the mechanisms determining year-class strength in a particular locality.

The recent development of testable hypotheses concerning the mechanisms determining survival in the early life history testify both to progress in thought and technique, and recognition of the complexity of the systems involved. It is almost too much to expect that the totality of the environmental components could be characterized by a single annual value covering all the time and space scales involved for any one stock.

The significance of environmental effects is nevertheless accepted even if they cannot be specified. For North Atlantic cod, the most convincing evidence is to be seen in the 1940–1950 recovery of the stock at West Greenland (Dickson *et al.*, 1994). The Greenland stocks, and the northern components of the Labrador cod, are at the lower temperature boundary of the habitable range for cod. One could expect these stocks to re-expand in periods of climatic amelioration.

Environmental effects on fish stocks are, of course, best examined in the time series of recruitment in the individual area reviews and would therefore be out of place here. However, one would expect to see major short-term environmentally induced variations in recruitment reflected in variation in landings over and above the effect of changes in fishing in response to changing stock conditions.

Figure 11 illustrates the compilation of the landings data from Table 1 and provides a clear indication of a fundamental Atlantic-wide structure which can now be interpreted against the background of the underlying and uniform upward trend in exploitation.

The evidence of environmental effect on the Greenland cod stock has already been referred to. The Iceland and Northeast Arctic time series, both separately and together, show visual evidence of single multidecadal-

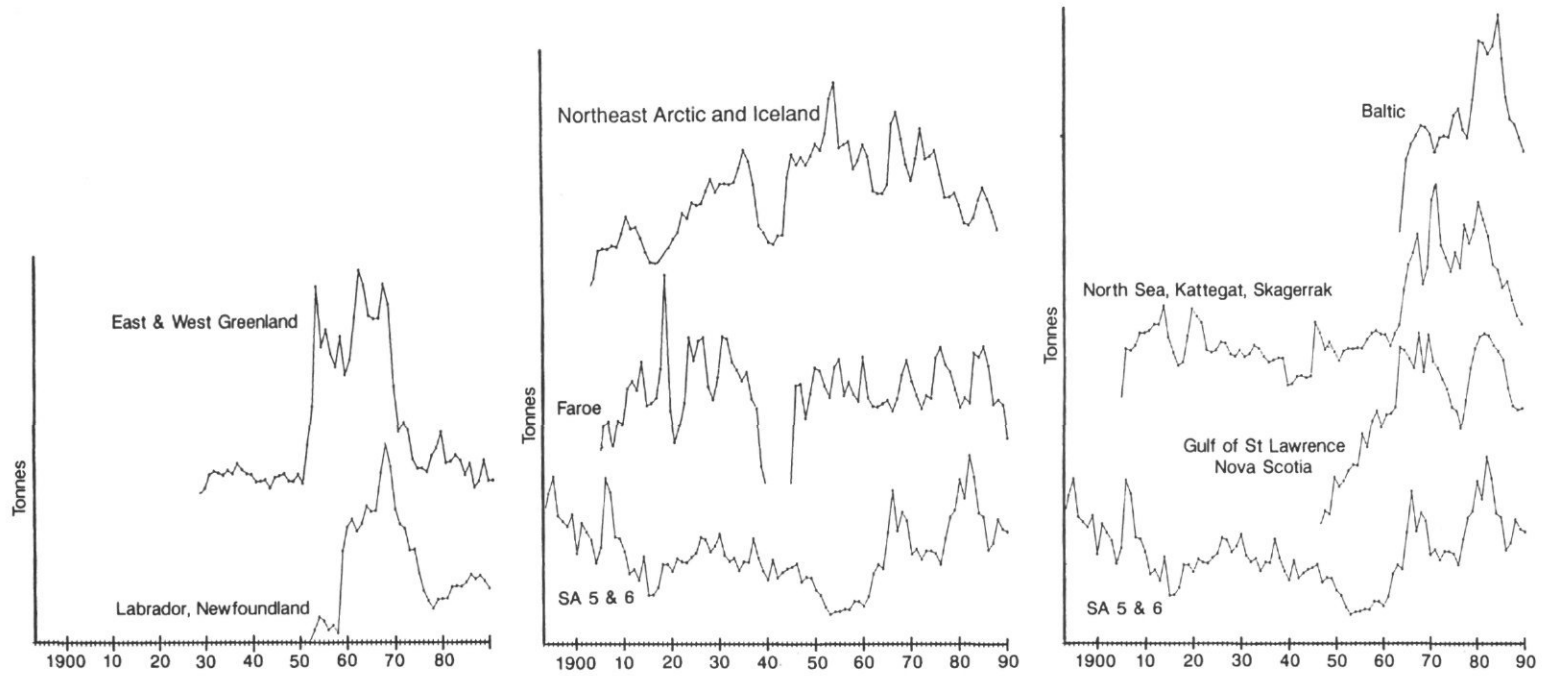


Figure 11. Compilation of cod landings from grouped cod stocks (Table 1).

induced rise to peak catches in the 1960s followed by a sustained decline. What are fairly obviously environmental periodicity and interannual variability are superimposed on this broader trend. The scale of the increase suggests that it involves more than increased exploitation over time and the key questions are how much of the long-term change is climatic, and whether the post-1950 downward trend in these stocks is evidence of a stock and recruitment decline. The patterns in the Arctic stocks are, however, quite different from the pattern of variation in the Faroe cod fishery. Following the initial development of the fishery, the variation there has been almost entirely of the shorter-term environmental type, with something like a five-year periodicity. Indeed, if one considered this array of stocks as a quasi-experimental situation, then the landings in the Faroe fishery could be interpreted as representing a "control" situation showing the profile of catches to be expected under gradually increasing exploitation in a situation where there was no environmental *trend* (as opposed to periodicity).

The North American, New England series from SA5 & 6 could be interpreted as showing a long-term climatic change which in visual terms appears to be a mirror image of the Arctic stocks. This is supported by the correlation shown in Figure 12. The result for 1906–1929 is indeterminate, but for 1930–1990 there is a negative correlation with $r^2 = 0.150$ over $n = 62$. This is only significant at the $p = 0.01$ level but would in fact be significant at $p = 0.001$ if the group of (ringed) outliers at low (and from the conditions prevailing at the time, surely suspect) 1940–1945 wartime catches in some of the Arctic stocks are excluded.

The correlation between the New England stocks and the North Sea cod 1906–1990 (Figure 13) is, however, positive, $r^2 = 0.318$, $n = 85$, $F = 38.66$, and $p<0.001$. This also looks convincing, though we note in Figure 11 that the effect on landings of the strong recruitment to the North Sea fishery in 1971/1972 has no such clear counterpart in the landings from stocks in SA5 and 6. Given the trends in exploitation described above, this relationship does therefore suggest a common effect, but with opposite sign in the two stock areas. Similar features can also be seen in the Nova Scotia time series in Figure 11. A third correlation of the Arctic Stock and the North Sea is "good in parts", but not significant.

Given the nature of the data and the scope for confounding factors we find the correlations somewhat surprising. The trend of increasing exploitation has been shown to be quite general. The opposing sign of the correlations is what one might expect of a climatic effect on a long time scale which affects stocks on both sides of the Atlantic at the *same* "ecological latitude" in the same way, but in a way which is reversed in the Arctic stocks. On the evidence, Faroe is at an ecological "point of balance".

The signs of the trend change from south to north. Further evidence of an environmental effect can be seen in Figure 11 by comparing recent catches from the North Sea and Baltic. They have suffered a comparable de-

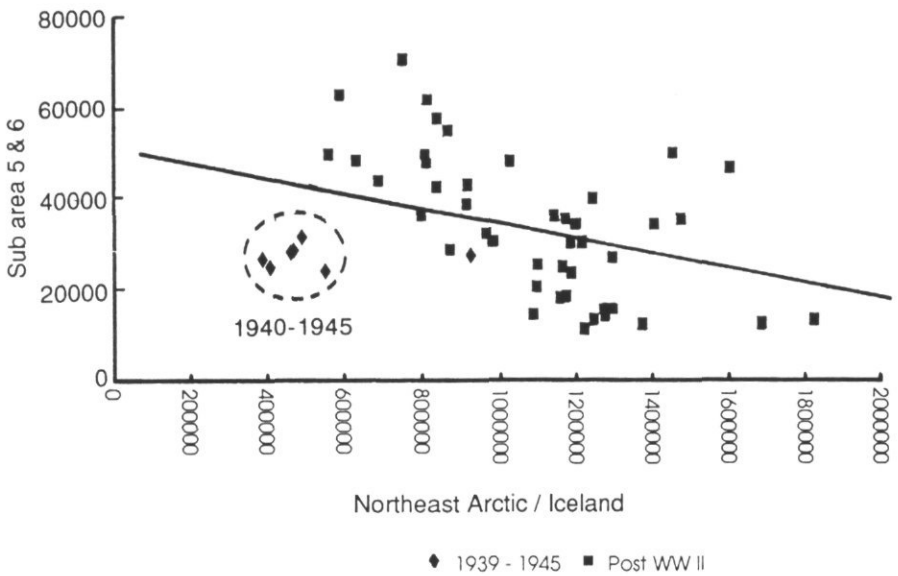


Figure 12. Regression of landings in Arctic (Northeast Arctic and Iceland) and NAFO S.A.5&6 cod stocks 1929–1990. ◆ 1939–1945; ■ post-World War II.

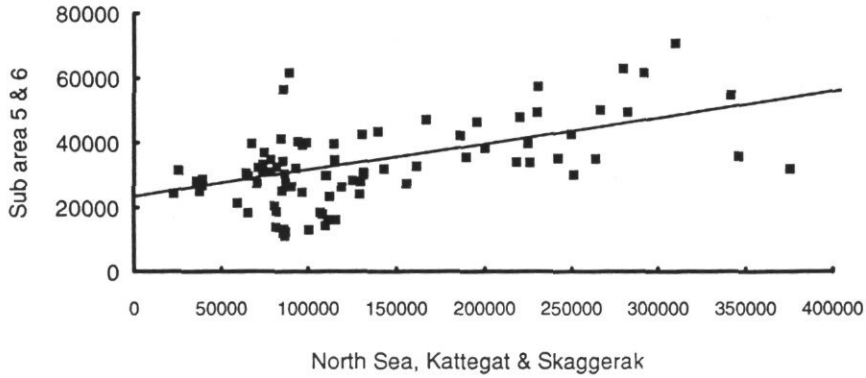


Figure 13. Regression of landings from North Sea and NAFO S.A.5&6 cod stocks 1906–1990.

cline, with a two-year lag into the Baltic. A similar feature can also be seen in the way the decline in the Labrador and Newfoundland catches lags behind the records for the Greenland fishery. Other analyses of individual stocks will consider likely environmental mechanisms responsible for these and similar effects. The present, admittedly simplistic approach does nevertheless argue in support of a widespread environmental trend affecting cod stocks through at least half the century, but with local effects superimposed in individual stocks, and in addition to the effect of fishing.

There are others better placed than us to identify the factors responsible. Dickson (1994) reminds us of classic papers that have established that "warming and salinification have been accompanied by radical northward shifts in the boundaries for a wide range of marine species". Ellet and Blindheim (1991) quote Ghil and Vautard's (1991) reconstruction of the principal component of the temperatures, the only example we know which purports to represent the northern hemisphere as a whole and thereby aggregates all the factors into a single annual figure. Ghil and Vautard's Figure 10 is reproduced with the Arctic cod catches in Figure 14 and the regression with Arctic cod catches (Arcto-Norwegian plus Iceland) in Figure 15, where $r^2 = 0.46$. It is actually difficult to find an environmental characteristic which, untuned, will correlate with fisheries data. This one just appeared without the usual diligent search and it is really quite difficult to escape the conclusion that this fits the broad trend of catches in the Arctic stocks quite well – up to the mid-1970s at least!

The entire time series might then be interpreted as showing the northward increasing relative abundance of cod comparable to the shift in boundaries referred to by Dickson and reflected here in the increased recruitment of cod to Arctic stocks. It might then be thought that the northward shift should be echoed by similar warming at the southern boundary of the distribution, which might be less then beneficial to recruitment there. From the negative sign of the North American/Arctic stock corre-

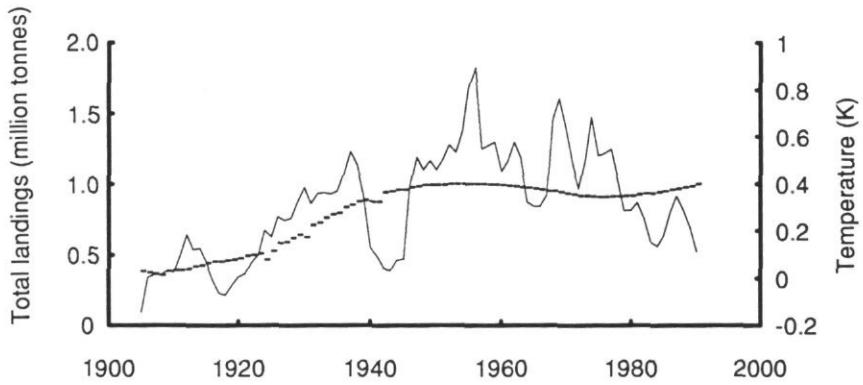


Figure 14. Comparison of combined Northeast Arctic and Iceland cod landings with the principal components of averaged surface air temperatures in the northern hemisphere (Ghil and Vautard, 1991). —— Total landings (million tonnes); - - - - - - Temperature (K).

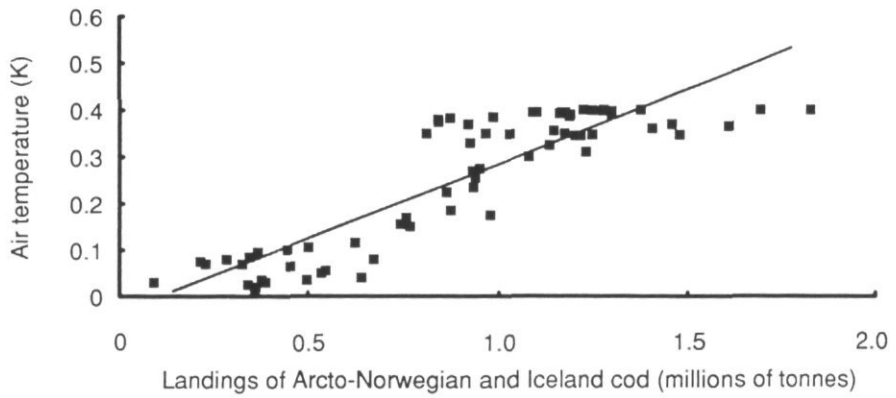


Figure 15. Regression of combined Northeast Arctic and Iceland cod landings on principal component of air temperature (as above).

lation and the positive North American/North Sea regression, that does indeed appear to be so. North Sea cod, for example, may not always benefit from colder climes, as Holden has proposed (1993) – but they may well be at a *disadvantage* on the southern boundary in the warm years. The two are not quite the same.

Figure 16 is a schematic interpretation, showing a hypothetical sinoidal band of increasing temperature covering the physiological range, which represents the potential for successful recruitment and therefore the potential geographical distribution of the stocks. As the physiological range moves northward with a warming trend there will be an increasing probability of good recruitment in warm years on the "cold" boundary, and a decreasing probability on the warm side. Hence the apparent inverse correlation between the Arctic stocks and those on the southern side, with the Faroe generally well within the range and showing relatively little response.

Whilst it is not yet possible to read the recent temperature changes in the context of a longer series, the continuing recent declines in cod stocks in some areas, e.g. Iceland/Faroe, do not appear to correspond to the Ghil and Vautard (1991) environmental principal component as convincingly as in the earlier years. A reduction in catches associated with reduced recruitment

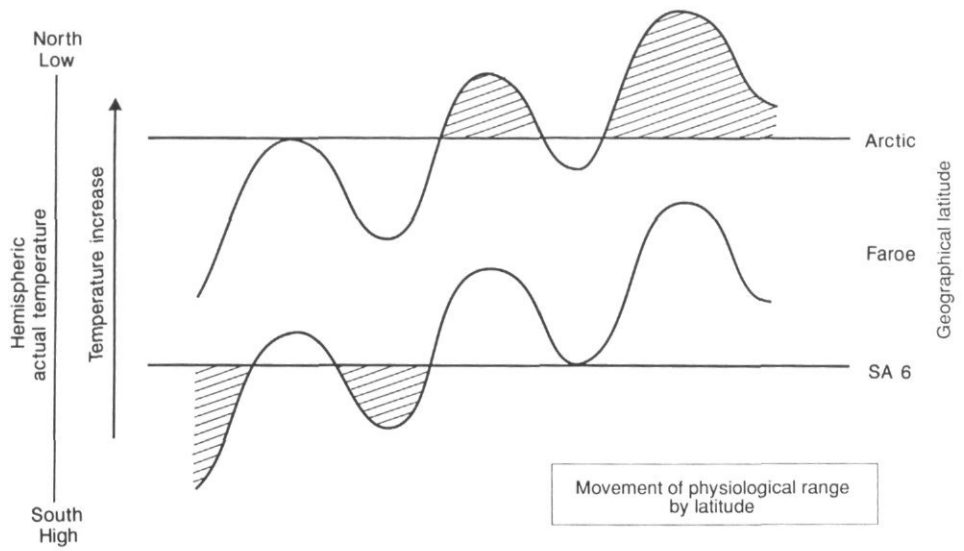


Figure 16. Schematic representation of trends in reproductive success with temperature as an index of favourable environmental conditions.

against the run of environmental expectation could occur as a result of a stock and recruitment relationship. The long-lived, late-maturing Arctic cod stocks on both sides of the Atlantic would be the most vulnerable to such an effect under sustained high levels of exploitation.

So what does the evidence of the time series amount to? First, a generally upward trend in catches into the mid-1960s was to be expected as fisheries were expanded and existing stocks were fished to a "lower" equilibrium level of standing stock. But whilst almost all stocks taken individually (and SA5 & 6 and North Sea series correlated together) conform to this pattern, the inverse relation between SA5 & 6 and the Arctic, even within the increasing trend, suggests that the effect of increasing exploitation has been superimposed on some wider pan-Atlantic scale environmental change most evident in the middle years of the century. By the statistical definition the correlation between some sets of catches and the Ghil and Vautard principal component parameter can hardly be fortuitous even though one may find it too facile, and as colleagues will hasten to point out it gives no indication of the mechanisms involved. But we think it is useful to have this wider evidence of changes in stocks and catches over such a geographical scale and which can be associated with a single environmental index, albeit a proxy for the real events, in a rational way. That the index is a derivative of temperature will confirm long-held presumptions and perhaps strengthen existing convictions, helping to focus forthcoming investigations.

Conclusion

We conclude from this analysis that the magnitude of variation in the POTENTIAL – the potential – for North Atlantic cod production has been strongly influenced by environmental circumstances, though the Ghil and Vautard "index" is not necessarily the most appropriate or only index. Other ecosystem constraints determine the actual stock production and therefore yield potentials, and this is in turn modulated by exploitation and by management to the extent it has, or could, control exploitation.

Recognition that environmental factors exert an important influence is not new. However, while the stronger evidence is useful because it confirms common sense, it should NOT be taken to mean that an environmental influence affecting stock decline provides justification for discounting future stocks and allowing unrestrained increases in fishing in order to maximize yield now. The North Atlantic cod stocks seem now to be environmentally weakened relative to, say, the 1950s. They are then especially vulnerable and there is even greater necessity to avoid double exposure to the additional risk of recruitment overfishing. In these circumstances, the level of exploitation needs to be even more carefully controlled to provide the basis for a future recovery. It is not an excuse for a "free for all" bonanza! It represents, in a sense, an application of the precautionary principle in fisheries, and should only be rejected if there is incontrovertible evidence that the stock will be totally lost regardless of the level of exploitation. We find it difficult to conceive of circumstances where this could apply and, indeed, remain concerned that if exploitation maintains the apparently inexorable trend of the last forty years the truly great North Atlantic cod will disappear.

Acknowledgments

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Fishery and environmental factors affecting trends and fluctuations in the Georges Bank and Gulf of Maine Atlantic cod stocks: an overview

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The Georges Bank and Gulf of Maine Atlantic cod stocks have been commercially exploited for centuries, and continue today to support important commercial and recreational fisheries in both the United States and Canada. Prior to 1960, the two stocks were fished exclusively by the United States. During the 1960s, marked increases in exploitation occurred due to the development of Canadian and distant-water fisheries on Georges Bank. Total landings from the two stocks increased from 14 400 t in 1960 to 57 500 t in 1966, but subsequently declined to 30 000 t in 1976. Under extended fisheries jurisdiction – enacted in 1977 by both the USA and Canada – landings and stock sizes initially increased and a record-high catch (71 000 t) was attained in 1982. However, during the late 1980s and early 1990s, fishing effort and fishing mortality also increased to record-high levels, resulting in marked reductions in spawning-stock size. Research vessel indices, commercial c.p.u.e. indices, and VPA results all indicate that biomass levels in both stocks are now at record-lows. Although it is clear that fishery-induced perturbations have had a major impact on the Georges Bank and Gulf of Maine stocks, environmental and biotic influences may also have affected the stocks. These influences are not easily discernible, given the magnitude of the fishery-induced changes. Biophysical processes appear to be extremely important during the first year of life of cod and affect growth, mortality, and year-class strength. These processes are reviewed and discussed in relation to their impacts on various life history stages of cod. Current and future research studies aimed at differentiating environmental from fishery-related factors affecting recruitment and abundance of cod in the Georges Bank–Gulf of Maine region are discussed.

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Introduction

On 14 May 1602, the sailing ship "Concord" – in search of sassafras trees to obtain quantities of sassafras extract for treating syphilis in Europe – completed a 50-day trans-Atlantic voyage from Falmouth, England to "a mighty headland" in the New World. Near this promontory, the "Concord" came to anchor in 15 fathoms [27 m] where such a "great store of codfish" was taken that the area was named Cape Cod (Jensen, 1972). Sassafras trees were also found in abundance, but it was cod that was to become the source of original wealth for both the early New England colonists and for the nation that was to become the United States (Serchuk and Wigley, 1992)

The earliest USA fisheries for Atlantic cod (*Gadus morhua*) began in the 1600s in nearshore waters off the states of Maine and Massachusetts. By the early 1700s, however, vessels had started to fish much farther offshore, with the Georges Bank fishery developing between 1720 and 1750. By the end of the nineteenth century, the offshore fisheries supported a thriving domestic industry; in 1880, greater than 12 000 t of cod were

landed from Georges Bank by the 163 schooners taking part in the fishery.

Continuous commercial landings statistics for cod exist from 1893 onward (Table 1). Total landings of cod from the Gulf of Maine and Georges Bank regions [ICNAF/NAFO Subareas 5 and 6: Fig. 1] exceeded 60 000 t in both 1895 and 1906, but declined to less than 20 000 t in 1915–1916 (Fig. 2). Between 1920 and 1940, cod was generally taken as a by-catch in the offshore fishery for haddock (*Melanogrammus aeglefinus*) – which had rapidly expanded in the early 1920s owing to development of a packaged trade in quick-frozen haddock fillets. During this 20-year period, annual landings of cod were relatively stable, fluctuating between 24 000 and 41 000 t and averaging 33 000 t annually. Cod catches declined in the 1940s and early 1950s, reaching a record-low of 11 000 t in 1953.

In the 1960s, Canadian and distant-water fisheries developed on Georges Bank, resulting in a rapid increase in fishing effort for cod (Table 2). Cod landings increased from 14 000 t in 1960 to 58 000 t in 1966, but afterward declined sharply to 30 000 t in 1976. In 1977,

Table 1. USA commercial landings (tonnes, live) of Atlantic cod from the Georges Bank (NAFO Division 5Z) and Gulf of Maine (NAFO Division 5Y) cod stocks (1893–1959). Prior to 1932, landings can only be assigned to Subarea 5.

Year	NAFO Subarea 5	Year	NAFO Subarea 5	NAFO Division 5Z	NAFO Division 5Y	Totals Subarea 5
1893	47 425					
1894	55 916					
1895	62 095	1930	41 341	–	–	41 341
1896	48 001	1931	33 338	–	–	33 338
1897	45 928	1932		25 122	5858	30 980
1898	44 150	1933		25 155	7025	32 180
1899	48 290	1934		15 976	11 619	27 595
1900	33 999	1935		21 162	9679	30 841
1901	45 238	1936		23 349	7442	30 791
1902	41 957	1937		32 282	7432	39 714
1903	39 024	1938		24 891	7547	32 438
1904	30 396	1939		22 048	5504	27 552
1905	36 316	1940		18 418	5836	24 254
1906	61 667	1941		25 453	6124	31 577
1907	56 516	1942		18 333	6679	25 012
1908	40 397	1943		17 341	9397	26 738
1909	39 672	1944		17 632	10 516	28 148
1910	34 796	1945		14 251	14 532	28 783
1911	26 427	1946		20 875	9248	30 123
1912	27 961	1947		16 582	6916	23 498
1913	24 101	1948		17 640	7462	25 102
1914	32 818	1949		17 681	7033	24 714
1915	18 459	1950		15 389	5062	20 451
1916	18 786	1951		14 791	3567	18 358
1917	21 330	1952		10 904	3011	13 915
1918	29 799	1953		8105	3121	11 226
1919	29 953	1954		8826	3411	12 237
1920	27 345	1955		9286	3171	12 457
1921	32 044	1956		10 535	2693	13 228
1922	30 847	1957		10 598	2562	13 160
1923	30 498	1958		11 582	4670	16 252
1924	32 639	1959		12 423	3795	16 218
1925	34 320					
1926	40 102					
1927	39 335					
1928	34 743					
1929	37 021					

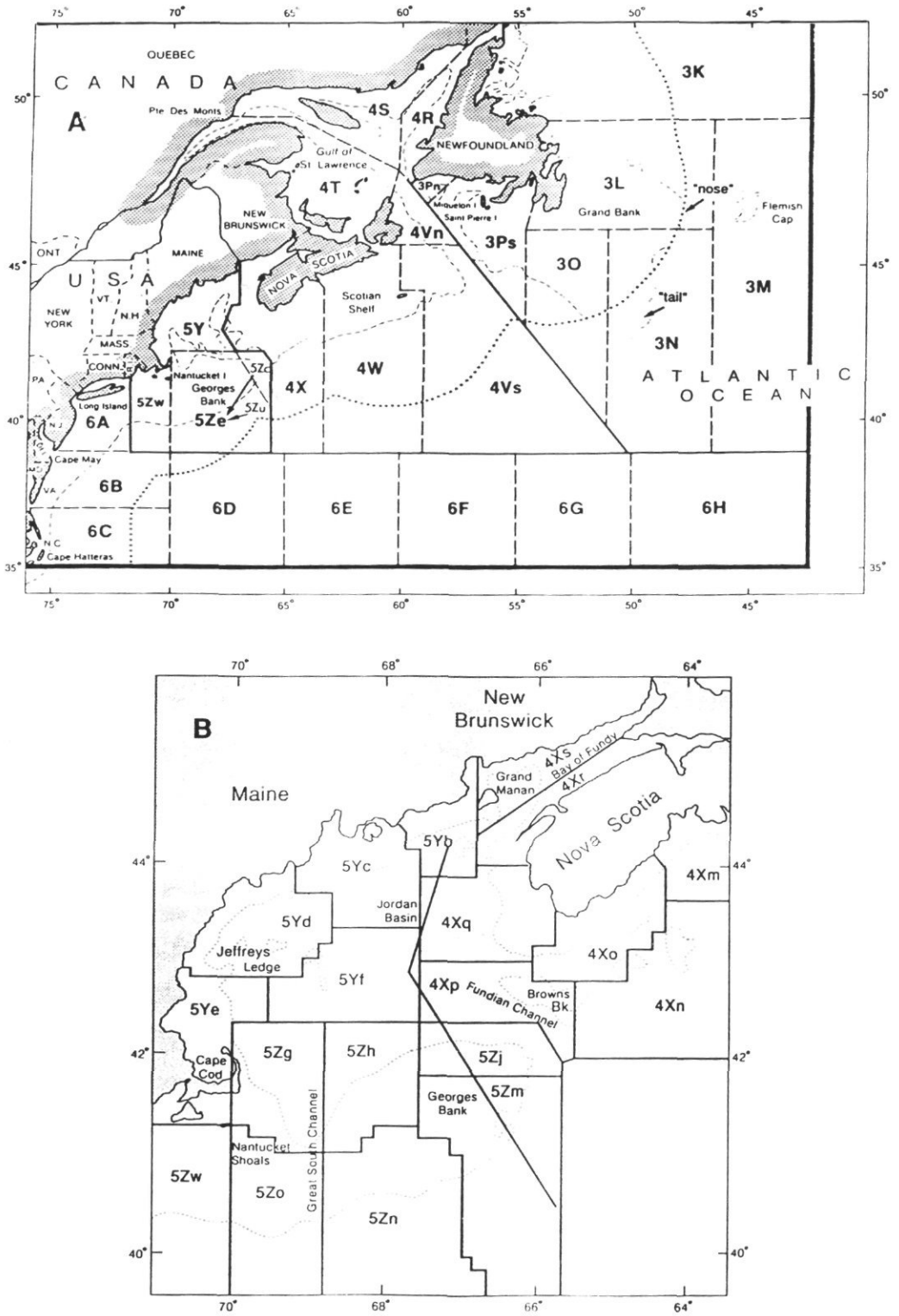


Figure 1. (A) Map depicting NAFO Subareas 3–6, and (B) statistical unit areas in the Gulf of Maine and Georges Bank (from Serchuk and Wigley, 1992).

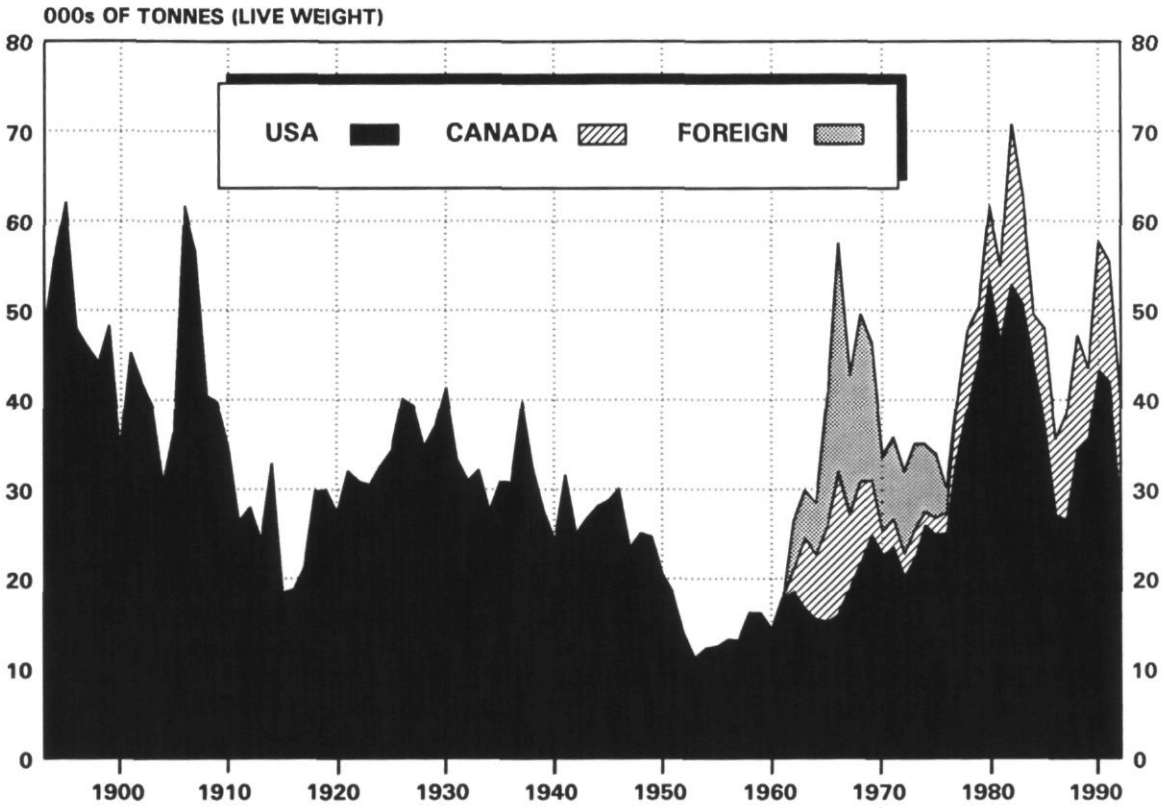


Figure 2. Total reported commercial landings of cod from the Georges Bank and Gulf of Maine stocks (1893–1992).

the USA and Canada independently enacted extended fisheries jurisdiction which prohibited distant-water fleets from fishing cod (and other species) in the USA and Canadian exclusive economic zones. By this time, the Georges Bank stocks of haddock, herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus*), and silver hake (*Merluccius bilinearis*) had already collapsed from overfishing ascribed largely to the distant-water fleets (Mayo *et al.*, 1992). Cod – which had always been a significant component of the groundfish complex in the Gulf of Maine and Georges Bank regions – had now become the most dominant component. Total cod landings (solely USA and Canadian) doubled between 1977 and 1982 (30 000 to 71 000 t, a record-high), declined to 36 000 t in 1986, but increased to 58 000 t in 1990. In 1992, however, landings fell to 39 000 t.

Since 1977, cod has annually accounted for more catch (by weight) than any other species in the USA Atlantic coast groundfish fishery. In recent years, cod has been so dominant that USA commercial landings of cod have typically exceeded those from haddock, redfish (*Sebastes fasciatus*), pollock (*Pollachius virens*), and six major species of flatfish combined (US Department of Commerce, 1992). In addition, between 3000 and 8000 t of cod are taken annually in recreational fisheries (Serchuk and Wigley, 1992).

Given the importance of cod off the northeast coast of the United States, in this paper we review the changes that have occurred over the past 30 years to the Georges Bank and Gulf of Maine cod stocks, and evaluate the influence of fishery and environmental factors in affecting stock size fluctuations, recruitment, growth, and maturation.

Stock definitions

In waters west of Nova Scotia and south of the Fundian Channel (i.e., NAFO Subareas 5 and 6), cod have been distinguished into three or possibly four major groups: (1) Georges Bank; (2) Gulf of Maine; and (3) one or two groups in the Southern New England–Middle Atlantic area (Wise, 1963; Serchuk and Wigley, 1992). Little interchange of cod occurs between the Gulf of Maine and Georges Bank groups, as inferred from tagging studies (Smith, 1902; Schroeder, 1930; North American

Table 2. Commercial landings (tonnes, live) of Atlantic cod from Georges Bank and South (NAFO Division 5Z and Statistical Area 6), and the Gulf of Maine (NAFO Division 5Y) (1960–1992).

	Georges Bank and South				Gulf of Maine				Grand Totals			
Year	USA	Canada	Other	Total	USA	Canada	Other	Total	USA	Canada	Other	Total
1960	10 834	19	–	10 853	3448	129	–	3577	14 282	148	–	14 430
1961	14 453	223	55	14 731	3216	18	–	3234	17 669	241	55	17 965
1962	15 637	2404	5445	23 486	2989	83	–	3072	18 626	2487	5445	26 558
1963	14 139	7832	5218	27 189	2595	3	133	2731	16 734	7835	5351	29 920
1964	12 325	7108	5732	25 165	3226	25	–	3251	15 551	7133	5732	28 416
1965	11 410	10 598	16 325	38 333	3780	148	–	3928	15 190	10 746	16 325	40 696
1966	11 990	15 601	25 543	53 134	4008	384	–	4392	15 998	15 985	25 543	57 526
1967	13 157	8232	15 363	36 752	5676	297	–	5973	18 833	8529	15 363	42 725
1968	15 279	9127	18 730	43 136	6360	61	–	6421	21 639	9188	18 730	49 557
1969	16 782	5997	15 160	37 939	8157	59	268	8484	24 939	6056	15 428	46 423
1970	14 899	2583	8170	25 652	7812	26	423	8261	22 711	2609	8593	33 913
1971	16 178	2979	9022	28 179	7380	119	163	7662	23 558	3098	9185	35 841
1972	13 406	2545	9108	25 059	6776	53	88	6917	20 182	2598	9196	31 976
1973	16 202	3220	9501	28 923	6069	68	9	6146	22 271	3288	9510	35 069
1974	18 377	1374	7580	27 331	7639	120	5	7764	26 016	1494	7585	35 095
1975	16 017	1847	7144	25 008	8903	86	26	9015	24 920	1933	7170	34 023
1976	14 906	2328	2692	19 926	10 172	16	–	10 188	25 078	2344	2692	30 114
1977	21 138	6173	56	27 367	12 426	–	–	12 426	33 564	6173	56	39 793
1978	26 579	8778	–	35 357	12 426	–	–	12 426	39 005	8778	–	47 783
1979	32 645	5978	–	38 623	11 680	–	–	11 680	44 325	5978	–	50 303
1980	40 053	8063	–	48 116	13 528	–	–	13 528	53 581	8063	–	61 644
1981	33 849	8499	–	42 348	12 534	–	–	12 534	46 383	8499	–	54 882
1982	39 333	17 824	–	57 157	13 582	–	–	13 582	52 915	17 824	–	70 739
1983	36 756	12 130	–	48 886	13 981	–	–	13 981	50 737	12 130	–	62 867
1984	32 915	5763	–	38 678	10 806	–	–	10 806	43 721	5763	–	49 484
1985	26 828	10 443	–	37 271	10 693	–	–	10 693	37 521	10 443	–	47 964
1986	17 490	8411	–	25 901	9664	–	–	9664	27 154	8411	–	35 565
1987	19 035	11 845	–	30 880	7527	–	–	7527	26 562	11 845	–	38 407
1988	26 310	12 932	–	39 242	7958	–	–	7958	34 268	12 932	–	47 200
1989	25 097	8001	–	33 098	10 397	–	–	10 397	35 494	8001	–	43 495
1990	28 193	14 310	–	42 503	15 154	–	–	15 154	43 347	14 310	–	57 657
1991	24 175	13 455	–	37 630	17 781	–	–	17 781	41 956	13 455	–	55 411
1992	16 855	11 669	–	28 524	10 915	–	–	10 915	27 770	11 669	–	39 439

Council on Fishery Investigations, 1932, 1935; Wise, 1963), *Lernaeocera* infestation patterns (Sherman and Wise, 1961), spawning time data (Colton *et al.*, 1979), otolith features (Penttila, 1988), and growth rate analyses (Penttila and Gifford, 1976; Serchuk and Wood, 1979). However, significant intermixing of fish occurs between cod on Georges Bank and those in the Southern New England–Middle Atlantic region; a seasonal southwesterly movement of adult cod from the South Channel area of Georges Bank occurs in early winter (Dec–Jan) followed by a northeasterly return in late spring–early summer (May–June) (Fig. 3). In addition, there are well-defined seasonal movements of juvenile cod between the Georges Bank and Southern New England areas (Wigley and Gabriel, 1991; Wigley and Serchuk, 1992).

Management of cod in NAFO Subarea 5 was initiated in 1973 when the International Commission for the Northwest Atlantic Fisheries (ICNAF) established separate catch quotas (TACs) for the Georges Bank (Division 5Z) and Gulf of Maine (Division 5Y) cod stocks (ICNAF, 1973). Subsequently, both stocks were managed by TACs during 1974–1976 (ICNAF, 1976). With the implementation of extended fisheries jurisdiction in 1977, the USA and Canada independently assumed responsibility for the management of the fisheries resources within their respective and, at the time, overlapping 200-mile fishery zones. The Georges Bank cod stock, however, was clearly a transboundary resource.

In the management program enacted by the USA in 1977, the two cod management units established by ICNAF were adopted but the "Georges Bank" stock unit was enlarged (Division 5Z and Subarea 6) to include the cod occurring in the Southern New England–Middle Atlantic region. This recognized that extensive mixing of fish occurred between the two areas, and that strong demographic affinities existed between the cod in these regions (Serchuk and Wood, 1979). Canada also initially considered the "Georges Bank" stock as encompassing the cod in Division 5Z and Subarea 6 (Bowen, 1987; Hunt, 1988). However, in 1989, Canada re-examined the definitions of management units for groundfish species on Georges Bank [in light of the separate USA and Canadian management systems and the delimitation in 1984 of a maritime boundary between the USA and Canada in the Gulf of Maine/Georges Bank area], and concluded that the "Georges Bank" cod stock could be partitioned into two management units: (1) eastern Georges Bank cod [unit areas 5Zj and 5Zm; Fig. 1]; and (2) central and western Georges Bank cod [the remainder of Division 5Z and Subarea 6] (Hunt, 1989). Since 1989, Canada has therefore treated the cod on Georges Bank as comprised of two separate units (CAFSAC, 1989; Halliday and Pinhorn, 1990).

Although further work on the structure of the cod stocks in Subarea 5 is certainly warranted, for the purposes of this paper the stock units recognized by the USA are employed, viz. a Georges Bank stock (Division 5Z and Subarea 6) and a Gulf of Maine stock (Division 5Y). These stock categorizations also correspond well with the traditional areas used in sampling and reporting catches, thereby facilitating the use of the long time-series of existing data.

Physical environment

The Gulf of Maine–Georges Bank region is bordered on the east, north, and west by the coasts of Nova Scotia, New Brunswick, and the New England States (Fig. 4). The Gulf is open at the surface to the North Atlantic Ocean to the south. Below about 50 m depth, however, Georges Bank forms a southern boundary for the Gulf, making it semi-enclosed. The Gulf is connected to the deep North Atlantic Ocean by only two major channels – the Northeast Channel between Georges Bank and the Scotian Shelf, and the Great South Channel between Georges Bank and the Nantucket Shoals to the west. The interior of the Gulf is characterized by several deep basins (>200 m) separated by a number of shallow ridges, ledges, and banks. The largest and deepest of these basins are (1) Georges Basin near the mouth of the Northeast Channel; (2) Jordan Basin to the northeast; and (3) Wilkinson Basin in the southwestern Gulf. The Jordan and Wilkinson Basins are separated by an irregular, shallower topography which extends from the coast toward the central Gulf.

Georges Bank is a large (300 × 150 km) shallow bank that appears to be an eastward extension of the U.S. continental shelf. The Bank has a steep slope on its northern edge and a broad, flat, gently sloping southern flank. To the west, the Bank is separated from the rest of the continental shelf by the Great South Channel. The central region of the Bank is quite shallow, with scattered areas less than 20 m deep, and the bottom is characterized by large-amplitude sand waves. The rest of the Bank is sandy and flat, with regions of gravel on the northern and eastern parts of the Bank (Valentine and Lough, 1991).

To the west of Georges Bank, the continental shelf south of New England is broad and flat. The bottom is generally sandy, except for an area of silt located on the outer shelf southwest of Martha's Vineyard (Garrison and McMaster, 1966). The Nantucket Shoals region, southeast of Nantucket, has sand waves similar to those on central Georges Bank. Patches of gravel are found on the western flank of the Great South Channel.

The Gulf of Maine and Georges Bank are part of an extended coastal current system which flows southward from Labrador, through the Gulf region to the Middle

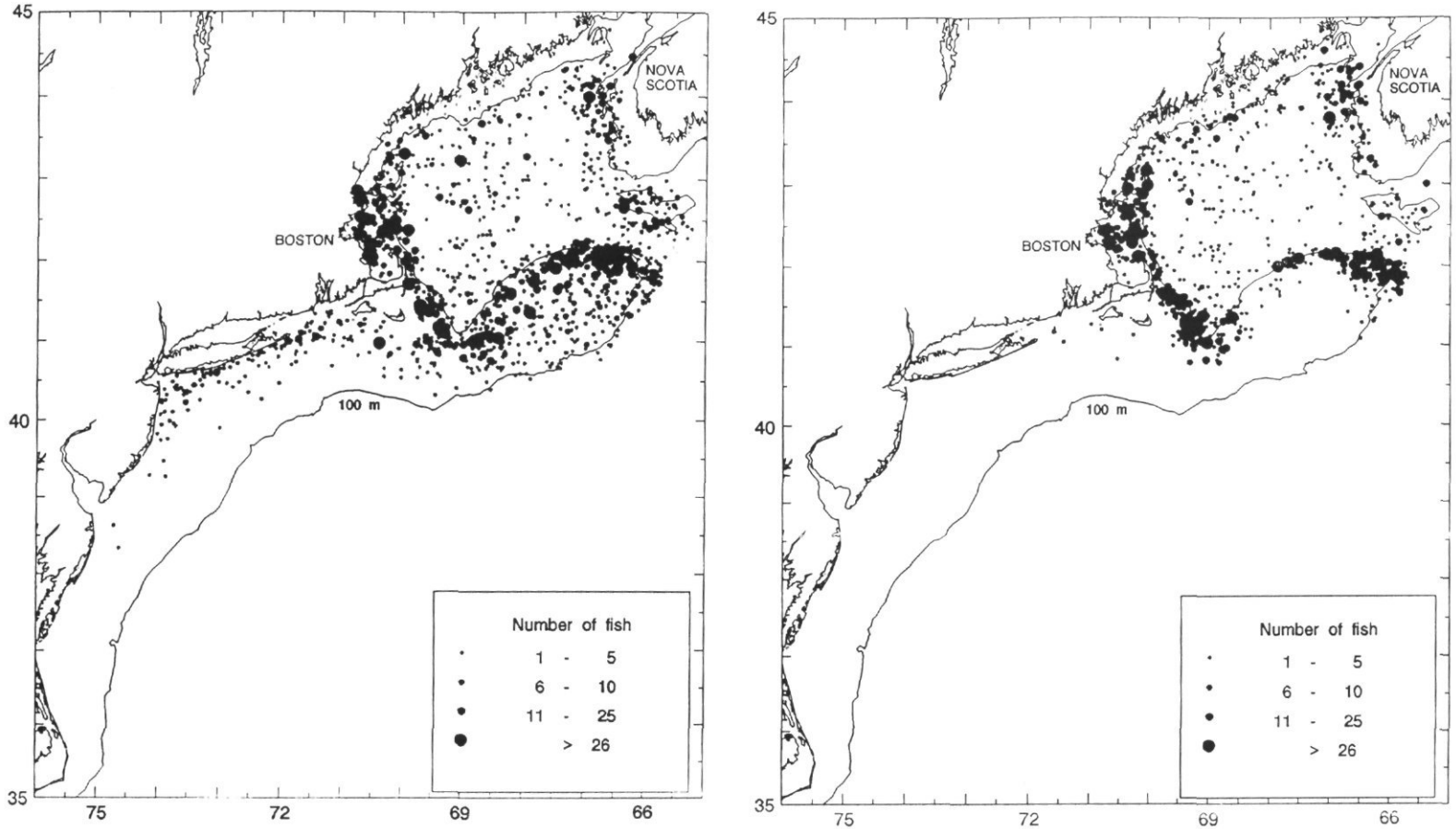


Figure 3. Geographic distribution (number/tow) of adult (≥37 cm) Atlantic cod, *Gadus morhua*, collected during NEFSC spring (left) and autumn (right) research vessel bottom-trawl surveys (1982–1992) in the Gulf of Maine, Georges Bank, and Southern New England–Middle Atlantic regions. Each dot represents a survey tow in which cod were caught.

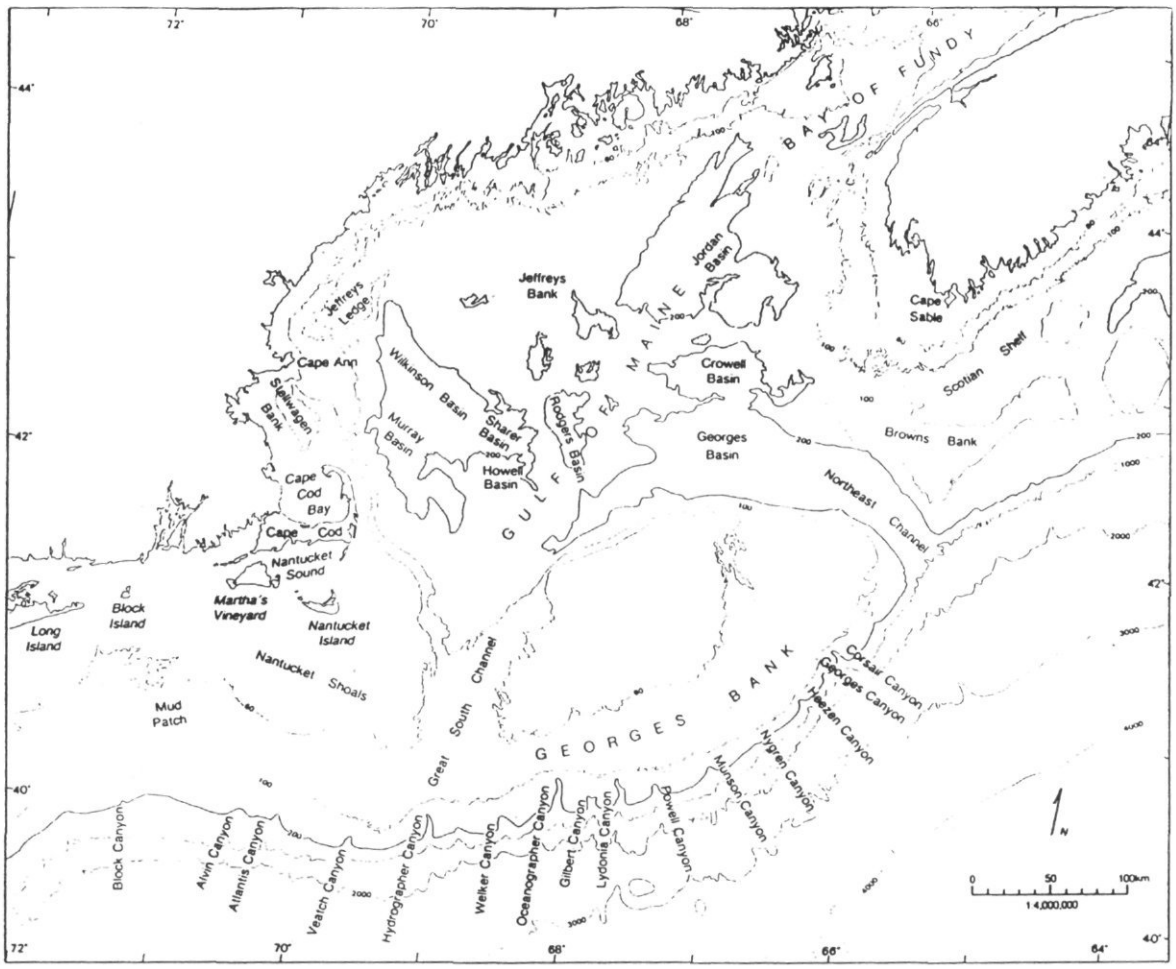


Figure 4. Topographic map showing the location of the Gulf of Maine and Georges Bank in relation to the New England shelf and the Scotian shelf. The topography inside the 60-m isobath is simplified (from Butman and Beardsley, 1987).

Atlantic Bight (Chapman and Beardsley, 1989; Fig. 5). Locally, the waters are derived from two primary water masses: (1) cold, low salinity water which flows southward from the Scotian Shelf and enters the Gulf of Maine system around Cape Sable (Smith, 1983), and (2) warm, high salinity Slope Water which enters the Gulf at depth through the Northeast Channel (Ramp *et al.*, 1985). Within the Gulf, these waters are mixed and subsequently modified by local atmospheric heating/cooling, precipitation, and coastal runoff. Because of the cyclonic circulation pattern in the region, water is carried around the Gulf to the southwest. From here, surface waters penetrate onto the northwestern side of Georges Bank (Hopkins and Garfield, 1981), entering a strong, eastward flow along the northern edge of the Bank (Fig. 6). The flow then turns south and then southwestward along the wide, southern flank of the Bank. At the Great South Channel, a portion of the flow turns north to form a recirculating gyre around the Bank, while the majority of the flow continues westward south of Nantucket Shoals and into the Middle Atlantic Bight. Along the edge of the shelf from Georges Bank to the Middle Atlantic Bight, a sharp hydrographic front exists between the shelf waters and the warmer, more saline, offshore Slope Water.

The water motions in the region are dominated by strong tidal currents, particularly in the shallow central area of Georges Bank. The mean clockwise circulation around the Bank results, in large part, from rectification of the tidal currents by the bathymetry (Loder, 1980). Wind events also generate strong, transient currents which can result in the exchange of water between regions. Warm core Gulf Stream rings often impinge against the shelf break and may entrain large amounts of

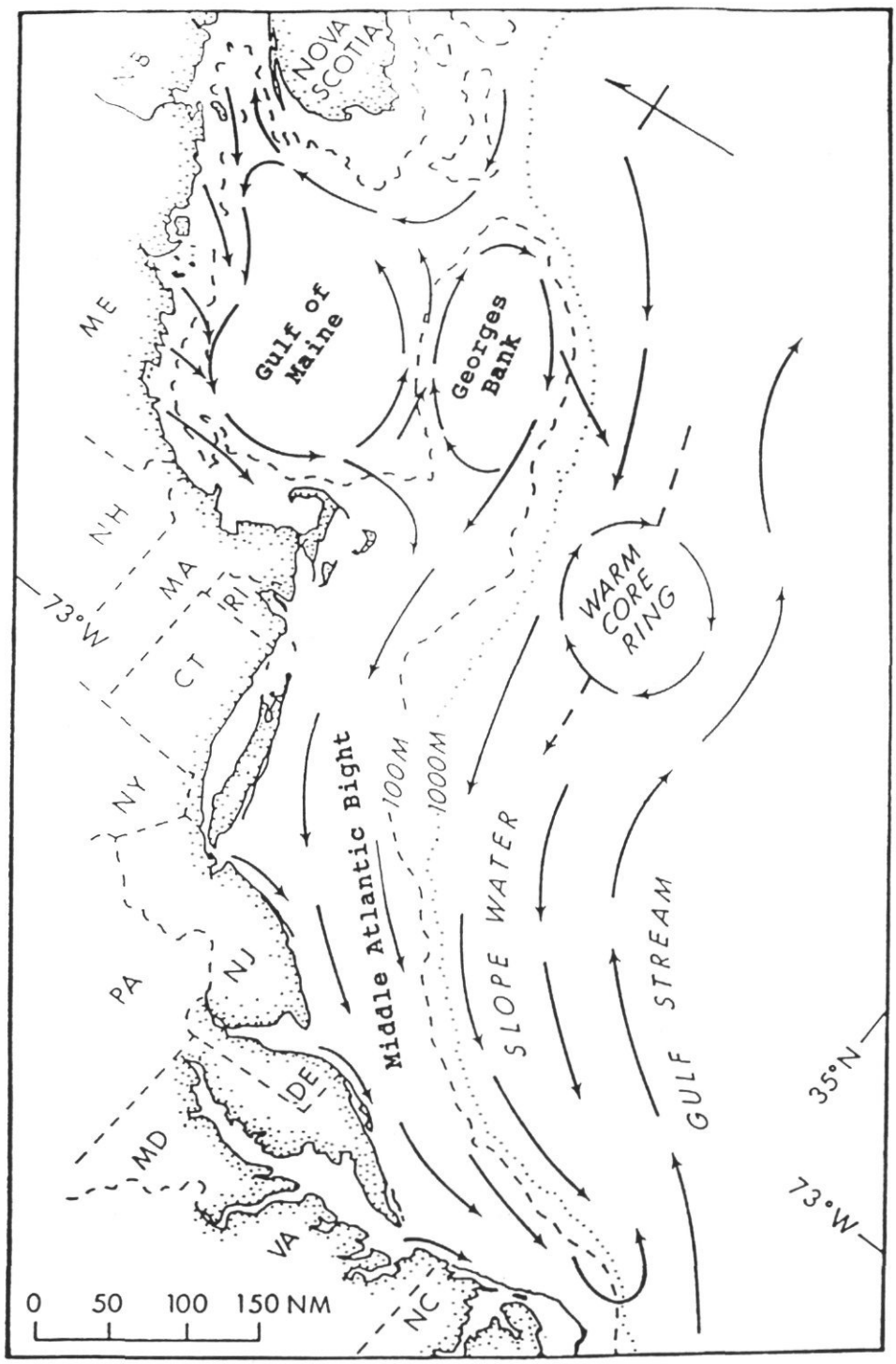


Figure 5. Generalized surface-layer water circulation patterns in the Gulf of Maine, Georges Bank, and Middle Atlantic regions (modified from Ingham *et al.*, 1982).

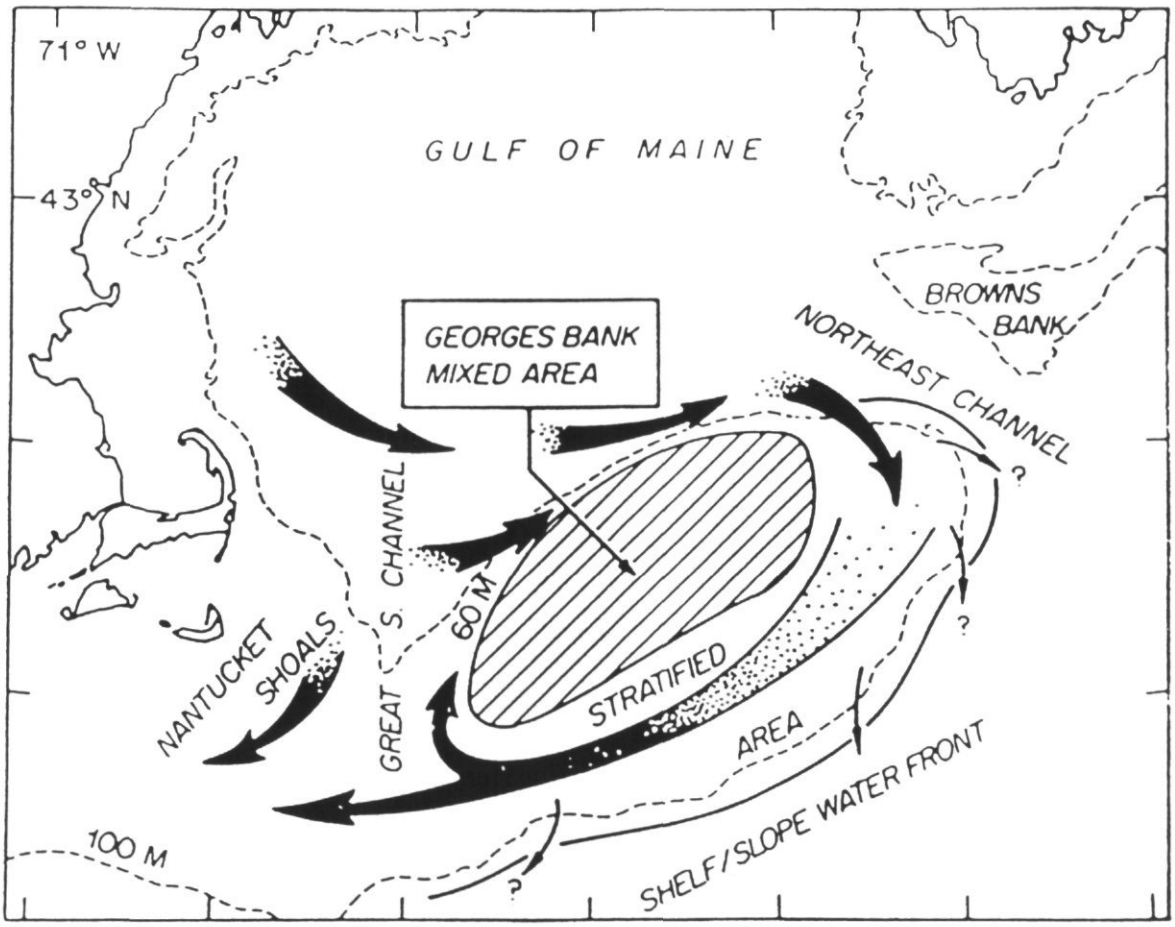


Figure 6. Schematic representation of the well-mixed and stratified water masses on Georges Bank and mean circulation flows (arrows) during spring and summer (from Lough, 1984).

water from Georges Bank and the Middle Atlantic Bight into the Slope region.

Water properties throughout the region undergo a characteristic seasonal cycle. In winter, atmospheric cooling and strong winds mix the water column from surface to a depth of about 100 m in the Gulf of Maine (Hopkins and Garfield, 1981), and to the bottom on Georges Bank and much of the Middle Atlantic Bight. During spring, surface heating and the seasonal decrease in wind forcing cause the surface waters to warm – inducing the development of vertical stratification with respect to temperature and density. In the central portion of the Bank and on Nantucket Shoals (<60 m), tidal currents are strong enough to keep the water column well mixed year round. Stratification continues to develop through the summer and into the fall, when seasonal cooling and winds again cause a return to the vertically well-mixed winter conditions. The annual minimum surface water temperature is about 4°C and occurs in March. The annual maximum surface temperature occurs during August–September at about 14–16°C on Georges Bank, and at about 18–20°C in the western Gulf of Maine and the northern Middle Atlantic Bight (Mountain and Holzwarth, 1989). Bottom temperatures in the Gulf of Maine show little seasonal pattern, but are generally higher in the eastern Gulf (6–9°C) than in the western Gulf (5–7°C), because of the influence of the Slope Water inflow through the Northeast Channel (Mountain and Jessen, 1987). On Georges Bank, maximum bottom temperatures occur in August–September at about 12–16°C.

The Gulf of Maine–Georges Bank regions experience significant inter-annual variability in water temperature (Fig. 7). Measurements from the USA (Northeast Fisheries Science Center) trawl survey program indicate a change of about 2°C in the Bank-wide spring average

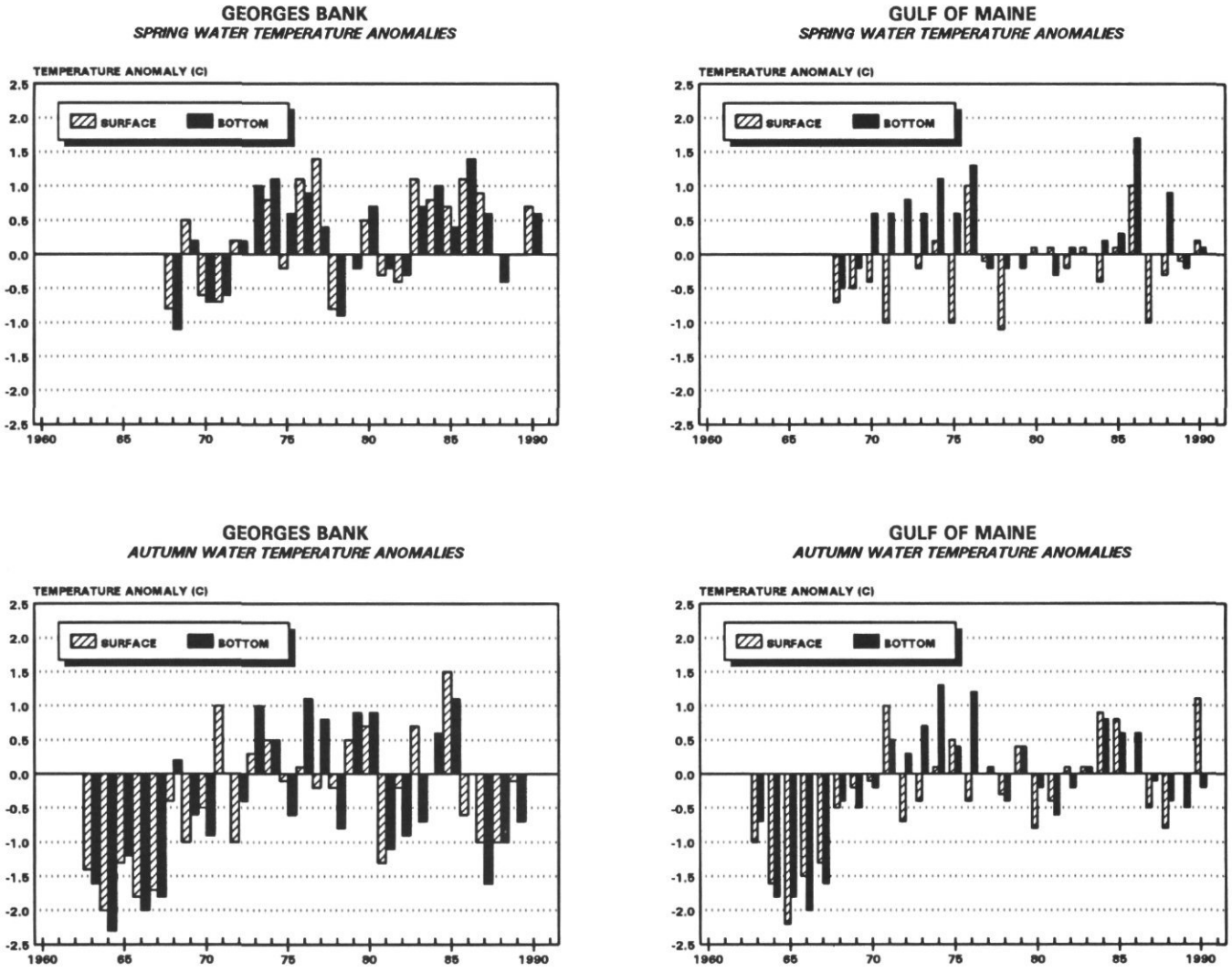


Figure 7. Average spring and autumn water temperature anomalies (surface and bottom) on Georges Bank and in the Gulf of Maine (1963–1990). Data derived from NEFSC spring and autumn research vessel bottom-trawl surveys.

water temperature between the cool 1960s and the warm mid-1970s. The years around 1980 were intermediate between the two earlier periods, while the last half of the 1980s was comparable to the mid-1970s (Holzwarth and Mountain, 1992).

Commercial fishery

Landings trends

During the past 30 years, commercial landings from both the Georges Bank and Gulf of Maine stocks have increased and attained record-high levels (Table 2). In the Georges Bank stock, landings initially peaked in 1966 at 53 000 t due to marked increases in exploitation by distant-water fishing fleets (primarily from the USSR, Spain, and Poland). Landings by these fleets, which had begun to fish cod on Georges Bank in 1961, increased dramatically from 55 t in 1961 to 25 500 t in 1966 (Fig. 8). As well, Canadian landings – which were just 200 t in 1961 – increased to 15 600 t in 1966. In contrast, USA landings of Georges Bank cod remained relatively stable, varying between 10 800 and 16 800 t during 1960–1969 and averaging 13 000 t per year. After 1968, distant-water and Canadian landings declined and, by 1976, total landings of Georges Bank cod had fallen to 20 000 t, the lowest since 1961. During 1974–1976, the Georges Bank cod fishery was regulated by ICNAF under a 35 000 t TAC, but annual catches during these years never exceeded 27 000 t.

Following the implementation in 1977 of extended fisheries jurisdiction by both Canada and the USA, Georges Bank cod landings again increased. Although USA catches peaked at 40 000 t in 1980, total catches (and Canadian landings) peaked in 1982 at 57 000 t (17 800 t, Canadian). Thereafter, catches declined, reaching a post-1976 low of 25 900 t in 1986. Total landings increased during 1987–1990 (attaining 42 500 t in 1990), but have since diminished to 28 500 t in 1992.

In the Gulf of Maine stock, virtually all landings have been by the USA fleet (Tables 1 and 2; Fig. 8). Landings peaked in 1945 at 14 500 t but then declined sharply, reaching a record-low of 2600 t in 1957. From 1960 until the early 1980s, Gulf of Maine landings steadily increased, doubling between 1964 and 1968 (3250 to 6400 t) and doubling again between 1968 and 1980 (6400 to 13 500 t). ICNAF TACs were implemented during 1973–1976 (10 000 t TAC in 1973–1975; 8000 t TAC in 1976) but only the 1976 TAC was constraining – and was overrun.

During 1976–1985, Gulf of Maine cod landings exceeded 10 000 t in every year and averaged 12 200 t per annum. Landings declined to less than 8000 t in 1987–1988, but subsequently increased – reaching a record-high level of 17 800 t in 1991. In 1992, however, total cod landings plummeted to 11 000 t.

Although USA and Canadian management programs for cod have been in place since 1977, catches of cod from both stocks have not been effectively controlled (Anthony, 1990; Serchuk and Wigley, 1992). Catch quotas were eliminated from the USA management program in 1982 in favor of indirect controls on fishing effort, such as minimum mesh sizes, minimum fish sizes, and closed areas. Quota management has been a part of the recommended Canadian approach to regulating the Georges Bank fishery since 1978, but TACs on Canadian catches were not implemented until 1985, after the Gulf of Maine/Georges Bank maritime boundary dispute between the USA and Canada had been resolved by the International Court of Justice. Independent and/or unilateral management actions by the two countries, however, have not proved successful in constraining exploitation. Management objectives differ between the two nations and each country has pursued management strategies without regard for one another. As of now, a cooperative and coordinated joint USA/Canadian approach to the harvesting and conservation of transboundary fishery resources (e.g., Georges Bank cod) has yet to be established.

Stock abundance and biomass indices

Trends in commercial catch per unit effort (c.p.u.e.)

USA commercial c.p.u.e. indices for the Georges Bank and Gulf of Maine stocks are available from 1965 onwards. These indices are based on otter trawl trips and were derived based on all trips in which cod were landed, and for "directed" trips in which cod constituted 50% or more of the total trip catch by weight. During 1965–1992, otter trawl landings accounted for 86% of USA Georges Bank cod catches and for 68% of USA Gulf of Maine cod catches.

For Georges Bank cod, both total and directed c.p.u.e. indices have, since 1970, generally exhibited trends (Fig. 8). C.p.u.e. values increased during the early and mid-1970s, peaked in the late 1970s and early 1980s, and then declined precipitously between 1983 and 1987. Catch rates increased slightly in 1990, but have since fallen; in 1992, both the total and directed c.p.u.e. indices were at record-low levels. Canadian c.p.u.e. indices are not considered to be reliable indicators of stock abundance (Hunt, 1990), and are not presented here as they have not been used in any of the recent Canadian assessments of the Georges Bank cod stock (Hunt and Buzeta, 1992).

For the Gulf of Maine stock, c.p.u.e. values increased

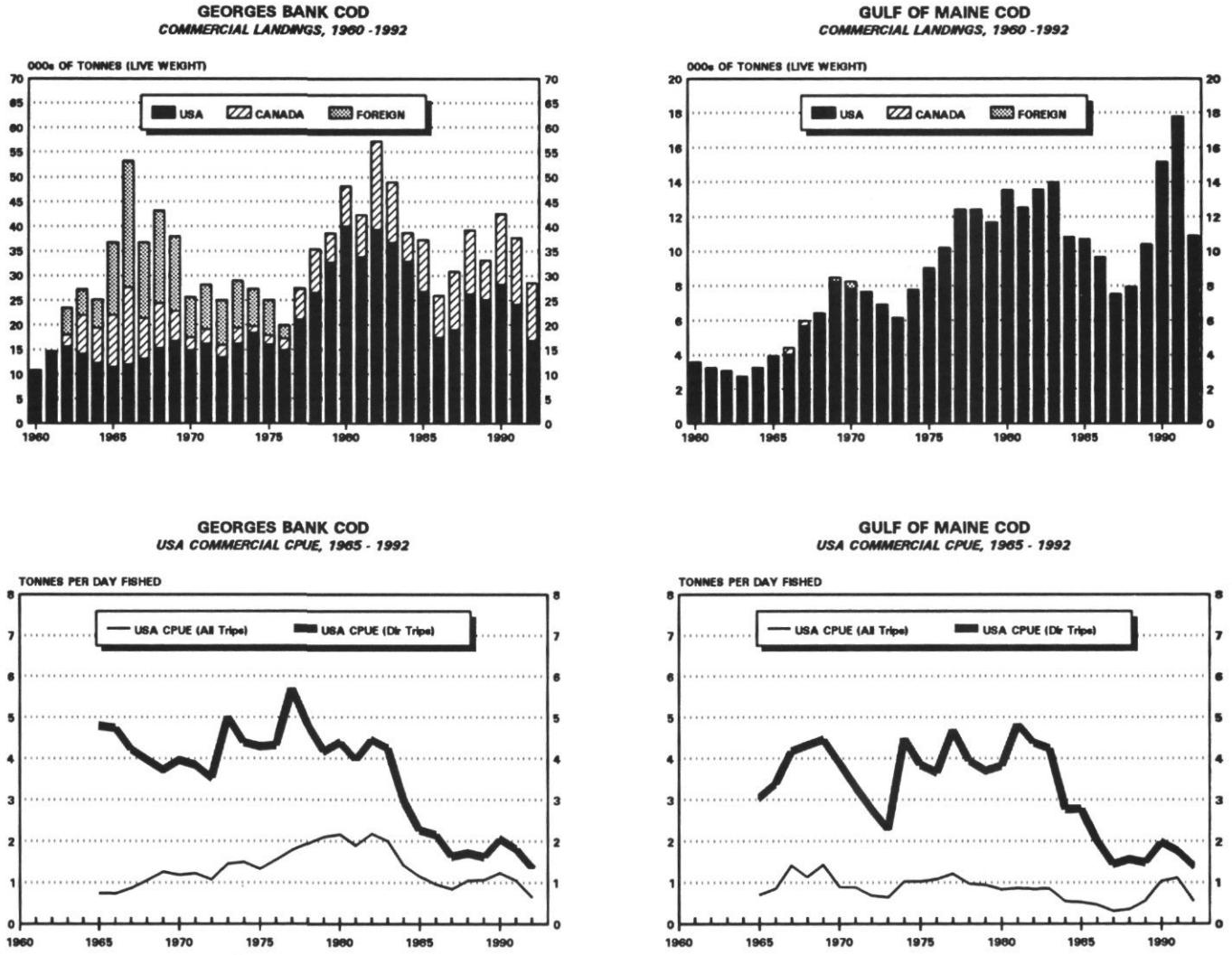


Figure 8. Total commercial landings (top) and USA commercial catch per day fished (bottom) of cod from the Georges Bank (Division 5Z and Subarea 6) and Gulf of Maine (Division 5Y) stocks.

during the late 1960s, declined during the early 1970s, sharply increased in 1974, and then stabilized at a relatively high level during 1975–1983 (Fig. 8). Subsequently, c.p.u.e. indices declined, reaching record-low levels in 1987. Between 1988 and 1991, the c.p.u.e. indices again increased, but in 1992 both the total and directed indices declined to near-record lows.

Taken at face value, the time series of c.p.u.e. values for both stocks suggest that exploitable biomass peaked during the late 1970s and early 1980s, but has since declined – in each stock – to historic low levels. On a relative basis, the present stock levels are probably even lower than indicated by the c.p.u.e. data because the c.p.u.e. indices have not been adjusted for increases in fleet efficiency in recent years.

USA otter trawl effort increased markedly after 1976 (Fig. 9). In the Georges Bank fishery, USA trawling effort for cod (nominal days fished) rose by 71% between 1977 and 1988 (11 700 to 19 800 days fished), while in the Gulf of Maine fishery trawling effort nearly doubled (7400 to 13 000 days fished). During the past few years, effort in both fisheries has been at or near historically high levels.

Trends in research vessel survey indices

Stratified-random bottom trawl surveys of the Georges Bank and Gulf of Maine regions have been conducted by the Northeast Fisheries Science Center (NEFSC) each autumn since 1963 and each spring since 1968 using the research vessels "Albatross IV" and "Delaware II" (Azarovitz, 1981). The data from these surveys have been used to derive standardized indices of relative abundance and biomass of cod (stratified mean catch per tow in number and weight, respectively) for both the Georges Bank and Gulf of Maine stocks.

For Georges Bank cod, the spring and autumn NEFSC survey indices show similar trends (Fig. 10). Survey biomass indices were relatively low and stable during 1963–1971, fluctuated at a generally higher level between 1972 and 1981, but have since declined to record-low values. Elevated survey biomass indices in 1969–1970, 1972–1973, 1978, 1981, and 1984–1985 reflect above-average recruitment of the 1966, 1971, 1975, 1980, and 1983 year classes.

For the Gulf of Maine stock, the time series of survey indices suggests that stock biomass was high in (1) the early 1960s; (2) during the late 1960s–early 1970s; and (3) and in the late 1970s–early 1980s. After 1985, however, both the spring and autumn survey biomass indices steadily declined, reaching record-low levels during 1989–1991 (Fig. 10). In 1992 [as in 1973], the spring and autumn indices were discrepant; the spring index markedly increased (due to a large contribution of fish from the strong 1987 year class) while the autumn index declined. Recruitment indices for the Gulf of Maine

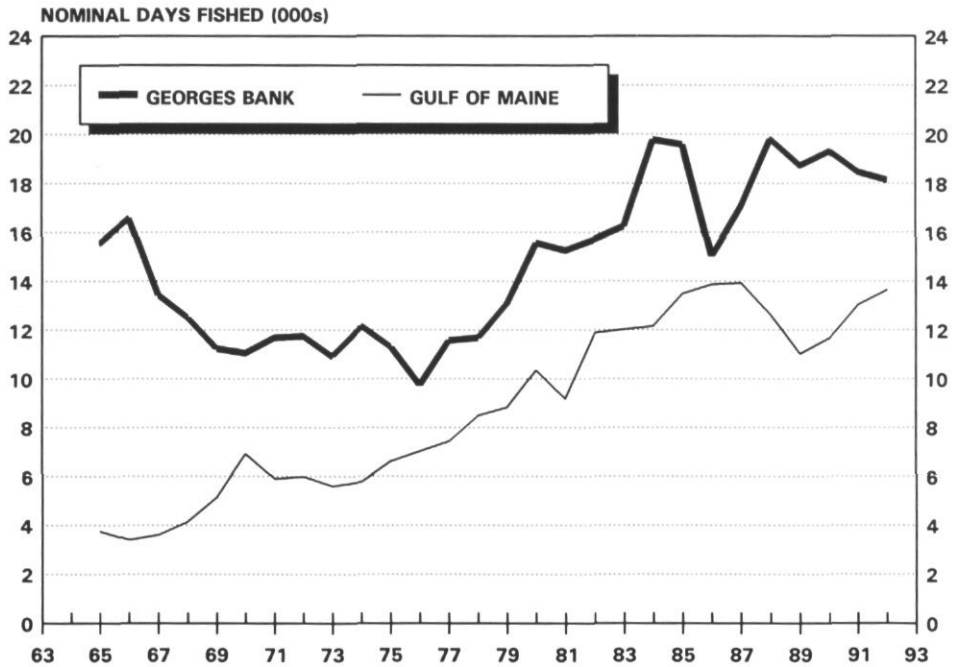


Figure 9. USA commercial otter trawl effort (nominal days fished) for trips landing cod from the Georges Bank and Gulf of Maine stocks (1965–1992).

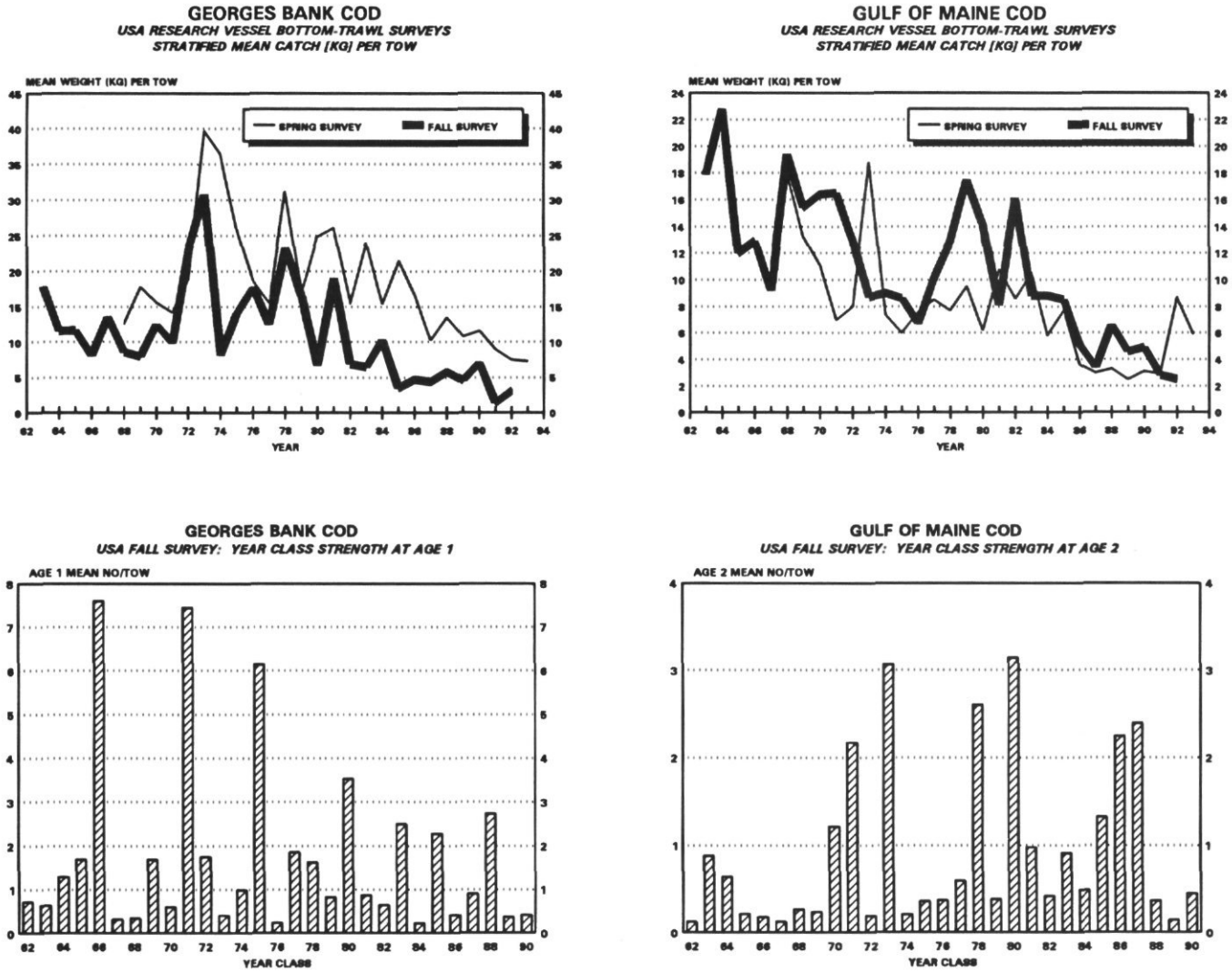


Figure 10. Standardized stratified mean catch per tow indices (top) and survey recruitment indices (bottom) for the Georges Bank and Gulf of Maine cod stocks from NEFSC spring and autumn bottom-trawl surveys (1963–1992).

stock (survey number-per-tow indices at age 2) indicate that the 1971, 1973, 1978, 1980, 1986, and 1987 year classes were all above average.

Trends in stock size, recruitment, and fishing mortality

Estimates of stock size, recruitment, and fishing mortality for the Georges Bank and Gulf of Maine cod stocks are available from virtual population analyses (VPA). For Georges Bank cod, the VPA covers the 1978–1992 period (Serchuk *et al.*, 1993); for the Gulf of Maine stock, the VPA extends from 1982–1992 (Mayo *et al.*, 1993).

During the past 10–15 years, marked reductions in the abundance of both cod stocks have occurred coincident with increases in fishing mortality rates. In the Georges Bank stock, spawning-stock biomass (SSB) declined by over 40% between 1980 and 1985 (93 000 to 55 000 t) while fishing mortality rates increased by 50% (Fig. 11). SSB increased in 1987 to 66 000 t and stabilized at about 70 000 t during 1988–1990 due to strong recruitment from the 1983 and 1985 cohorts. Fishing mortality, however, continued to rise, and increased from F = 0.63 in 1989 to a record-high F = 1.07 in 1991 (a 70% increase). SSB subsequently declined sharply in 1991 and fell to a record-low of 41 000 t in 1992. Further declines in SSB are expected in 1993 and 1994 when the 1989–1991 year classes, all below average in abundance (i.e., below 21 million fish at age 1), recruit to the spawning stock.

In the Gulf of Maine stock, fishing mortality increased from F = 0.62 in 1982 to above F = 1.0 during 1985–1987 (Fig. 11). In this same time period (1982–1987), SSB declined from 25 700 t to 13 900 t. Because of above-average recruitment of the 1986 year class and the exceptionally strong 1987 year class, SSB increased sharply in 1989 and reached a record-high level of 27 500 t in 1990. However, poor recruitment of the 1988–1990 year classes, coupled with fishing mortality rates above F = 1.0 in both 1990 and 1991, resulted in SSB declining in 1992 to a record-low of 13 600 t. SSB of Gulf of Maine cod is expected to decline below 12 000 t in 1993 as the 1987 cohort (which accounted for over 60% of the catch and SSB in 1992) is further fished down.

The striking declines in biomass in both the Georges Bank and Gulf of Maine cod stocks have occurred during a period when landings, fishing effort, and fishing mortality have increased to record-high levels. For both stocks, recent fishing mortality rates have far exceeded the levels generally associated with stock replacement (F_{med} or $F_{20\%}$) or growth overfishing (F_{max}). On an annual basis, the fisheries on the two stocks currently remove between 40 and 60% of the exploitable biomass. Factors other than fishing may also have affected the stocks but these influences are not easily discernible given the magnitude of the fishery-induced perturbations.

Environmental and biotic processes affecting cod life history

Despite the long history of exploitation of cod in the Georges Bank–Gulf of Maine region, it has only been rather recently that sufficient information has been obtained to begin sorting out the environmental factors from the fishery events affecting cod abundance. This information has come largely from a time series of research vessel surveys and accompanying biological studies, which indicate that environmental effects are most significant during the first year of life. Attempts to correlate recruitment and egg/larval abundance of Georges Bank cod have failed so far (Smith *et al.*, 1981; Fogarty *et al.*, 1987), but significant correlations have been observed between recruitment and trawl survey catches of 0-group and 1-year cod on Georges Bank (Serchuk *et al.*, 1993). This supports the inference that factors controlling cod year-class success operate chiefly during the first year of life.

Approximate mortality estimates in late-larval and postlarval stages of cod (≥99.9%) are typically as high or higher than mortality in the egg and early larval stages (Sissenwine *et al.*, 1984); thus a small change in natural mortality at these late larval or juvenile stages could make the difference between a strong or weak year class. Given the high mortality rates in both the early and late 0-group stages, Sissenwine (1984) concluded that recruitment is likely to be a function of highly variable processes occurring throughout the first year of life.

While density-dependent mortality in late-larval and juvenile stages is important in regulating year-class size, a general view is emerging that the major variability in recruitment ("bumper" vs. "bust" year classes) is largely due to density-independent mortality during the egg and early larval stages. Based on a comprehensive review of egg and larval predation mortality, Bailey and Houde (1989) concluded that year-class strength is established very early (i.e., at the egg and larval stages), but that predation on later stages can have moderate to large effects on recruitment (i.e., altering year-class strength by an order of magnitude or less). Myers and Cadigan (1993a) examined juvenile mortality data from six cod stocks and found strong evidence of density-dependent mortality within cohorts, as well as a negative autocorrelation between adjoining cohorts. The Georges Bank and Gulf of Maine stocks were included in these analyses and generally fit the patterns seen in the other stocks, except that density-dependent mortality was not evident for Georges Bank cod, possibly due to the very low abundance level of this stock. Little interannual vari-

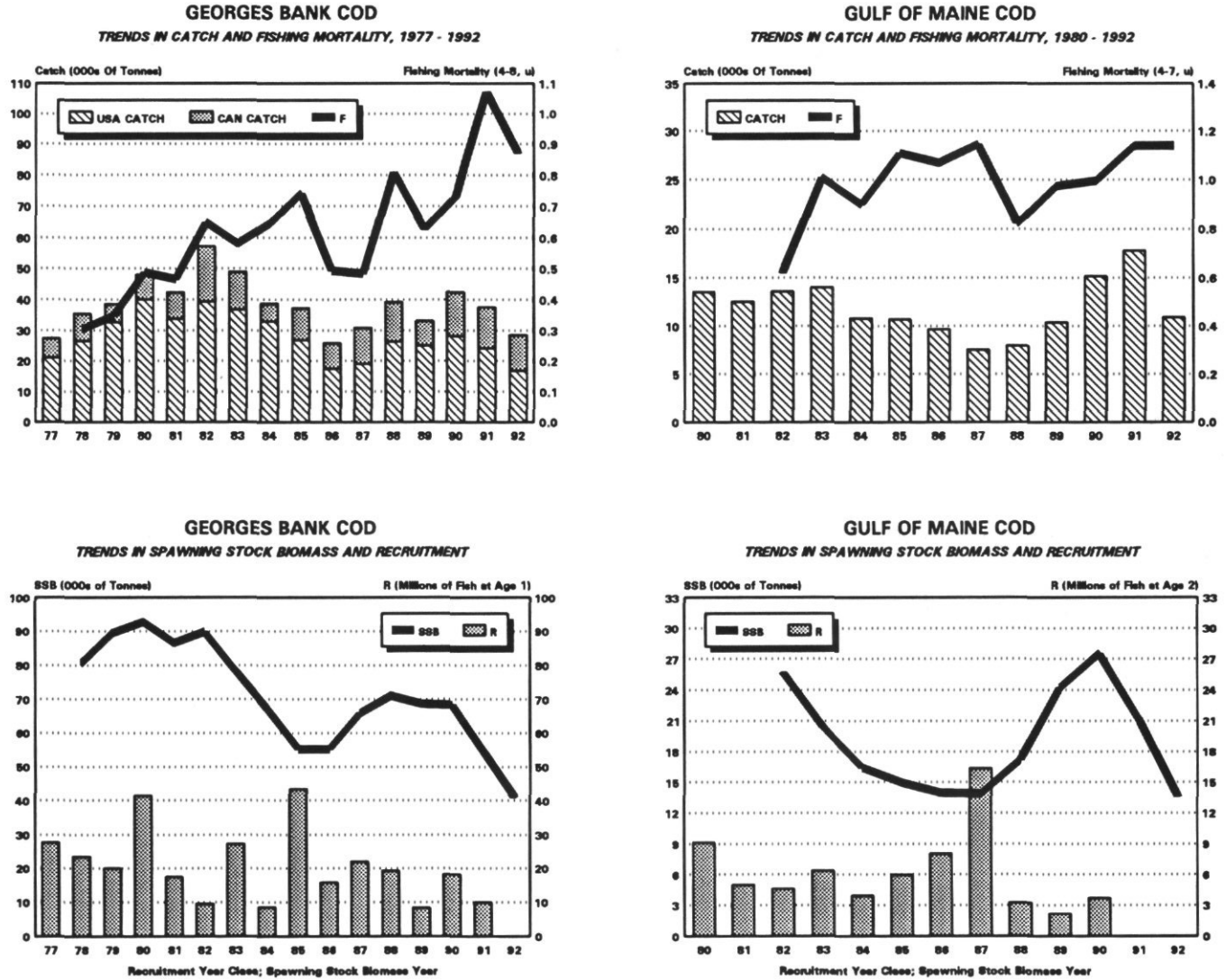


Figure 11. Trends in commercial catches and fishing mortality (top) and spawning-stock biomass and recruitment (bottom) for the Georges Bank and Gulf of Maine cod stocks derived from VPA analyses. Data derived from 1993 assessments (from Serchuk *et al.*, 1993; Mayo *et al.*, 1993).

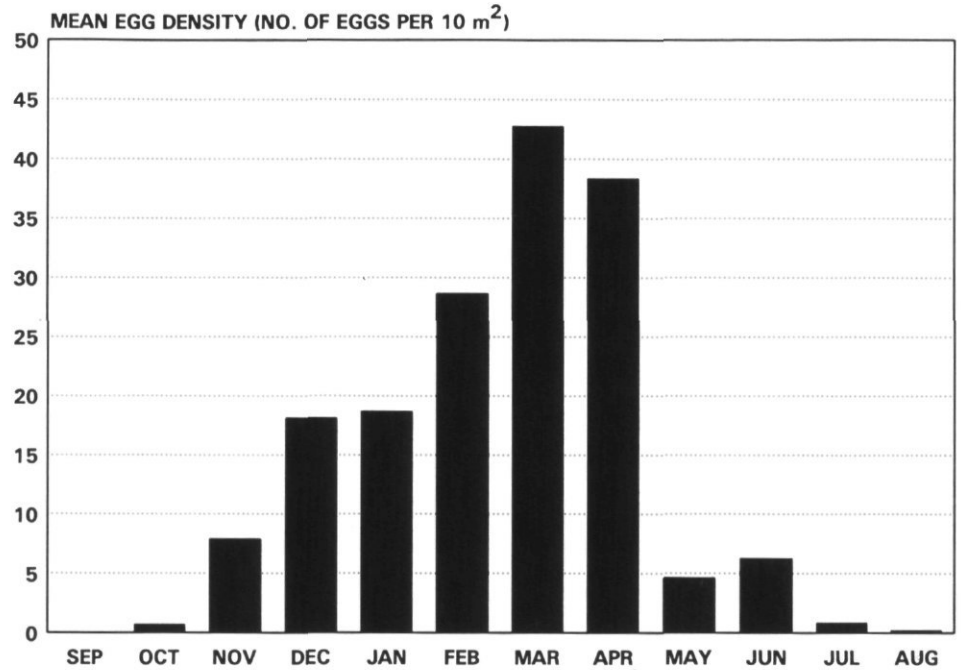


Figure 12. Average monthly egg densities of Atlantic cod off the northeastern coast of the United States (1978–1987) (from Berrien and Sibunka, 1993).

ability was found in the density-independent component of juvenile cod mortality (Myers and Cadigan, 1993b). Myers and Cadigan concluded that the major variability in year-class strength of cod (and in many other marine demersal species) was determined during the larval stage, but that this variability was subsequently attenuated by density-dependent mortality during the juvenile stage.

A number of mechanisms associated with physical factors could influence survival of eggs and early-stage larvae, including advection, food supply, temperature, and predation. Postlarval stages would be less affected by advection, but their growth and predation susceptibility would certainly be affected by food supply and temperature. For Georges Bank cod, energy balance calculations and food habits studies (Fogarty *et al.*, 1987) indicate that predation is the principal natural mortality affecting postlarval survival. Hence, the modes by which physical factors influence the survival of postlarvae are likely to be indirect – via effects on cod growth (food supply and temperature) and predation vulnerability (available juvenile habitat, and match/mismatch in the spatial/temporal distributions of juvenile cod and their predators).

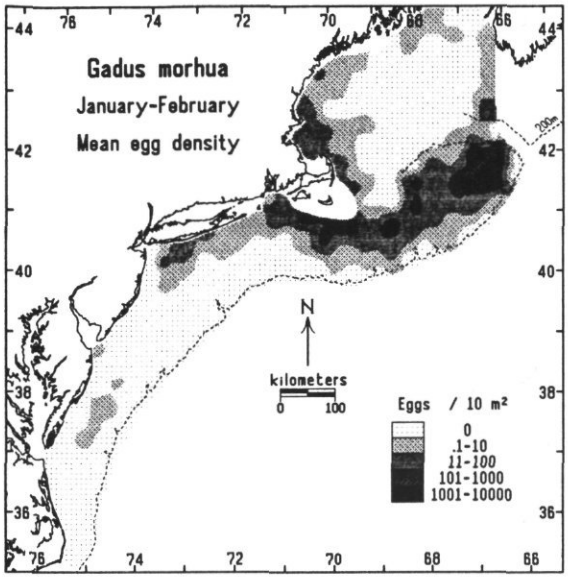
The basic features of the life history of cod in relation to both environmental and biotic processes are outlined below, as background for the review – presented in the subsequent section – on the environmental influences affecting cod. Current and future research studies aimed at differentiating environmental from fishery-related factors affecting recruitment and abundance of cod in the Georges Bank – Gulf of Maine region are discussed in the concluding section of the paper.

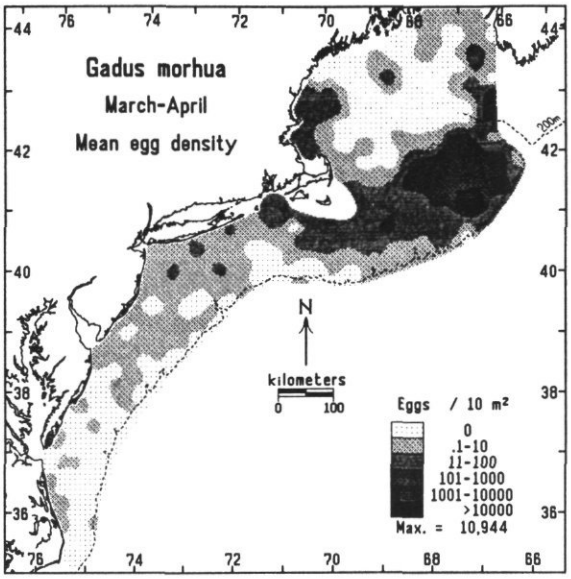
Life history features

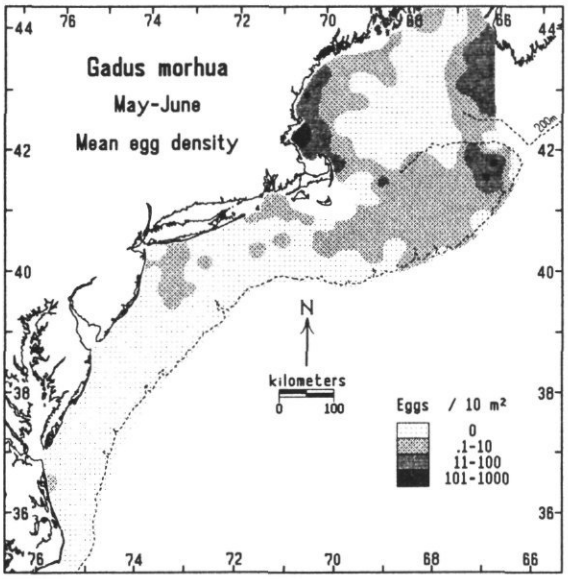
Spawning time and location

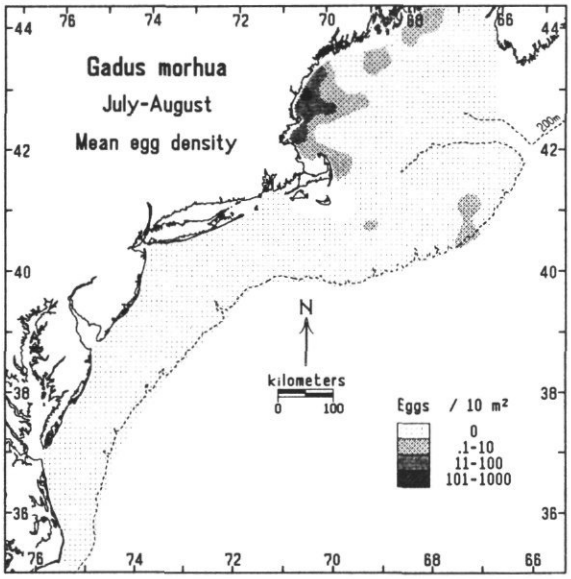
Spawning of cod in the Gulf of Maine–Georges Bank region exhibits a pronounced seasonal cycle. Monthly composite distributions of egg densities from an 11-year series (1977–1987) of ichthyoplankton surveys (i.e., the US MARMAP study) indicate that cod spawning occurs primarily between November and June, with peak spawning in March and April (Berrien and Sibunka, 1993; Fig. 12). Based on geographic distributions of cod eggs and larvae (Figs. 13 and 14), principal spawning areas occur on Georges Bank, in Southern New Eng-

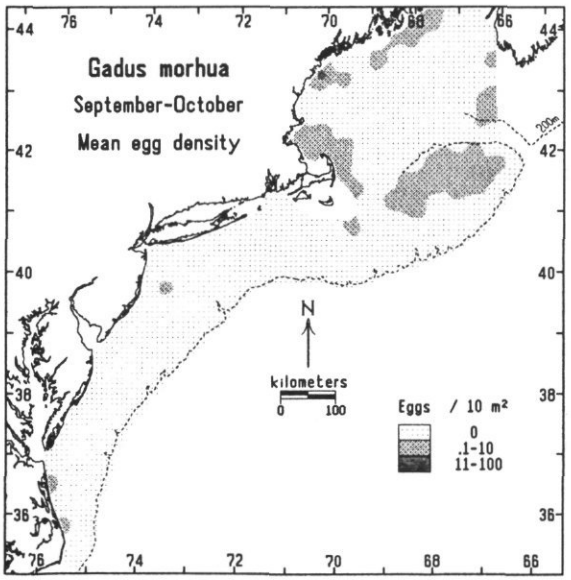
Figure 13. Composite bimonthly geographic distributions of Atlantic cod eggs off the northeastern coast of the United States from MARMAP surveys (1977–1987).

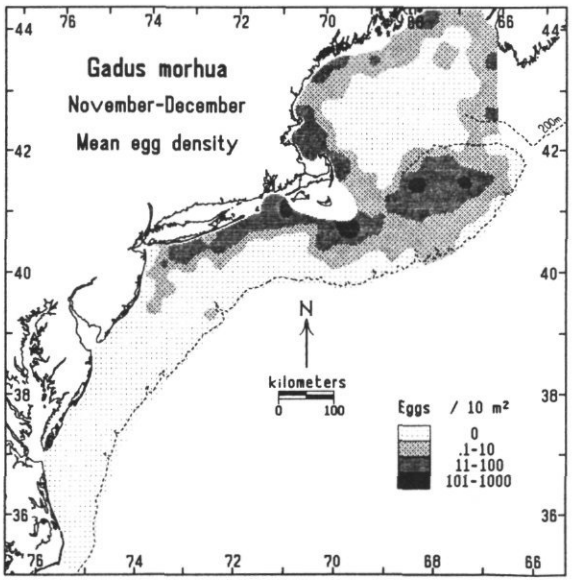

Gadus morhua
January-February
Mean egg density
N
kilometers
0 100
Eggs / 10 m²
0
.1-10
11-100
101-1000
1001-10000

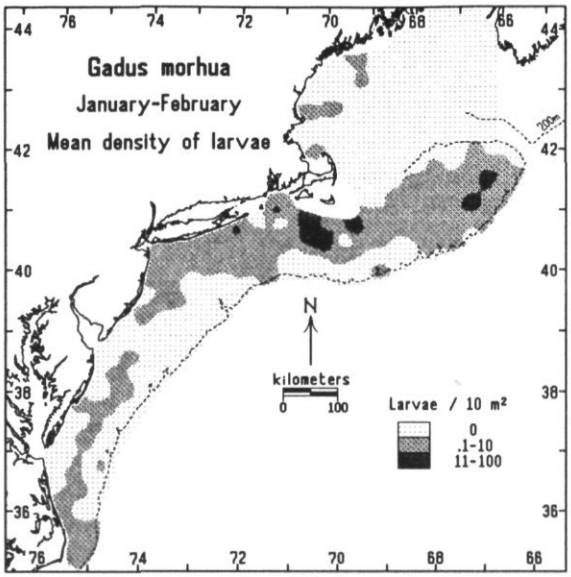

Gadus morhua
March-April
Mean egg density
N
kilometers
0 100
Eggs / 10 m²
0
.1-10
11-100
101-1000
1001-10000
>10000
Max. = 10,944

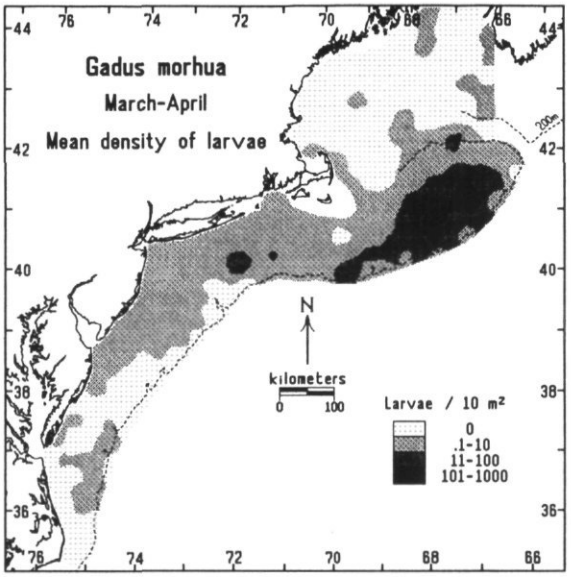

Gadus morhua
May-June
Mean egg density
N
kilometers
0 100
Eggs / 10 m²
0
.1-10
11-100
101-1000

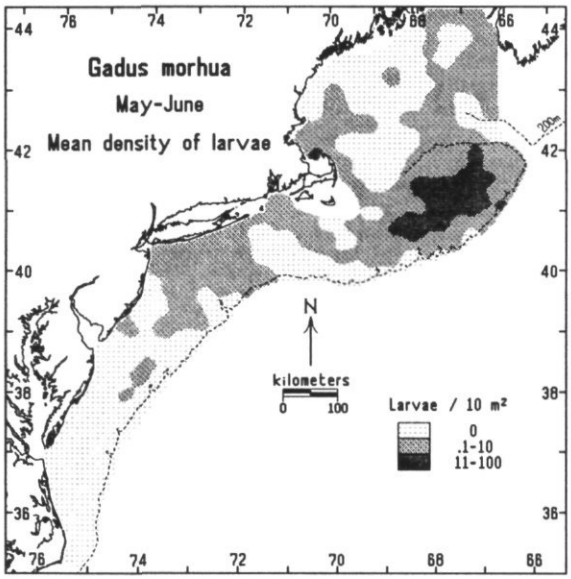

Gadus morhua
July-August
Mean egg density
N
kilometers
0 100
Eggs / 10 m²
0
.1-10
11-100
101-1000

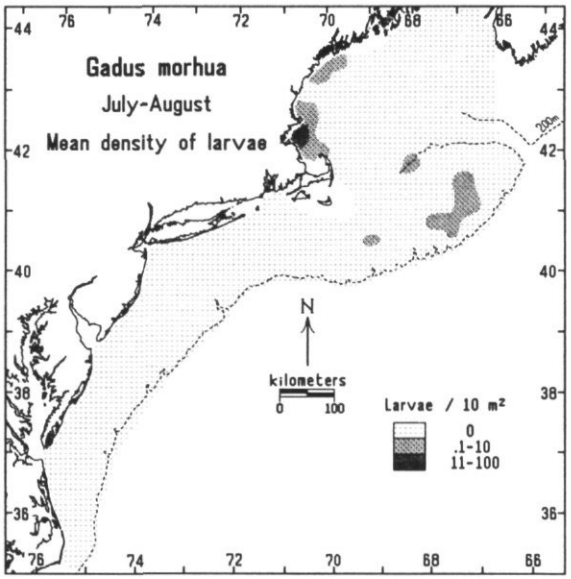

Gadus morhua
September-October
Mean egg density
N
kilometers
0 100
Eggs / 10 m²
0
.1-10
11-100

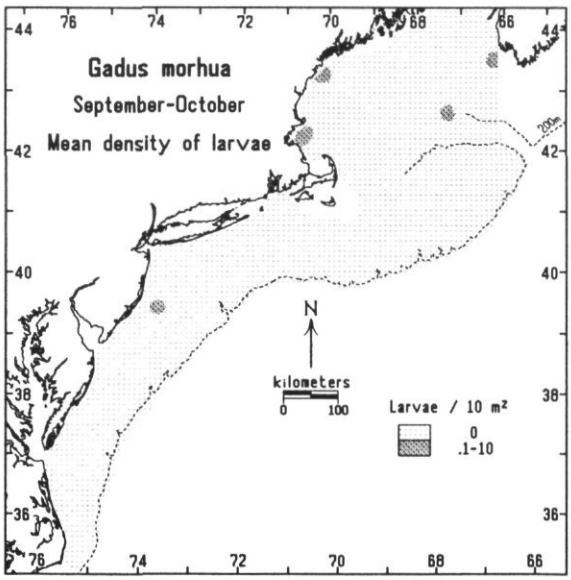

Gadus morhua
November-December
Mean egg density
N
kilometers
0 100
Eggs / 10 m²
0
.1-10
11-100
101-1000

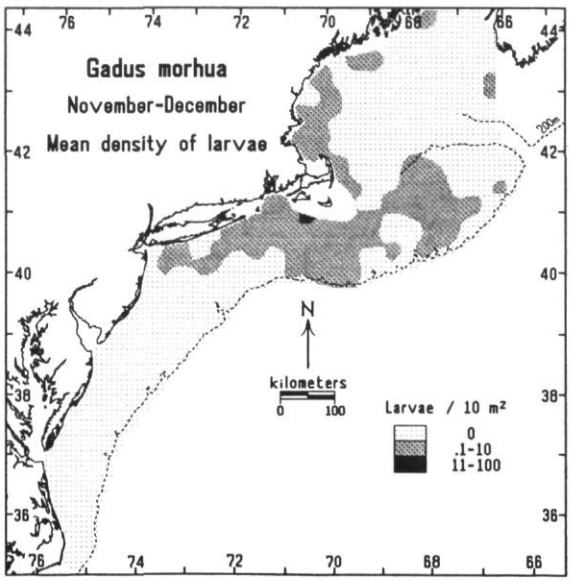

Gadus morhua
January-February
Mean density of larvae
N
kilometers
0 100
Larvae / 10 m²
0
.1-10
11-100


Gadus morhua
March-April
Mean density of larvae
N
kilometers
0 100
Larvae / 10 m²
0
.1-10
11-100
101-1000


Gadus morhua
May-June
Mean density of larvae
N
kilometers
0 100
Larvae / 10 m²
0
.1-10
11-100


Gadus morhua
July-August
Mean density of larvae
N
kilometers
0 100
Larvae / 10 m²
0
.1-10
11-100


Gadus morhua
September-October
Mean density of larvae
N
kilometers
0 100
Larvae / 10 m²
0
.1-10


Gadus morhua
November-December
Mean density of larvae
N
kilometers
0 100
Larvae / 10 m²
0
.1-10
11-100

land, and along the western Gulf of Maine (Morse *et al.*, 1987; Smith and Morse, unpub. data; Berrien and Sibunka, 1993). On Georges Bank and in Southern New England, cod eggs are most abundant during November through April; generally, the highest densities of eggs occur on Georges Bank in March. In the western Gulf of Maine, eggs are abundant between November and June, with some concentrations occurring even in July (Fig. 13).

Distribution of early life stages

Eggs spawned on the northeastern portion of Georges Bank generally drift southwesterly in the clockwise gyre normally present on the Bank (Fig. 6). At typical early spring temperatures, the eggs hatch in about two to three weeks (Laurence and Rogers, 1976). Identifiable egg, larval, and pelagic juvenile patches have been followed from spawning on northeastern Georges Bank, and have been shown to be advected along the southern flank of the Bank in a sheared flow field (Smith *et al.*, 1981; Morse *et al.*, 1987; Lough and Bolz, 1989). A variable fraction of the eggs and larvae reaching the western part of the Bank near the Great South Channel are caught up in the gyre (as are the eggs and larvae spawned in the South Channel area) and are recirculated around the Bank. Some fraction, however, is advected westward to the Southern New England and Middle Atlantic regions. In unusual years, a significant fraction of larvae can be transported off Georges Bank and into Middle Atlantic waters (e.g., as occurred in 1987 with haddock larvae; see Polacheck *et al.*, 1992), although some spawning of cod also occurs in the southerly areas.

It is not known to what degree eggs and larvae are transported northeastwards from Georges Bank (i.e., to the Scotian Shelf), but advective losses do occur, especially in early spring when the Georges Bank gyre is weaker and storm events are more frequent. Eggs and larvae spawned in the Gulf of Maine tend to drift south and eastward (towards Georges Bank) owing to the counter-clockwise Gulf of Maine gyre. However, the extent of exchange of cod offspring between the Gulf of Maine and Georges Bank regions is unknown.

During early spring on Georges Bank, the waters are well mixed and eggs and larvae are broadly distributed throughout the water column (Lough and Potter, 1993). Late-stage larvae and pelagic juveniles are located progressively deeper in the water column; by the time juveniles have grown to 40 mm, most are associated with the bottom. The diel vertical movement of cod appears to be strongly related to the light–dark cycle. Larvae tend to be found deeper by day than at night, with larger fish having a greater vertical range. Recently settled juveniles remain on the bottom during the day but migrate 3–5 m into the water column at night.

Lough and Bolz (1989) found evidence for continuous recruitment of both cod and haddock larvae onto the central shoals area (<60–70 m) of Georges Bank. At depths less than 70 m, retention of larvae appears to be enhanced via interactions with cross-isobath tidal currents. Based on results from an advection model, Werner *et al.* (1993) reported that cod larvae are transported westward along the southern flank of the Bank – and are more likely to be retained on the Bank – when the larvae occur shoalward of the 70-m isobath and are near the bottom. In late spring, when stratification begins, the Georges Bank gyre intensifies and reinforces the tidally-rectified recirculation pattern (Butman *et al.*, 1987). Hence, both the time and strength of stratification influence the retention of larval cod on Georges Bank.

Prior to settling to the bottom in early summer, pelagic juveniles (20–50 mm) are broadly distributed over the entire Bank (Lough *et al.*, 1989).

Growth and mortality of 0-group cod

The growth of larval cod on Georges Bank has been described by Gompertz-type curves based on daily growth increments of otoliths (Bolz and Lough, 1988). Growth rate increases from 0.13 mm/day after hatching to about 1.0 mm/day at 100 days of age. In June, pelagic juveniles range from 20 to 50 mm in length, and most juveniles are between 50 and 80 mm in size by the end of July (Lough *et al.*, 1989). By the end of their first year of life, Georges Bank cod reach an average length of 26 cm (Penttila and Gifford, 1976).

The mortality rate of cod eggs on Georges Bank has been estimated from ichthyoplankton surveys conducted from 1979 to 1987; daily mortality estimates range from 2% to 20%, and average 10% per day over the 20-day egg incubation period (pers. comm., Peter Berrien). Average mortality of cod larvae on Georges Bank [derived from 1977–1984 ichthyoplankton surveys] is estimated at 4% per day during the approximate 100-day period between hatching (4 mm) and 20 mm size (Morse, 1989).

Using these mortality estimates, total instantaneous natural mortality for the 120 days between fertilization and 20 mm size is M = 6.0 [i.e., ($M_{egg} = 0.1 \times 20$) + ($M_{4–20\ mm\ larvae} = 0.04 \times 100$)]. Total mortality from the

Figure 14. Composite bimonthly geographic distributions of Atlantic cod larvae off the northeastern coast of the United States from MARMAP surveys (1977–1987).

egg stage to recruitment at age 1 is estimated to be M_t = 13.8, viz.:

$$M_t = -\ln (R/E)$$
$$= -\ln [(2.2 \times 10^7)/(21.7 \times 10^{12})]$$
$$= 13.8$$

where R = average number of age 1 recruits for the 1979–1984 cohorts and E = average number of eggs spawned during 1979–1984.

By subtraction (13.8 − 6.0), total instantaneous mortality for the postlarval stage is M = 7.8. These rates thus correspond to overall mortalities (expectations of death) during the egg, larval, and postlarval stages of 86%, 98%, and >99.9%, respectively. The level of postlarval mortality (>99.9%) during 1979–1984 is similar to that estimated by Sissenwine *et al.* (1984) for the 1974–1980 period.

Larval and postlarval mortality rates can also be derived by comparing direct estimates of postlarval (≥20 mm) cod abundance for the 1986 and 1987 Georges Bank cohorts [from June surveys using a 10 m^2 MOCNESS sampler] with estimates of eggs spawned and age 1 recruits for these year classes (unpubl. data, Peter Berrien and Gregory Lough). These data indicate that total egg and larval mortality rates in 1986 and 1987 were M_t = 6.8 (99.9%) and M_t = 5.6 (99.6%), respectively. Postlarval mortality (from about mid-June until age 1) was M_t = 6.2 (99.8%) in 1986 and M_t = 6.8 (99.9%) in 1987. These values are consistent with the 1974–1980 and 1977–1987 averaged estimates, and again demonstrate that postlarval mortality in cod is comparable to that experienced in the egg and larval stages.

Prey and predators of 0-group stages

In the Georges Bank–Gulf of Maine region, the prey of larval cod consists of zooplankton. Yolk sac and first-feeding larvae prey primarily on small plankton such as copepod nauplii, phytoplankton, and lamellibranch larvae. With the exception of the yolk-sac stage, cod larvae feed on the same prey species throughout their early life, selecting the most numerically dominant prey (Kane, 1984; Buckley and Lough, 1987; Auditore *et al.*, 1994).

Prey size plays an important role; as cod grow larger, they tend to select larger size prey items. On Georges Bank, cod larvae feed on copepod nauplii, copepodites, and adults of *Calanus finmarchicus, Pseudocalanus* spp., *Oithona similis,* and *Centropages typicus*. As pelagic and recently settled juveniles, cod shift to epibenthic prey and swarming species that – like cod – also undergo diel vertical migrations. These food items include mysids (*Neomysis americana*), amphipods (*Gammarus annulatus*, *Themisto gaudichaudii*, *T. compressa*), chaetognaths (*Sagitta elegans*), and euphausiids (*Meganyctiphanes norvegica*) (Auditore *et al.*, 1988; Perry and Neilson, 1988; Lough *et al.*, 1989).

Much less is known of the predation on young cod in the Georges Bank–Gulf of Maine region than of their prey and feeding. Cod larvae and pelagic juveniles are themselves likely predators of smaller cod larvae (Laurence *et al.*, 1981). However, to date, there is little direct evidence of cannibalism. Mackerel are confirmed fish predators of cod and haddock larvae, and herring very likely also prey on small cod larvae (Michaels, 1991). Dogfish, silver hake, squid, larger cod, and many other piscivores prey on juvenile cod (Edwards and Bowman, 1979).

Despite limited direct evidence, the importance of predation as a dominant source of pre-recruit mortality in many fish populations is now a widely accepted assumption (Hunter, 1981; Sissenwine, 1984; Houde, 1987, 1989; Bailey and Houde, 1989). However, there are insufficient data from the studies on Georges Bank and in the Gulf of Maine to reliably quantify egg and larval predation mortality, let alone partition these mortalities among the various predators. New research initiatives currently underway on Georges Bank are designed to address these questions (see concluding section on Future Research).

Post-juvenile growth and maturation

Georges Bank cod grow more rapidly than Gulf of Maine cod. Penttila and Gifford (1976) fitted von Bertalanffy growth curves for cod collected from research vessel surveys in the early 1970s and found that at age 2 (January 1) Georges Bank cod averaged 39.9 cm in length while Gulf of Maine cod were only 26.4 cm long. The von Bertalanffy parameters for the two stocks are as follows:

	L_{inf}	K	t_0
Georges Bank	148.1	0.120	−0.616
Gulf of Maine	146.5	0.116	0.285

Based on mean weights-at-age in commercial catches, the growth rates of Georges Bank and Gulf of Maine cod appear to be intermediate compared with those in other North Atlantic cod stocks (Fig. 15).

Georges Bank cod mature earlier than Gulf of Maine cod, and fish in both stocks appear to mature earlier – and at a smaller size – than in most other North Atlantic stocks (Table 3). During the early 1970s, Georges Bank cod reached 50% maturity at about 2.8 years old as compared to 3.5 years for cod in the Gulf of Maine (Livingstone and Dery, 1976). Recently, however, the A_{50} values have declined in both stocks and are now 1.8 and 2.2 years, respectively (O'Brien *et al.*, 1993; Table 3). These A_{50} values are probably the lowest in any North Atlantic cod stock, including the North Sea stock, where cod display even faster somatic growth than on Georges Bank (Table 3, Fig. 15).

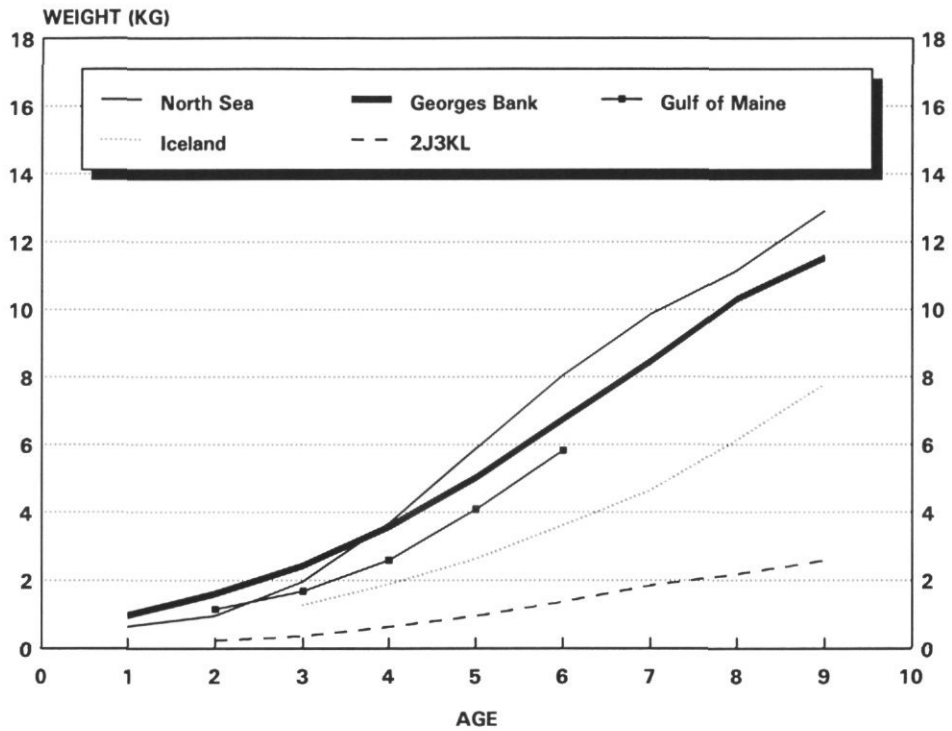


Figure 15. Mean catch weight-at-age values for five North Atlantic cod stocks. Values depicted are those used in the most recent stock assessments.

Of the few studies conducted on cod maturation in the Georges Bank–Gulf of Maine area, only the most recently completed study (O'Brien, 1990) is temporally and spatially comprehensive. This study, based on data from NEFSC spring research surveys collected during 1970–1990, indicates that both length and age at maturation have declined in both stocks over the past two decades. On Georges Bank, the estimated median age (A_{50}) and median length (L_{50}) at maturity for female cod declined from 2.7 year and 53.4 cm for the 1970 year

Table 3. Median age at maturity (A_{50}) and median length at maturity (L_{50}) of Atlantic cod in various North Atlantic stocks. Data are provided for females (F) and males (M), or sexes combined (C).

Area	Time period	A_{50} (years)			L_{50} (cm)			Source of data
		F	C	M	F	C	M	
Georges Bank	1972	2.9	–	2.6	51.5	–	44.0	Livingstone and Dery (1976)
	1985–1990	1.7	–	1.9	38.8	–	41.0	O'Brien *et al.* (1993)
Gulf of Maine	1878	4.0	–	3.0	–	–	–	Earll (1880)
	1972	3.5	–	3.5	–	–	–	Livingstone and Dery (1976)
	1985–1990	2.1	–	2.3	32.1	–	36.0	O'Brien *et al.* (1993)
Nova Scotia to Cape Hatteras	1977	–	–	–	49.6	–	53.7	Morse (1979)
Scotian Shelf	1963	5.0	–	3.9	52.0	–	51.0	Beacham (1983)
	1978	2.0	–	2.0	35.0	–	38.0	Beacham (1983)
NAFO Area 2J3KL	–	–	6.0	–	–	49.7	–	Xu *et al.* (1991)
Iceland	–	–	3.4	–	–	–	–	ICES (1993a)
North Sea	–	–	3.7	–	–	–	–	ICES (1993b)

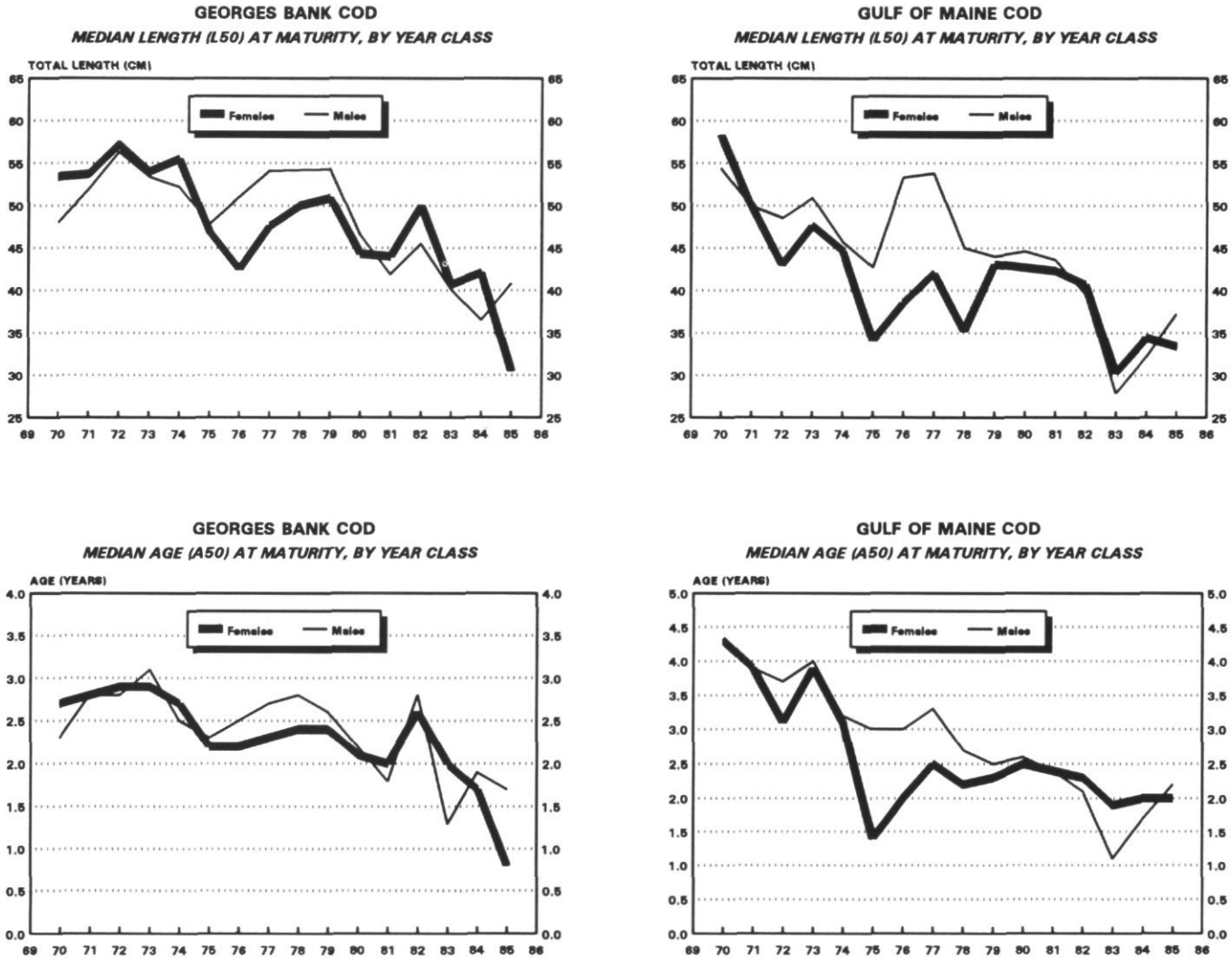


Figure 16. Trends in median length at maturity, by year class (top) and median age at maturity, by year class (bottom) for the Georges Bank and Gulf of Maine cod stocks. Data derived from NEFSC bottom trawl surveys.

class to 0.8 years and 30.5 cm, respectively, for the 1985 year class (Fig. 16). Similar trends have occurred in Gulf of Maine cod for the same year classes; A_{50} and L_{50} values for females declined from 4.3 years and 58.3 cm (1970 year class) to 2.0 years and 33.4 cm (1985 year class). In both stocks, A_{50} and L_{50} for males have declined in tandem with those for females (Fig. 16).

The accelerated maturation rates in both stocks have occurred over a time period during which marked reductions in stock abundance have occurred. Changes in maturation show a significant correlation with changes in abundance of the two stocks, but not with annual changes in water temperatures (O'Brien, 1990).

Food and feeding of juvenile and adult cod

Extensive studies of food habits of fishes on Georges Bank and in the Gulf of Maine have been conducted in conjunction with the NEFSC research vessel surveys in these areas (Grosslein *et al.*, 1980). These studies show that the diet of juvenile and adult cod in both areas is basically similar to that found in other North Atlantic cod stocks; fish represent the major prey item (in terms of percentage weight of stomach contents), followed by crustaceans and mollusks (Edwards and Bowman, 1979; Fig. 17). On Georges Bank, fish comprised 62% of the diet of cod during 1969–1972, with about 15% each for crustacea and mollusks (Langton and Bowman, 1980). During the same time period, the diet of Gulf of Maine cod was comprised of 70% fish, 26% crustaceans, and 1% mollusks. The major fish prey of cod in both areas was clupeids (chiefly *Clupea harengus*), but flounders and other gadids were also consumed on Georges Bank, while redfish, mackerel, and other gadids were taken as prey in the Gulf of Maine (Langton and Bowman, 1980).

The principal crustaceans consumed by cod in both areas are decapod crabs and shrimp. Of the mollusks eaten, squid constitute the major prey of Gulf of Maine cod, while the discarded remains of sea scallops (from scallop vessels shucking at sea) are often an important molluscan component of the diet of Georges Bank cod (Langton and Bowman, 1980; Bowman and Michaels, 1984). Juvenile cod (6–10 cm) consume some fish but depend most heavily on amphipods and small decapod shrimp. Larger crustacea and more fish are eaten by cod as they grow. By the time cod attain a length of 50–60 cm, their overall diet is about half fish and half invertebrates; thereafter, the proportion of fish in the diet continues to increase (Bowman and Michaels, 1984).

During the mid-1960s and early 1970s, large declines in fish biomass occurred on Georges Bank due to intensive fisheries exploitation (Mayo *et al.*, 1992). Comparisons of cod diets before and after this period indicated a change in diet composition; the percent frequency occurrence of fish (all species) in cod stomachs dropped from 37% in 1963–1966 to 29% in 1973–1976 (Grosslein

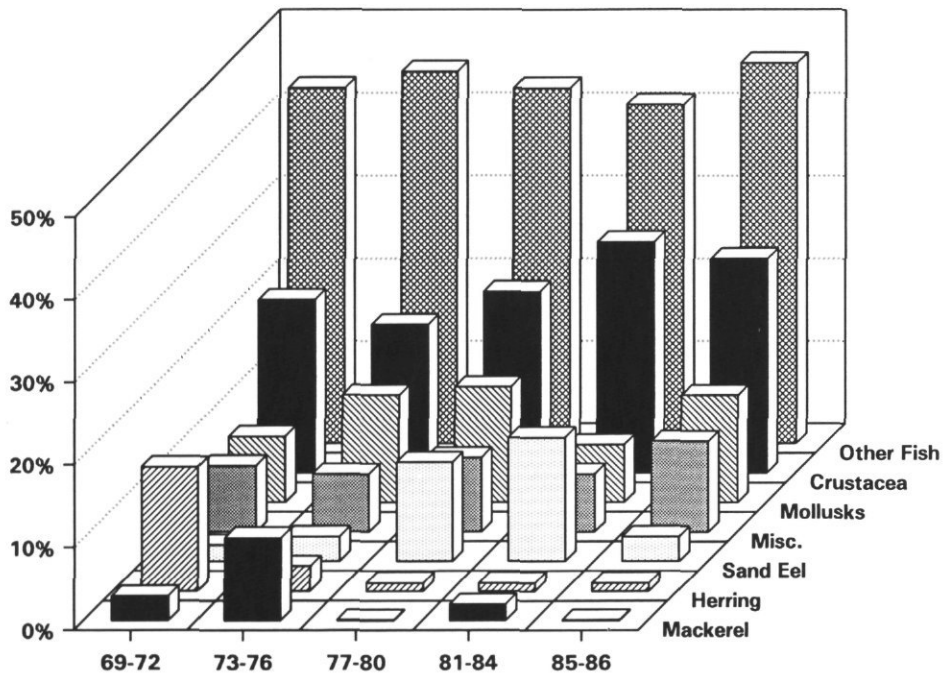


Figure 17. Diet composition (% by weight of prey) of Atlantic cod off the northeast coast of the United States (1969–1986).

et al., 1980). The reduced incidence of fish in the diet of cod was due to decreased consumption of gadids, since the incidence of clupeids remained unchanged (Grosslein *et al.*, 1980). Although the stomach sampling protocols were quite different between the 1963–1966 and 1973–1976 periods (and hence the data not strictly comparable), the reduced incidence of gadids in the post-1972 diet appears to be a real reflection of the diminished abundance and availability of the Georges Bank gadid stocks. On the other hand, sea herring abundance was considerably greater on Georges Bank during 1963–1966 than in 1973–1976, yet the frequency of occurrence of clupeidae in cod stomachs was virtually the same in both time periods (Grosslein *et al.*, 1980). In more recent years (1977–1986), cod diets in both the Gulf of Maine and on Georges Bank have shown a lower fraction of fish balanced by an increased proportion of invertebrate prey (Fig. 17). This apparent shift could be a reflection of reduced availability of preferred fish prey and partial compensation (substitution) of invertebrate prey for fish (ICES, 1992).

Estimates of daily ration for cod in the Georges Bank–Gulf of Maine region range from about 1–2% body weight per day (Edwards and Bowman, 1979; Grosslein *et al.*, 1980; Cohen and Grosslein, 1981; Durbin *et al.*, 1983). These estimates are somewhat higher than the daily ration estimates of 0.8–1.0% body weight per day for similar-sized cod (50–60 cm) in the North Sea (Daan, 1973) – despite the fact that mean weight of gut contents is more than twice as great in North Sea cod (Ursin *et al.*, 1985) and both stocks have similar growth rates (Ursin, 1984). However, the mean stomach content weights of cod on the Scotian Shelf and off Newfoundland are also much larger than those observed on Georges Bank, but growth rates of cod in these areas are much slower (Ursin, 1984; Ursin *et al.*, 1985). Recent analyses of cod food habits data by the ICES Multispecies Assessment Working Group indicate that for most North Atlantic cod stocks stomach content weight is inversely correlated with temperature; the lower mean stomach content weights of cod off the northeastern United States are thought to result from higher ambient water temperatures (ICES, 1992). The fraction of fish in the diet of Georges Bank/Gulf of Maine cod is also generally lower than observed in other North Atlantic cod stocks (ICES, 1992). More investigations on the effects of prey size and prey type (as well as temperature) on digestion rates are considered to be essential in resolving these apparent paradoxes, as well as to obtain more accurate estimates of consumption rates by cod and other species (Ursin *et al.*, 1985).

A measure of the relative importance of cod as a piscivore on Georges Bank is provided within the framework of energy budget calculations for Georges Bank. Fish consumption by cod represented only 3% of the total estimated production of fish (including pre-recruit stages) and just 4% of the pre-recruit fish production component for the periods 1964–1966 and 1973–1975 (Sissenwine *et al.*, 1984). By comparison, the consumption of fish by silver hake represented 55% and 67% of the total estimated fish production and 69% and 93% of the pre-recruit fish production. While there is considerable uncertainty about the accuracy of the absolute values of the energy budget calculations, they provide a reasonable basis for concluding that cod is not the controlling fish predator in the Georges Bank and Gulf of Maine regions. Given that the biomass of both cod stocks has recently sharply declined while other piscivorous species (notably spiny dogfish) have markedly increased (US Department of Commerce, 1992), it is believed that cod plays only a minor role in regulating the current production and composition of the finfish biomass in the Georges Bank/Gulf of Maine ecosystems.

Environmental factors affecting cod

Seasonal and interannual changes in the environmental conditions on Georges Bank and in the Gulf of Maine exert influences on the cod stocks – in terms of both their distribution and abundance. Environmental factors affecting the abundance of cod most likely occur at the early life history stages. While a number of physical and biological properties and processes can potentially influence growth and survival of cod larvae and juveniles, different properties or physical processes may be important during each of the different life stages. Many hypotheses have been proposed linking environmental conditions and cod recruitment success, but so far few relationships have been established based on actual observations and none have yet led to an in-depth understanding of the actual mechanisms involved.

Temperature

The environmental influence most easy to document is the effect of temperature changes on stock distributions. During NEFSC spring trawl surveys, when bottom water temperatures are 4–6°C, adult cod are widely dispersed across Georges Bank (Fig. 3). In autumn, when bottom water temperatures are above 10°C, the distribution of cod shifts with the highest concentrations of adults found in the cooler, deeper waters off the northern side of the Bank and in the northern part of the Great South Channel (Fig. 3). A similar seasonal pattern is also evident for juvenile fish (Wigley and Serchuk, 1992). Interannual changes in temperature also affect cod distribution patterns. Mountain and Murawski (1992) compared the average bottom water temperature on Georges Bank during spring NEFSC

surveys with the average temperature at which cod were caught in the surveys. The two temperature series were related ($p < 0.05$) with a regression slope of 0.58, such that for each degree increase in Georges Bank temperature the average catch temperature increased by 0.58°C. These findings suggest that cod compensated for about 40% of the interannual changes in temperature by changing their spatial distribution. However, this interannual temperature compensation could not simply be explained by movements of fish between depths (e.g., shallow to deep) or across latitudes (e.g., north–south shifts).

Optimum spawning and hatching temperatures for cod are between 5 and 7°C, which typically occur on Georges Bank in March and April (Heyerdahl and Livingstone, 1982). However, water temperatures and peak spawning vary from year to year (Smith, 1985). In warm to moderate winters, peak spawning can occur as early as December, but during unusually cold winters the spawning peak may be delayed until the end of April (Smith *et al.*, 1981). Although temperature clearly affects the timing of peak spawning, there is so far no indication that overall egg production is affected by temperature. During the period 1978–1987, Berrien and Sibunka (1993) reported a downward trend in cod egg abundance over the entire northeast shelf region (Middle Atlantic to the Gulf of Maine). Temperature data (Holzwarth and Mountain, 1992) indicate that the second half of this decade was about 1°C warmer than the first half; water temperatures in the 1983–1987 period were comparable to the warm mid-1970s, particularly on Georges Bank (Fig. 7). However, the decline in cod egg production is most likely due to the sharp decline in spawning-stock biomass that occurred between 1980 and 1986 (Fig. 11).

In several stocks of Atlantic cod, higher water temperatures have been associated with higher growth rates (Taylor, 1957). In the autumn (during the latter part of the growing season for cod off the US coast), bottom temperatures on Georges Bank (Holzwarth and Mountain, 1992) are warmer (8.6–13.4°C) than in the Gulf of Maine (5.8–9.2°C). The accelerated growth and maturation rates of Georges Bank cod compared to Gulf of Maine cod may thus be partly due to higher average temperatures on Georges Bank. Georges Bank also appears to have higher fish production than the Gulf of Maine; this production is represented largely by juvenile fish which would be potential prey for cod (Cohen and Grosslein, 1987). However, as noted earlier, no correlation exists between maturation rates and bottom water temperatures. The significant correlations found in both stocks between maturation and abundance (O'Brien, 1990) suggest that the acceleration of maturation is a compensatory response associated with reduced stock size levels in recent years.

Based on ichthyoplankton data collected during the 1977–1984 MARMAP surveys, Morse (1989) reported that both larval growth of cod and length-dependent larval mortality were positively correlated with water temperatures in the Georges Bank–Gulf of Maine region, and postulated that the increased metabolic requirements of predators were primarily responsible for the higher larval mortality. Larval metabolic requirements also increase with temperature. Buckley *et al.* (1992) recorded larval cod mortalities ranging from 2 to 10% per day in predator-free tanks at a constant temperature of 7°C, and at prey densities of 10–500 plankters/l which provided normal larval cod growth rates of 8–10% per day. Thus, even under near-optimal conditions, some cod larvae will not survive. Since both larval metabolic requirements and larval growth (at food densities above a critical level) increase with temperature, temperature must also play a role – independently of predation – in regulating larval mortality .

Studies of the copepod populations sampled with 0.333 mm mesh during the 1977–1984 MARMAP surveys showed: (1) no correlation between water column temperature and total copepod abundance on Georges Bank and in the western Gulf of Maine; (2) no correlation between temperature and *C. finmarchicus* on Georges Bank; and (3) a negative correlation between temperature and *C. finmarchicus* in the Gulf of Maine (Meise-Munns *et al.*, 1990). These results seemingly indicate that during spring, food of the larger cod larvae is less plentiful (or, at least, no different) at higher water temperatures. It is recognized that most of the diet of smaller cod larvae comprises smaller-bodied copepod species not fully sampled by the 0.333 mm mesh. However, no evidence exists to suggest that food supplies at higher water temperatures are insufficient to sustain higher growth rates. As such, part of the increase in mortality with temperature is likely attributable to intrinsic temperature effects.

Koslow *et al.* (1987) considered the influence of a number of climatic variables on recruitment in various cod stocks in the Northwest Atlantic, and found that both local and large-scale winds were significant correlates for a number of stocks but sea-surface temperatures generally were not. Although the Georges Bank cod stock was not included in this study, subsequent analysis of Georges Bank recruitment (Serchuk *et al.*, 1993) and spring and fall temperature anomaly estimates (Holzwarth and Mountain, 1992) revealed no correlation between recruitment and the local interannual temperature patterns.

Advection

The characteristic circulation pattern on Georges Bank transports gadid ichthyoplankton from spawning areas

on the northeastern part of the Bank to the southwest. The rate of water movement is such that, by the time watermasses reach the Great South Channel, many larvae have moved shoalwards and are thus retained on the Bank. Variability in the circulation pattern, however, can result in a greater or lesser advective losses of larvae from the Bank.

Polacheck *et al.* (1992) documented an unusual westward drift of haddock larvae from Georges Bank into the Middle Atlantic region in the spring of 1987. The larvae appeared to have survived through the summer and autumn because of unusually cool bottom water temperatures on the outer half of the shelf. Georges Bank cod larvae were not similarly advected into the mid-Atlantic area in 1987, but this may occur in some years. In general, however, advective losses of larvae would be less significant to recruitment success for cod than haddock, because cod has a more protracted spawning season.

Gulf Stream warm-core eddies near the southern edge of Georges Bank may play an important role in some years in both entraining larvae and in moving water on and off the shelf (Lough, 1982; Joyce and Wiebe, 1983). The southeast flank of Georges Bank is particularly vulnerable to advective losses during periods of strong northerly windstress (Walford, 1938; Cohen *et al.*, 1986). Myers and Drinkwater (1989) investigated the relationship between warm-core ring frequency and recruitment in a number of Northwest Atlantic fish stocks. Although there was a tendency for decreased recruitment with increased ring frequency, no relationship was found between warm-core rings and cod recruitment on Georges Bank.

Difficulties in identifying the influence of environmental processes on larval survival were illustrated by Cohen *et al.* (1986). Comparisons were made of the development of the 1981, 1982, and 1983 cod and haddock year classes on Georges Bank in relation to various physical processes which could affect larval survival. In 1982, after what appeared to be normal spawning, low larval abundance suggested unusually high egg and larval mortality. This mortality was most likely due to: (1) a large storm event in early April, which satellite imagery indicated drove a large amount of water off the southeastern flank of the Bank; (2) a Gulf Stream ring which entrained a large volume of water from the southeastern part of the Bank during March and April; or (3) a combination of these events.

Stratification

The development of water column stratification during spring on the southern flank of Georges Bank leads to increased phytoplankton and zooplankton in the vicinity of the pycnocline. This concentrating mechanism for the larval food organisms is believed to be important for the growth and survival of gadid larvae. Buckley and Lough (1987) investigated the effect of water column stratification on Georges Bank on the short-term growth and condition of haddock and cod larvae, and found that haddock larvae from a site where the water was well mixed were in poor condition, while larvae from a nearby site where the water was stratified were in good condition. Cod larval condition did not show as strong a relationship with stratification as did haddock. Cod collected at the same sites as haddock were in better condition and were faster growing. Cod larvae appear to be better adapted to winter conditions – when prey densities are generally lower. Haddock larvae require higher prey densities than cod and seem more adapted to spring conditions when prey are concentrated by stratification (Lough, 1984). The findings suggest that interannual changes in stratification conditions on Georges Bank could have a marked influence on the survival of haddock larvae and thereby affect recruitment, but probably a lesser effect on cod.

Turbulent mixing

Turbulent mixing generated by strong tidal currents and surface windstress on Georges Bank may affect the encounter rate between larvae and prey organisms (Rothschild and Osborn, 1988). Studies from other regions have indicated a relationship between water-column turbulence and larval feeding (Sundby and Fossum, 1990). Although information is not yet available on water turbulence and the feeding of cod larvae in the Georges Bank–Gulf of Maine region, Meise-Munns *et al.* (1990) found a significant positive correlation between total copepod abundance and windstress during February–April on both Georges Bank and in the western Gulf of Maine. Windstress could conceivably affect larval growth and mortality via effects on prey density and temperature, but specific linkages have not yet been established.

Fish food production

Although maturation rates of both Georges Bank and Gulf of Maine cod have been influenced by stock size, the faster growth and maturation rates of Georges Bank cod relative to Gulf of Maine cod may be due to environmental differences. As noted previously, water temperatures and apparent fish prey production on Georges Bank are higher than in the Gulf of Maine. However, secondary production (zooplankton and macrobenthos) appears to be about the same in both areas (Cohen and Grosslein, 1987) and the proportion of fish in the diet of Gulf of Maine cod is as high – or higher – than for Georges Bank cod (Langton and Bowman,

1980; Bowman and Michaels, 1984). Once again the pieces of the puzzle do not fit neatly into place.

Another problematic aspect is that somatic and gonadal development appear to be de-coupled in Georges Bank cod but not for cod in the Gulf of Maine. Mean lengths-at-age for Georges Bank cod do not show any trend over time, despite declines in age/size at maturity, whereas in the Gulf of Maine there is evidence for increased growth of cod along with faster maturation (O'Brien, 1990).

If Georges Bank cod were already at or near their physiological limit for growth, it is plausible that any excess energy might be diverted towards gonadal growth, resulting in acceleration of maturation. Although changes in maturation are usually associated with changes in growth, this is not always the case (Roff, 1982). If the Gulf of Maine is a less productive environment for cod (relative to Georges Bank), then an increase in available prey might enable the stock to shunt excess energy into both somatic and gonadal growth, thereby accelerating both growth and maturation rates. However, there are no data that indicate that secondary production in the Gulf of Maine has increased in recent years.

Predator/prey biomass changes

Large-scale fluctuations in abundance of mackerel, herring, and sand lance have occurred in the Georges Bank–Gulf of Maine region during the past several decades (Sherman, 1986). These species are not only prey for cod but also significant predators of cod eggs and larvae (Grosslein *et al.*, 1980; Michaels, 1991). The relative occurrence of mackerel/herring/sand lance in the diet of cod (Fig. 17) broadly reflects changes in the abundance levels of these prey. Empirical evidence exists that mackerel and herring exert predatory control on sand lance abundance (Fogarty *et al.*, 1991). Given these interactions, the predator–prey linkages among just these four species may be extraordinarily complex.

Presently, there are insufficient data to adequately quantify predation mortality on cod eggs, larvae, or juveniles. To obtain quantitatively reliable measures of critical rates, intensive studies of the first year of life – including a life table along with concurrent studies of physical/biological processes – are urgently needed.

Future research

Although many attempts have been made to correlate environmental variables with variations in stock abundance of cod, nearly all of these lack long-term predictive power and usually break down when re-examined with new data (Myers *et al.*, 1993a). Large-scale synchrony in recruitment patterns of cod stocks from Labrador to Nova Scotia were reported by Koslow (1984) and linked to large-scale meteorological pressure fields and offshore winds (Koslow *et al.*, 1987). Thompson and Page (1989), using more appropriate analytical methods, also detected a synchrony in recruitment patterns for these same cod stocks but showed that the correlation with large-scale weather patterns was not significant. More recently Myers *et al.* (1993a) reported a strong relationship between salinity and recruitment for cod stocks in the Newfoundland region, but the causal oceanographic and food chain mechanisms linking these variables were not identified. In another study of northern cod stocks (Grand Bank of Newfoundland, Labrador, and West and East Greenland Shelves), Myers *et al.* (1993b) examined cod spawning times in relation to seasonal cycles of plankton abundance, ocean temperature, water column stability, and oceanic transport; no consistent relationships between these features and cod spawning times were detected, and only a very general match existed between timing of larval production and planktonic food.

Cohen *et al.* (1991) updated and re-examined the time series of recruitment estimates for cod (and haddock) stocks throughout the entire Northwest Atlantic (including the Gulf of Maine and Georges Bank stocks) and found that these stocks fell into two groups: a northern group in the Labrador/Newfoundland region, and a southern group extending from the Gulf of St Lawrence to Georges Bank. Recruitment synchrony was stronger within the groups than between them, suggesting that local-scale physical factors exert more control over recruitment than large-scale climatic effects.

Attempts to link recruitment to physical environmental factors on Georges Bank have so far been unsuccessful (Fogarty *et al.*, 1987). Since cod recruitment appears to be a compound function of largely density-independent factors operating in the egg and larval stages and density-dependent factors operating during the juvenile period, correlation analysis alone will certainly be inadequate to sort out the controlling mechanisms. Achieving predictive capability will require a better quantitative understanding of the dynamics of key processes controlling growth and mortality throughout the first year of life. These processes are the focus of two new research initiatives on Georges Bank being conducted under the auspices of: (1) the US GLOBEC Program; and (2) the NOAA Coastal Ocean Program.

The goal of the US GLOBEC NW Atlantic/Georges Bank Study is to predict the potential effects of climate change on Georges Bank gadid stocks (US GLOBEC, 1992). The Program will involve intensive investigations of those processes believed to be most susceptible to alteration by climate change and which are likely to be important to the population dynamics of gadid larvae and their primary prey organisms, *Calanus* and *Pseudo-*

calanus. Three physical processes will be studied in detail: (1) stratification of the water column; (2) retention and loss of water from the Bank; and (3) frontal exchange processes. Concurrent biological studies will be conducted on feeding, growth (and physiological condition), abundance, distribution, and mortality of cod and haddock eggs/larvae (as well as principal zooplankton species). Identification of major invertebrate predators and estimation of predation rates on pelagic stages of 0-group gadids will also be attempted.

Studies of fish predation on larval and juvenile gadids will be conducted under the NOAA Coastal Ocean Program (COP) research initiative on predator/prey interactions in the Georges Bank ecosystem. The chief goal of the COP Georges Bank study is to understand the interactive effects of exploitation and interspecific interactions on the fish community dynamics of Georges Bank. This program involves: (1) retrospective studies of changes in fish biomass, species composition, and predator–prey interactions; (2) process-oriented studies in the field and laboratory on predation on 0-group stages, digestion rates, etc.; and (3) multispecies modelling to test and evaluate hypotheses about controlling mechanisms, and to examine long-term effects of different fishery management strategies on the productivity of the Georges Bank ecosystem.

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Possible causes of recent trends and fluctuations in Scotian Shelf/Gulf of Maine cod stocks

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Frank, K. T., Drinkwater, K. F., and Page, F. H. 1994. Possible causes of recent trends and fluctuations in Scotian Shelf/Gulf of Maine cod stocks. – ICES mar. Sci. Symp., 198: 110–120.

Three major cod stocks are generally recognized in the Scotian Shelf/Gulf of Maine region: one each on the eastern and western Scotian Shelf (ESS and WSS) and Georges Bank (GB). Spring spawning is common to all stocks with peak egg concentrations occurring on offshore banks during January/February (GB cod), March/April (WSS cod), and April/May (ESS cod). Fall spawning, an event quite exceptional among cod stocks, also occurred during November/December in ESS cod at locations identical to those in spring. During the past two decades landings averaged about 50 000 t in ESS cod, 22 000 t in WSS cod, and 17 000 t in GB cod. Annual fishing mortality rates (F) have, on average, ranged from 0.51 to 0.61, with an increase since the mid-1980s in ESS cod. Recent fishing mortalities in ESS and GB cod have been substantially in excess of their long-term mean and have contributed to declines of spawning-stock biomasses (SSB) to near-historic low levels. In ESS cod, strong year classes were produced during the 1970s coincident with low SSB with a reversal of this situation occurring in the 1980s. Prior to the mid-1980s there existed a strong inverse correlation between ESS cod recruitment and St Lawrence River discharge (RIV-SUM) and it disappeared with the addition of recruitment data from the 1980s, when year-class survival per unit of SSB was quite low and when environmental variability was well within the range of historical observations. This recent sequence of events on the eastern Scotian Shelf coincided with a change in spawning pattern to fall only, resulting from either a disappearance of the spring-spawning component or a switch to autumn spawning.

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Introduction

Important Canadian fisheries for cod (*Gadus morhua*) in the Western Atlantic exist outside of Newfoundland/Labrador waters. These "other" fisheries are supported by the cod stocks which inhabit the offshore waters of the Scotian Shelf and Gulf of Maine (Fig. 1) that together have accounted for about 20% of the total Canadian cod landings during the past decade. This geographic area also supports significant groundfish fisheries for haddock (*Melanogrammus aeglefinus*) and pollock (*Pollachius virens*), unlike the shelf regions to the north. In addition, the Scotian Shelf is among the best scientifically surveyed regions in Canadian waters. For example, during the past 20 years there have been three major ichthyoplankton surveys of the main spawning areas on the Scotian Shelf and Gulf of Maine: the Scotian Shelf Ichthyoplankton Program (1977–1982; O'Boyle *et al.*, 1984), the Fisheries Ecology Program (1983–1985; Hurley and Campana, 1989) and the recruitment program of the Ocean Production Enhancement Network (1991–1993). In addition, seasonal bottom trawl surveys of juvenile and adult groundfish have been conducted annually since 1970 (Page *et al.*, 1994). Collectively, this information provides the basic biological data for describing the seasonal and life stage-specific distributions of cod. Analytical stock assessments for cod provide time series estimates of biomass, recruitment, and fishing mortality. Drawing upon this background information we provide an overview of the life

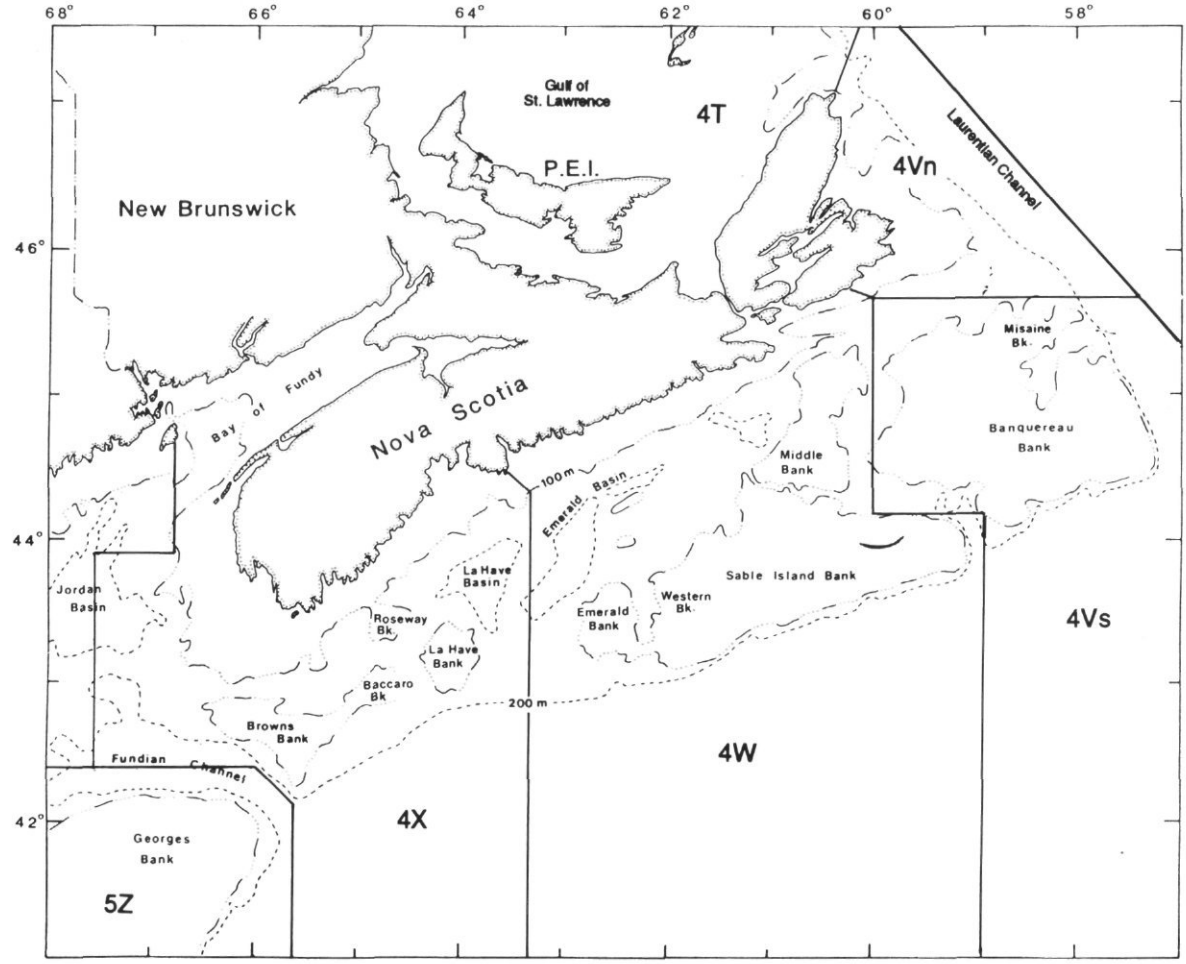


Figure 1. Map of the Scotian Shelf and Gulf of Maine showing bathymetry, NAFO Divisions, and place names referred to in the text.

history and population dynamics of the Scotian Shelf/Gulf of Maine cod stocks and speculate on the causes for the recent decline of the most productive stock in the region – the eastern Scotian Shelf cod.

Physical environment

The Scotian Shelf lies off Nova Scotia and has a length of 700 km and a width, defined by the 200 m isobath, varying from 250 km at its eastern end to 150 km to the west. The average depth over the shelf is about 90 m. The complex topography includes several deep basins (>200 m) near mid-shelf and a series of shallow (less than 50 m) banks further offshore (Fig. 1). A topographic ridge which includes Middle Bank separates the deeper shelf waters (>100 m) in the northeast from those to the southwest. The Scotian Shelf is separated bathymetrically from the southern Newfoundland shelf by the Laurentian Channel and from the Gulf of Maine by the Fundian Channel. The residual circulation is dominated by the Nova Scotian Current, a southwestward flow whose axis lies 50–70 km offshore and whose strength varies seasonally from a winter maximum to a summer minimum (Drinkwater *et al.*, 1979). Clockwise circulation patterns have been observed over the banks where detailed current measurements have been taken, e.g. Browns Bank (Smith, 1989) and Western Bank (Thompson and Griffin, in prep.). The density structure in summer in the western region consists of three layers: a near surface layer with salinities <32 and temperatures >5°C, a cold intermediate layer with salinities 32–33.5 and temperatures <5°C and a warm (>5°C), saline (>33.5) bottom layer. In winter the top two layers coalesce. In the eastern Scotian Shelf, there are only two

layers in summer, as the cold intermediate layer extends to the bottom.

Georges Bank, located in the offshore regions of the Gulf of Maine, is divided by the boundary between Canada and the United States. The depths on the Bank are typically 40–70 m, but reach as shallow as 20 m in the central region. The residual current consists of an anticyclonic eddy over the bank (Butman *et al.*, 1987). The strong tidal currents result in well-mixed water over the top of the Bank, even in summer (Garrett *et al.*, 1978).

Distribution of cod

Cod distributions on the Scotian Shelf/Gulf of Maine vary according to season and life stage. During late winter and early spring, spawning occurs on most of the major offshore banks. Starting from the west and moving east these include Georges, Browns, Emerald, Western, Middle, Sable Island and Banquereau. Smaller concentrations of spawning cod occur in the Bay of Fundy and along the southwestern shore of Nova Scotia (Fig. 2). Cod spawning concentrations also occur during the fall (October–December), particularly on the offshore banks within the eastern Scotian Shelf (Fig. 2). Cod-spawning aggregations were not evident on the shelf during the summer months; but they were found in the Sydney Bight region off Cape Breton in NAFO Division 4Vn.

Historical, broad-scale, ichthyoplankton surveys should provide a more exact definition of cod-spawning times and locations than collections of spawning cod made during standard trawl surveys. One such survey, the Scotian Shelf Ichthyoplankton Program (SSIP), conducted seasonal sampling across the Scotian Shelf during 1977–1982 (O'Boyle *et al.*, 1984). Peak concentrations cod eggs occurred during January/February on Georges Bank, March/April on Browns, and April/May on the banks to the east (Fig. 2). This pattern of progressively later spring spawning from west to east coincides roughly with the seasonal northward progression of the 3–4°C surface isotherms along the shelf (Drinkwater and Trites, 1987) and suggests that initiation of spawning is temperature-dependent. This composite picture generally supports the view obtained from the trawl surveys with some exceptions.

The concentration of spawning cod on Banquereau was not matched by overlapping peak egg concentrations; this could be the result of several factors, including increased strength of the along-shelf currents in this region or lack of recirculation features combined with the fact that the cod eggs are about 16 days old when they reach stage IV of development. In the fall, peak egg concentrations were associated with the offshore banks on the eastern half of the Scotian Shelf (Fig. 2). Egg concentrations were also high along the Nova Scotian coast in both the spring and fall.

The distributional pattern of yolk-sac and post-yolk-sac cod larvae (4–17 mm sl) was nearly identical to that of the eggs, which suggests that retention mechanisms associated with the banks are acting to minimize dispersal. Recent process-oriented studies on Georges, Browns Bank, and Western/Sable Island Bank have revealed that topographically induced eddies serve to enhance the retention of offspring in the vicinity of the spawning sites (Loder *et al.*, 1988; Smith *et al.*, 1989; Thompson and Griffin, in prep.).

The standard trawl surveys provided information on the seasonal distribution of juvenile cod (age 1). Peak abundances were evident on the offshore banks across the Scotian Shelf during all of the seasons surveyed and major concentrations were seen near the mouth and inner Bay of Fundy (Fig. 3). Juvenile cod are broadly distributed across the central shoal area of Georges Bank (Serchuk *et al.*, 1994). Significant age segregation of cod occurs on the eastern Scotian Shelf during the summer with adult fish tending to occupy deeper and colder water (Sinclair, 1991). However, such a pattern is not evident on the western Scotian Shelf, where considerable mixing occurs during spring, summer, and fall among juvenile and adult cod (Hurley *et al.*, 1991).

Springtime distributions of adult cod were highly aggregated and closely associated with the offshore banks. In the summer, which is generally considered to be a non-spawning period for cod, the adult distributions were widely dispersed. Fall cod distributions on the western Scotian Shelf resemble the summer distributions quite closely, although this was not the case to the east, where some pronounced aggregations were evident in the vicinity of Middle and Banquereau Bank. Fall aggregations were also evident along the edge of the Laurentian Channel and Cape Breton, which may reflect the migration of cod out of the Gulf of St Lawrence (McKenzie, 1956). It should also be noted that catch rates of cod were generally higher on the eastern Scotian Shelf during all three seasons examined (Fig. 4). Collectively, the defined management units correspond well with the seasonal distributional patterns of the three stocks at all life stages.

Cod growth

Growth rates differ substantially between the three stocks, with size differences evident at age 1 that persist through to adults. Long-term mean weight-at-age from commercial sampling shows that age 6 cod weigh 6.5 kg on Georges Bank, 3.8 kg on western Scotian Shelf, and 2.0 kg on the eastern Scotian Shelf (Fig. 5). Size-at-age gradients coincide with warmer, near-bottom water con-

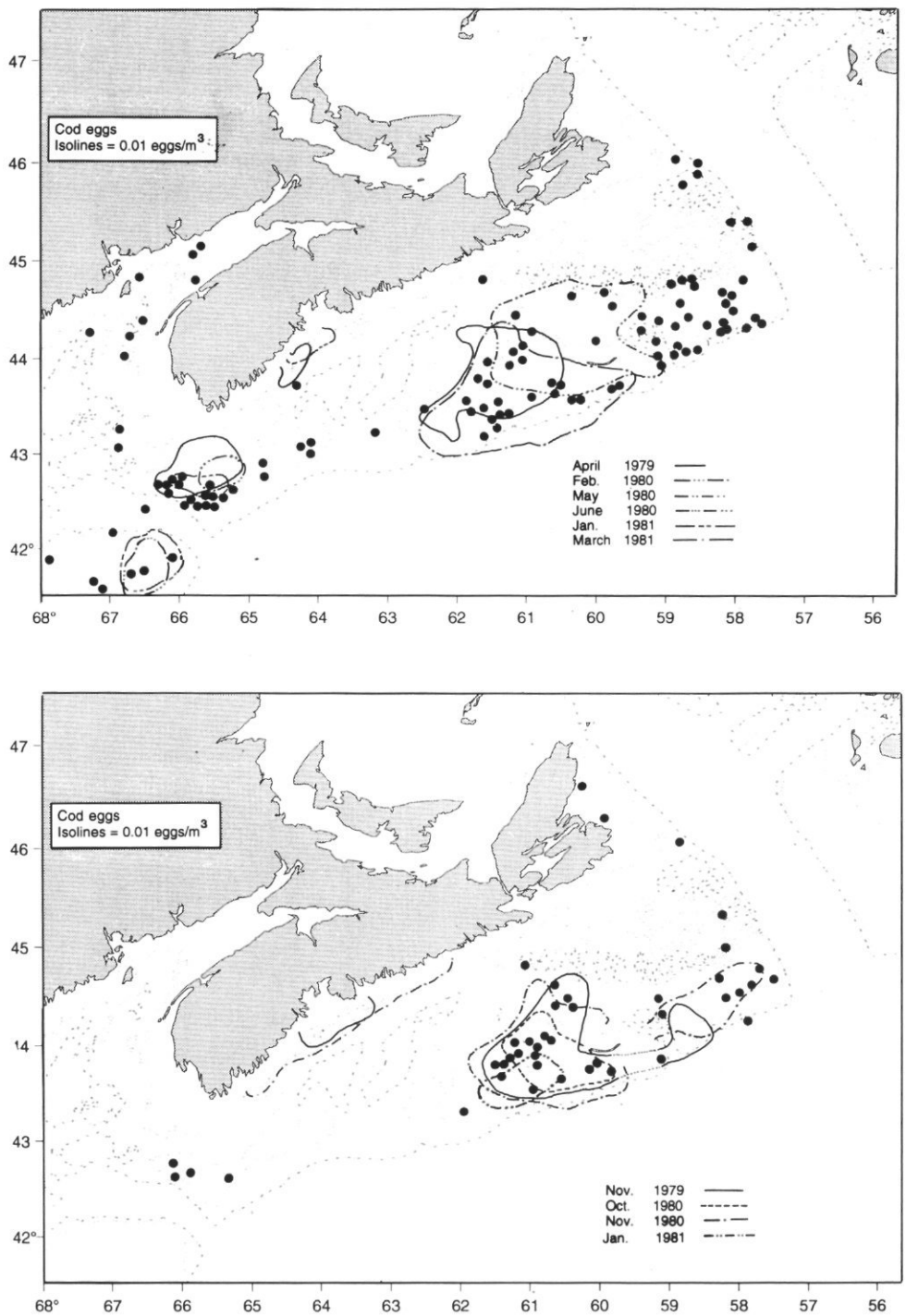


Figure 2. Isolines of cod egg concentrations equivalent to 0.01 eggs per m^3 from ichythyoplankton surveys conducted in the Scotian Shelf region. Cod eggs were stage IV, which corresponds to the time when the embryo begins to show a characteristic pigment pattern (about 16 days old at 4°C). Black dots show locations of cod in a ripe or spawning condition collected during spring and fall research vessel bottom-trawl surveys, 1979–1984. Top panel shows spring and bottom panel shows fall period.

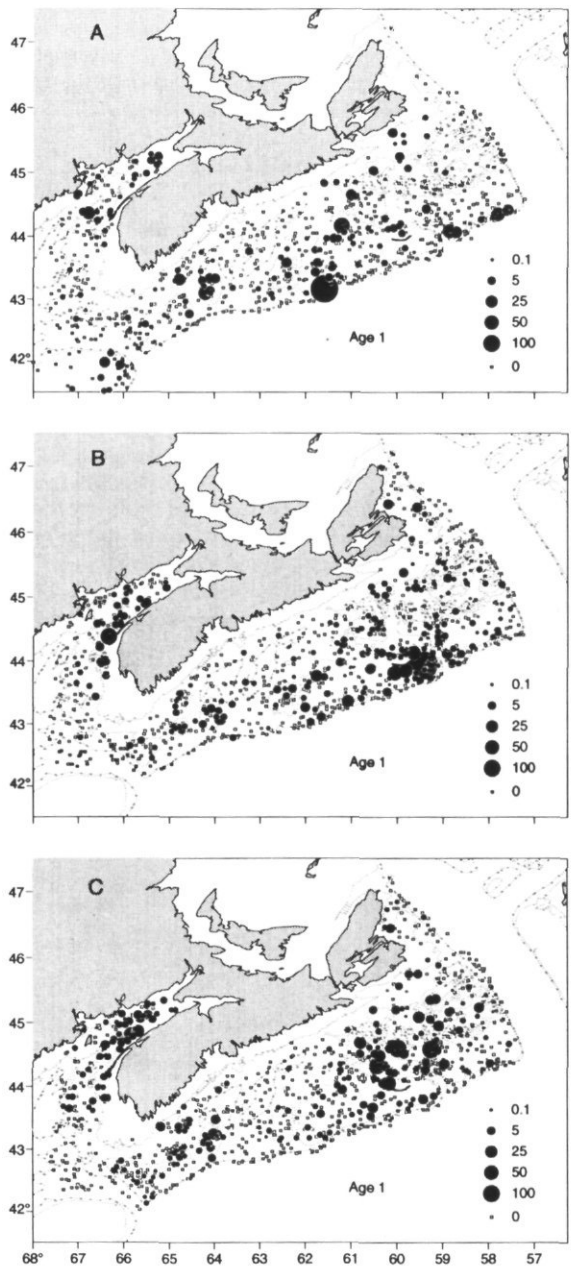


Figure 3. Distribution of juvenile cod (age 1 numbers/standard tow) from trawl surveys conducted during (A) spring (February–April), (B) summer (July), and (C) fall (October–December), 1979–1984, in the region of the Scotian Shelf. Note: summer and fall surveys did not include Georges Bank.

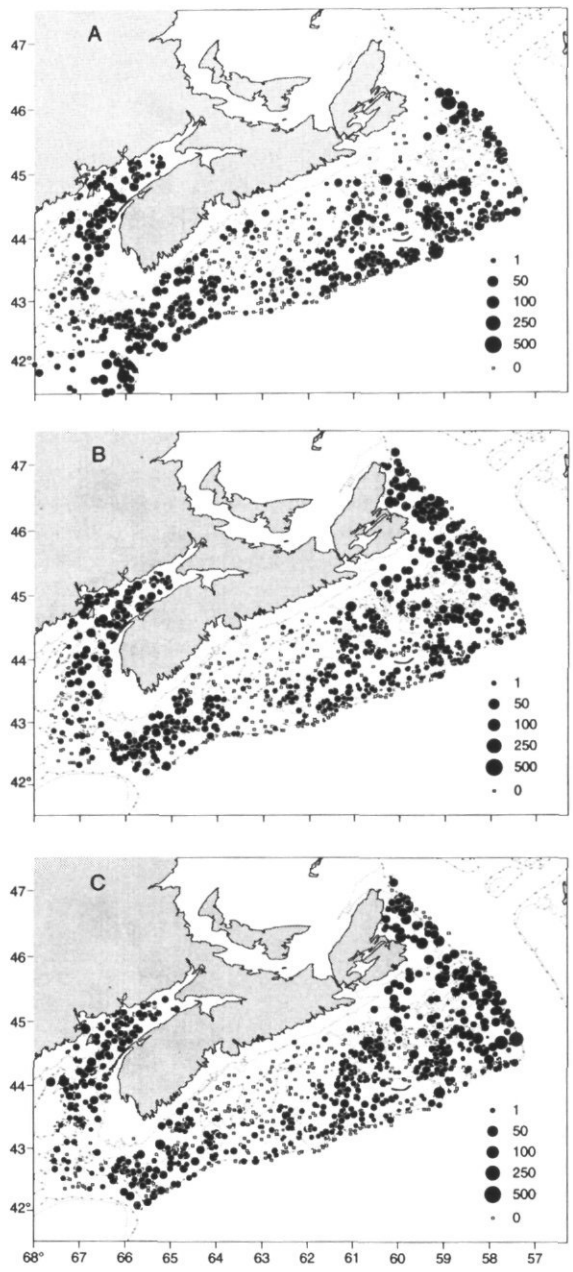


Figure 4. Distribution of adult cod (numbers/standard tow) from trawl surveys conducted during (A) spring (February–April), (B) summer (July), and (C) fall (October–December), 1979–1984, in the Scotian Shelf/Gulf of Maine region. In NAFO Division 4X and 5Z, age 3+ numbers are shown and in Division 4VW, age 6+ numbers are shown. Note: summer and fall surveys did not include Georges Bank.

ditions in the west relative to the east, with temperature differences ranging from 3 to 6°C in any month throughout the year (Fig. 5). Such growth differences have obvious implications for the fisheries exploiting these stocks. Weights-at-age have been declining since the early 1980s on the eastern Scotian Shelf and since the late 1980s on Georges Bank. No temporal trend was

evident from the western Scotian Shelf stock (Fig. 5). It is of interest to note that temperatures have been declining on the eastern half of the Scotian Shelf since the mid-1980s (Page and Losier, 1994) and near-bottom temperatures measured during the summer trawl surveys during 1970–1992 explain a significant proportion of the total variability in ESS age 6 cod weight ($r^2 = 0.36$, $n = 23$).

The fishery

Eastern Scotian Shelf

The Eastern Scotian Shelf cod is the most productive stock in the region with average landings in excess of 50 000 mt, an amount exceeding all other stocks in the region by two–threefold. Total landings ranged from 40 000 to 80 000 t in the years 1958 to 1974 and then declined rapidly to a low of 10 000 t in 1977 (Fig. 6). With the extension of jurisdiction to 200 miles in 1977, catches rose quickly and were above 50 000 t from 1980 to 1986. Recent landings have since declined to near historical low levels (Fig. 6). Foreign landings (dominated by Spain) were generally in excess of 40 000 t during the 1960s. However, since 1977 the foreign catch has only once exceeded 1000 t. Otter trawl catches typically account for 70% of the catch, with the remainder generated by longline, seines, and gillnets. Age 7+ contribute, on average, about 25% to the annual landings, with ages 3 to 5 making up about 50%. Estimates of annual fishing mortalities range from 0.22 to 1.56 with an indication of a temporal increase in F since the mid-1980s (Fig. 7). Recent fishing mortalities have been substantially in excess of their long-term mean (0.6) and above the targets established ($F_{0.1} = 0.2$). These have contributed to near historic low levels of spawning-stock biomass (SSB).

Western Scotian Shelf

On the western Scotian Shelf landings have averaged 22 000 t between 1948 and 1992 with peak landings in 1968, 1982, and 1991 (Fig. 6). The 1968 peak of 36 000 t was associated with large numbers of Canadian and foreign offshore trawlers that commenced fishing in this region in 1962. Unlike the cod fishery in the east, Canadian landings have generally dominated (74–100%) and there has been a roughly equal split between otter trawler and longline catches. Historically, the stock has been primarily exploited by an inshore fleet with less than 3000 t coming from the offshore grounds during 1947–1961. On average, less than 10% of age 7+ fish contribute to the annual landings compared to age 3 to 5, which generally make up 75% of the catch. Fishing mortalities have been estimated to range from 0.28 to 0.71 (Fig. 7). This relatively high fishing mortality, combined with high growth rates and a heavy dependence on incoming recruitment, cause the stock to be subject to rapid changes in abundance.

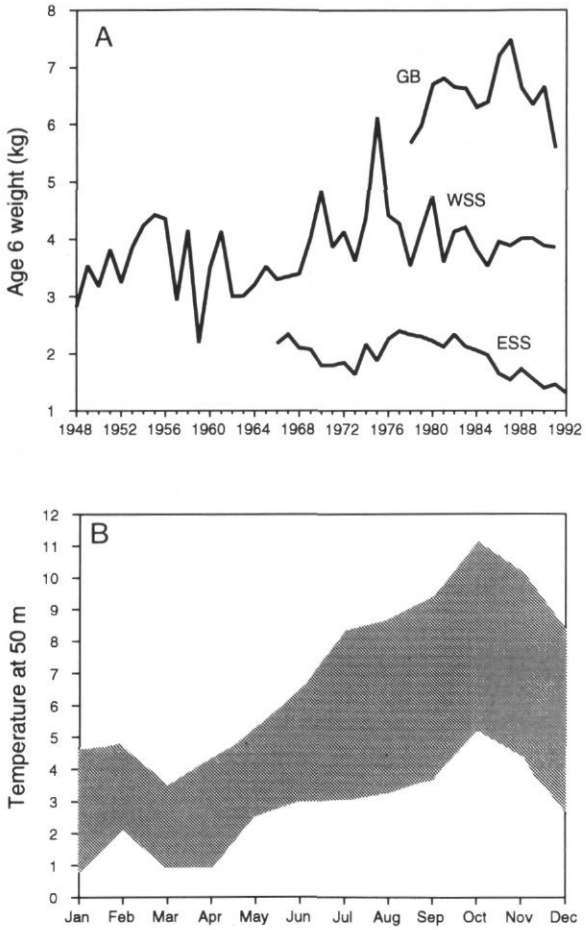


Figure 5. (A) Weight-at-age 6 from commercial samples of cod collected on Georges Bank, western Scotian Shelf, and eastern Scotian Shelf. These data were taken from analytical assessments of cod by Hunt and Buzeta (1992), Campana and Hamel (1992), and Mohn and MacEachern (1992). (B) Near-bottom, monthly mean temperature envelope representative of the offshore banks in the Scotian Shelf region based on data collected between 1910 and 1982 (Drinkwater and Trites, 1987). Upper bound represents conditions on Georges Bank; lower bound represents conditions on Banquereau Bank.

Georges Bank

Cod are taken by both Canada and the United States on Georges Bank. Total landings have averaged 17 000 t between 1978 and 1992, with a peak of 26 000 t in 1982 (Fig. 6). Since 1988 landings have averaged about 18 000 t. Otter trawl catch typically accounts for 60–70% of the

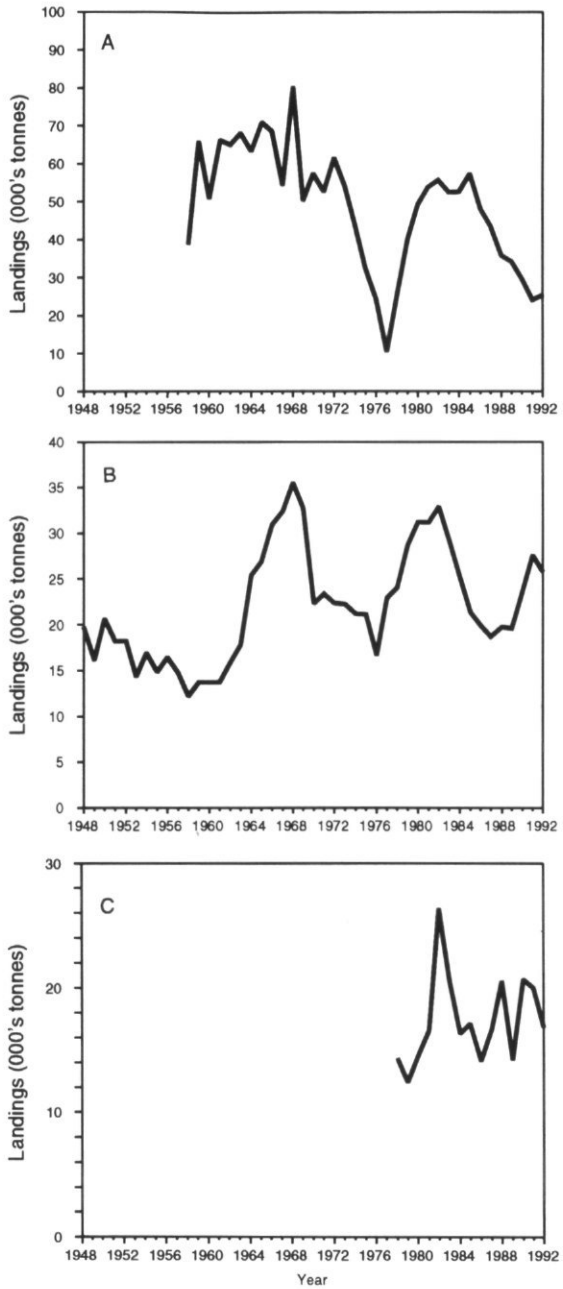


Figure 6. Total commercial landings of cod from the (A) eastern and (B) western Scotian Shelf, and (C) Georges Bank. Data sources same as indicated in legend for Figure 5A.

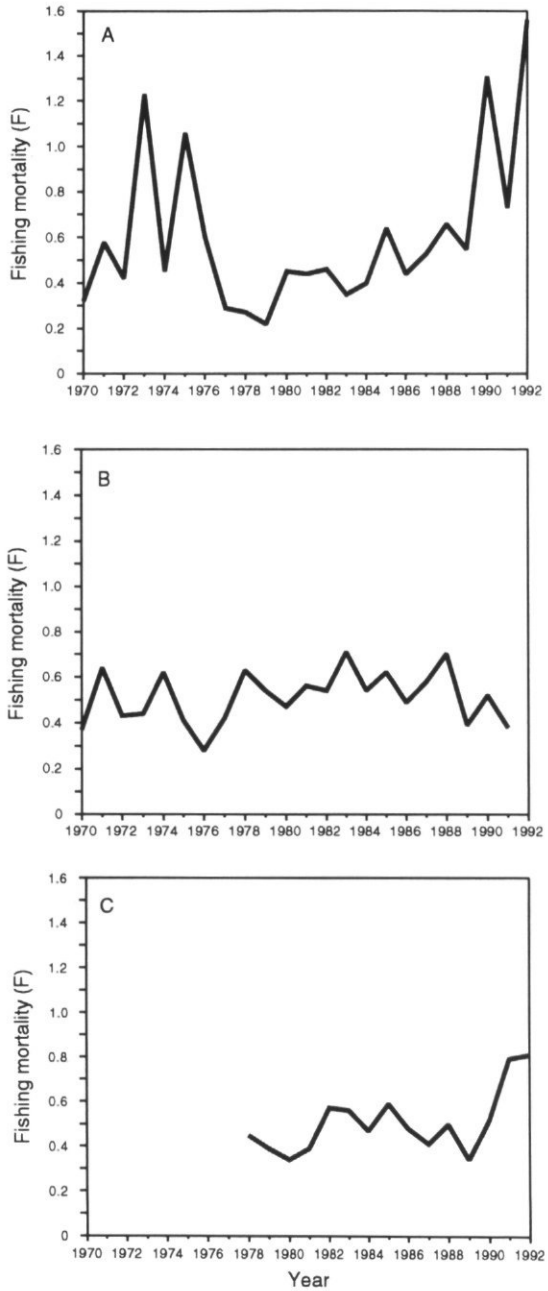


Figure 7. Trends in fishing mortality (F) for fully recruited ages of cod on the (A) eastern and (B) western Scotian Shelf, and (C) Georges Bank. Data sources same as indicated in legend for Figure 5A.

Canadian catch and Canada has taken about 65% of the combined (total) landings since 1984. Canada and the United States are the only countries to report catches of Georges Bank cod since 1987, but prior to 1987, there were substantial catches by the USSR and Portugal.

Sampling of the commercial landings was inadequate before 1978 to allow estimation of the catch-at-age, and discarding has further complicated attempts at catch reconstruction. The age composition of the catch re-

flects the very rapid growth rate (and high exploitation) characteristic of Georges Bank cod with ages 3 to 5, ages 1 and 2, and ages 7+ contributing, on average, 70%, 20%, and 4% to the annual landings, respectively. Similar to the western Scotian Shelf, Georges Bank is very much a recruitment-dependent fishery and hence subject to rapid changes in stock abundance. Estimates of annual fishing mortalities have averaged 0.51 (range 0.34–0.81) between 1970 and 1992, with recent estimates well above the long-term mean (Fig. 7).

Stock and recruitment

Since 1970, spawning-stock biomass has averaged 58 000 t, 63 000 t, and 42 000 t for cod on the eastern Scotian Shelf, western Scotian Shelf, and Georges Bank, respectively (Fig. 8). On the eastern Shelf, decreased exploitation during the mid-1980s and recruitment of the strong 1977–1980 year classes resulted in a peak in SSB (100 000 t) during the 1980s. Strong year classes were produced during the 1970s coincident with low SSB, with a reversal of this situation occurring in the 1980s (Fig. 8). In recent times both recruitment and SSB (<20 000 t) are at the lowest levels ever observed on the eastern Scotian Shelf. On the western Scotian Shelf, the SSB has fluctuated between 40 000 and 80 000 t since 1970 and is currently near its lowest level. Recruitment also appears to be independent of SSB (Fig. 8). The current SSB of Georges Bank cod is the lowest observed in time series, which began in 1978 and, as seen in the other stocks examined, recruitment is largely independent of SSB in all but the most recent years of observation.

Long-term mean recruitment levels differ considerably among the three stocks, with average recruitment estimated at age 1 of 64, 21, and 9 million fish for the eastern, western, and Georges Bank cod stocks. The magnitude of the difference in mean recruitment among the three stocks was surprising given the roughly similar mean spawning-stock levels. This difference appears largely due to events that occurred during the mid-1970s and early 1980s, when survival rates (recruitment/SSB) were exceptionally high in the east (Fig. 9). Since the mid-1980s survival rates have been similar among the three stocks.

It is also noteworthy that in the past recruitment of eastern Scotian Shelf cod was strongly correlated with river discharge (Drinkwater, 1987). In this case river discharge (or RIVSUM) represents the combined runoff from the St Lawrence, Saguenay, and Ottawa rivers, whose effects have been traced onto the Scotian Shelf (Sutcliffe *et al.*, 1976). High recruitment was associated with low annual runoff during the birth year (i.e. zero lag). Re-analysis of the data for the 1957 to 1979 year

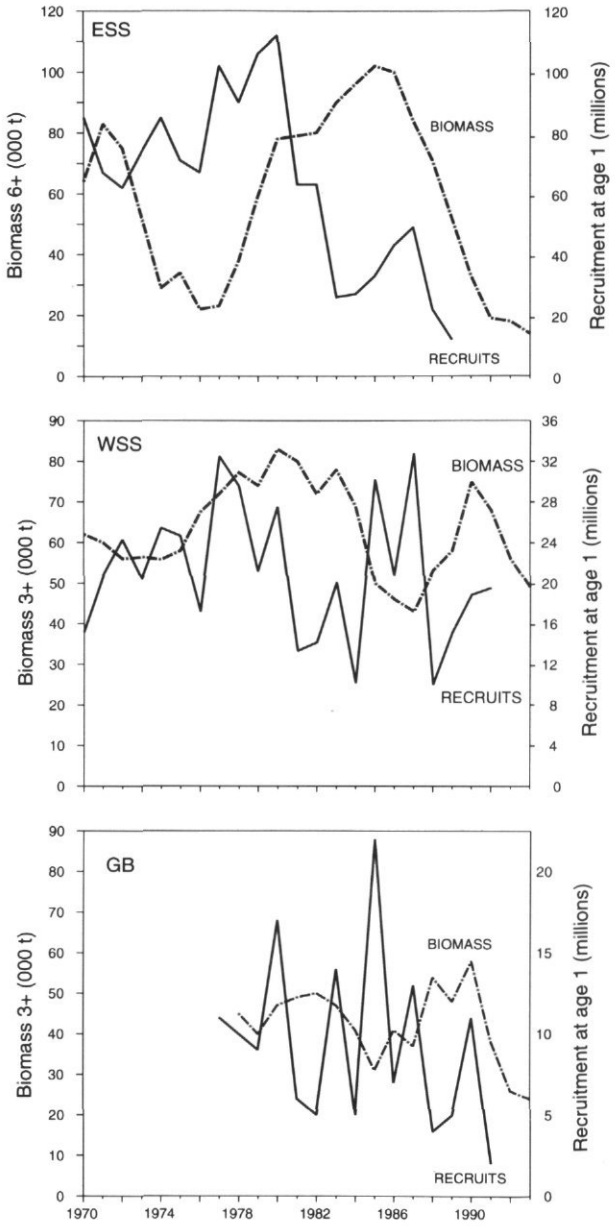


Figure 8. Trends in spawning-stock biomass and recruitment for the Scotian Shelf and Georges Bank cod stocks. Data sources same as indicated in legend for Figure 5A.

classes confirmed the relationship between recruitment and RIVSUM ($r = -0.77$, $n = 23$). Recruitment data for the subsequent 10 years were poorly predicted by RIVSUM, despite the fact that RIVSUM was within the historical range of observations (Fig. 10). The relationship between recruitment and RIVSUM for the entire time series was weak ($r = -0.47$, $n = 33$). The failed

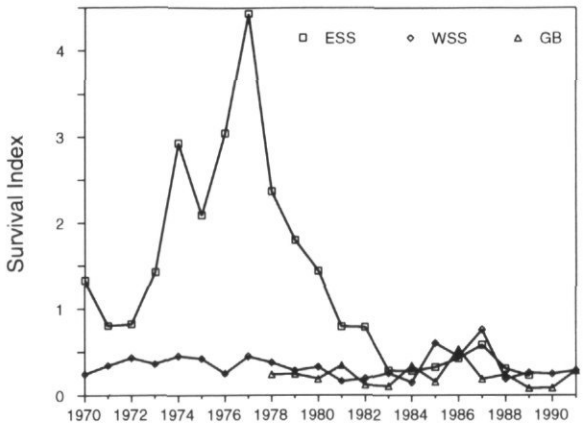


Figure 9. Survival index for each of the three cod stocks expressed as year-class size at age 1 divided by the spawning-stock biomass.

environmental correlation in eastern Scotian Shelf cod with the addition of recruitment data from 1980 onward, when year-class survival per unit of SSB was quite low and when environmental variability (as measured by RIVSUM) was well within the range of historical observations, suggests that intrinsic changes in production dynamics of the stock has occurred. It is also possible that other environmental factors have influenced the post-1980 recruitment pattern that were ineffective (at least compared to RIVSUM) prior to 1980.

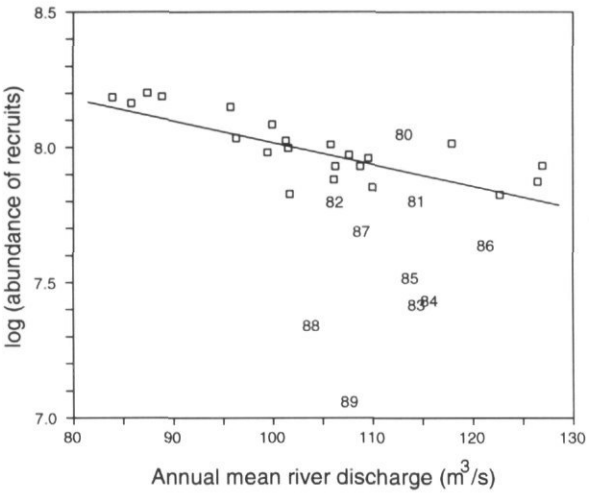


Figure 10. Relationship between recruitment (log transformed) for the 1957–1979 year classes of cod on the eastern Scotian Shelf based on VPA estimates from Mohn and MacEachern (1992) and the annual estimate of the combined runoff from the St Lawrence, Saguenay, and Ottawa rivers denoted as RIVSUM. The 1980–1989 year classes were omitted from the regression analysis and are shown (last two digits centred on estimate) to illustrate the failure of the relationship in recent times.

Eastern Scotian Shelf cod: causes of decline

Recent results of ichthyoplankton surveys conducted monthly on the eastern Scotian Shelf by the Ocean Production Enhancement Network (OPEN) suggest that there has been a change in the reproductive pattern of cod during the period in question (Miller *et al.*, submitted). Comparing the monthly occurrence of cod larvae from two time periods, during the conduct of SSIP (1977–1982) and OPEN (1991–1993), revealed a dramatic change in the spawning pattern. During SSIP, near equal production of cod larvae occurred during spring (45% of annual total) and late fall–early winter (52%; also see Brander and Hurley, 1992). The temporal pattern based on the OPEN surveys now shows an apparent concentration of cod larval production in the late fall–early winter period (>90%). It appears that spring spawning has all but ceased or that cod larval survival during springtime has been greatly reduced. Although it is difficult to determine which of these alternatives is correct, failure of the RIVSUM recruitment prediction is inconsistent with the poor springtime larval survival hypothesis. We may, however, be able to establish the time of this shift in the reproductive pattern.

For this we examine the temporal variation in length-at-age 1 (l_1) from the standard trawl surveys conducted during July on the Scotian Shelf. For any given year class, if survivors from the spring spawning of the previous year dominate, then l_1 should be relatively high because the fish are 15 months old. Conversely, if survivors from the fall spawning of the previous year dominate, then a low l_1 is expected because the fish are only 9 months old (Fig. 11). We therefore consider variation in l_1 as an index of spawning time. Because only spring spawning occurs on the western Scotian Shelf, l_1 measured in July provides an approximate length of an age 1 cod spawned during the spring of the previous year.

The l_1 time series for the eastern and western Scotian Shelf cod stocks were similar up to the mid-1980s, with an average length difference of about 2 cm (Fig. 11). This suggests that spring spawning on the eastern Scotian Shelf was making most of the contribution to annual recruitment. After this time period, the two length series diverged greatly with progressively smaller sizes evident among the eastern Scotian Shelf cod (Fig. 11). This situation apparently reflects the dominance of fall spawned survivors among these year classes. The timing of the shift in the reproduction pattern that occurred in

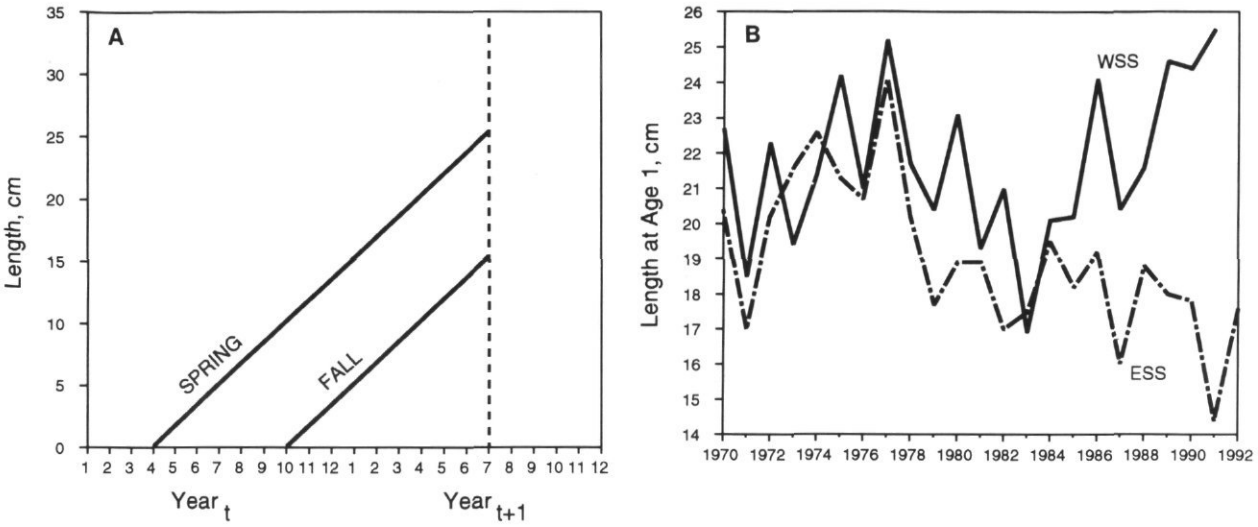


Figure 11. (A) A schematic to illustrate the use of l_1 as an index of spawning time. $Year_t$ is the birth year and growth is assumed to be constant. (B) Average length of age 1 cod from annual research vessel surveys conducted during July on the Scotian Shelf, 1970–1992.

the mid-1980s coincides closely with the recent period of low recruitment. In fact, the below average year classes were generally associated with low age 1 lengths, while strong year classes frequently coincided with high age 1 lengths (Fig. 12).

The last piece of information considered is the distribution of effort by the fishing fleet, which may give insights into cod distribution during the spring fishery on the eastern Scotian Shelf. It has been noted by Mohn and MacEachern (1992) that a dramatic change in the distribution of the fishery occurred during the first 4 months of the year between 1981 and 1991. In 1981, vessels fishing for cod were widely distributed over the shelf and in the vicinity of most of the offshore banks. In 1991, almost no vessels were fishing on the offshore banks and virtually all of the effort was directed along the slope of the Laurentian Channel. Further analysis of this situation on a year-by-year basis (Mohn, unpubl.) has revealed that almost no fleet activity occurred in the vicinity of Middle Bank and only sporadic activity existed on Sable Island Bank during the spring-spawning period from 1986 to 1992.

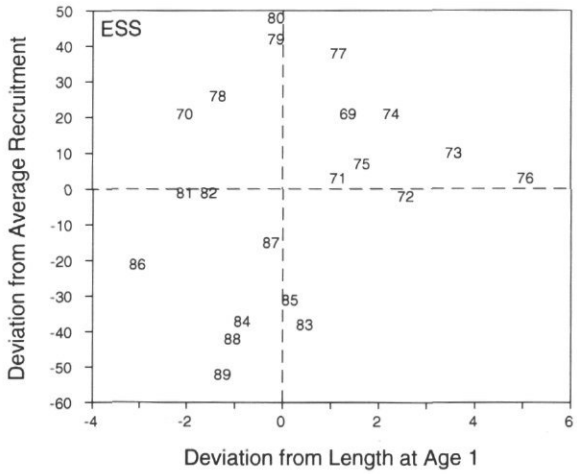


Figure 12. Relationship between recruitment anomalies and l_1 anomalies for the eastern Scotian Shelf cod stock. Two digit numbers show year class (centred on estimate).

Assuming that the fleet distribution reflects spawning concentrations, then these observations would suggest that around 1985 the spring-spawning component disappeared or became so low that it was not worth fishing. This suggestion is also consistent with the results of the analysis of the l_1 time series. Because it is largely unprecedented for marine fishes to change spawning locations from year to year, given the precise coupling between spatial processes and population structure (e.g. see Sinclair, 1988), we believe the evidence reviewed here suggests the loss of the spring-spawning component on the eastern Scotian Shelf. Such a loss could be due to over-fishing a discrete spawning component or a cross-over in spawning time from spring to fall due to changes in maturation rate as reported for herring by Winters *et al.* (1986). This latter hypothesis is supported, in part, by the declining weights-at-age that occurred during the past decade (Fig. 5) that correlate strongly with near-

bottom water temperatures. While the cause(s) of the recent decline remains unconfirmed, it remains to be seen whether or not historical levels of cod production can be achieved on the eastern Scotian Shelf with limited or no spring spawning.

Acknowledgments

We are grateful to the many individuals who have contributed to maintaining the research-vessel survey series and who have conducted the analytical assessments of cod on the Scotian Shelf and Georges Bank. J. Simon assisted in many important technical ways as usual. We also thank Dr R. J. M. Beverton and Jean-Jacques Maguire for many helpful suggestions on the manuscript.

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Fluctuations in the cod stocks of the Gulf of St Lawrence

Ghislain A. Chouinard and Alain Fréchet

Chouinard, G. A., and Fréchet, A. 1994. Fluctuations in the cod stocks of the Gulf of St Lawrence – ICES mar. Sci. Symp., 198: 121–139.

The Gulf of St Lawrence is a semi-enclosed sea connected to the Northwest Atlantic Ocean by the Strait of Belle Isle and Cabot Strait. Two Atlantic cod stocks (*Gadus morhua*) inhabit the area; the southern (NAFO 4T-Vn (Jan.–Apr.)) and northern (NAFO 3Pn,4RS) Gulf of St Lawrence stocks. Catches since 1960 have averaged 54 000 t and 76 000 t, respectively. In recent years about 80% of the landings were made by otter trawls and seines. For both stocks, abundance was low in the mid-1970s and in recent years, and was highest in the early 1980s. Landings, abundance, and recruitment trends between the two stocks are relatively similar. Production for both stocks has been low in recent years. Although fishing mortality has fluctuated over the time periods examined, abundance changes appear to be related more to recruitment fluctuations. An index of survival calculated as the ratio of recruitment numbers to parental biomass indicates that, for both stocks, lower levels of spawning biomass in the 1970s produced good recruitment, while the number of recruits produced from the large spawning biomass of the early 1980s was low. Although the lower index of survival in the 1980s corresponds with a period of colder conditions (greater ice extent, lower water temperatures), there is little correlation when the entire time period is examined. The index of survival was weakly correlated with freshwater discharge in the southern Gulf. Until factors influencing survival are more clearly understood, direct estimates of pre-recruit abundance are likely to be more helpful in predicting short-term stock trends.

Le Golfe du St Laurent est une mer semi-fermée, reliée à l'Atlantique nord-ouest par le Détroit de Belle-Isle et le Détroit de Cabot. Deux stocks de morue (*Gadus morhua*) habitent cette zone: le stock du sud du Golfe du St Laurent (OPANO 4T-Vn (jan-avr)) ainsi que celui du nord (OPANO 3Pn,4RS). Les prises moyennes depuis 1960 sur ces stocks ont été de 54 000 t et de 76 000 t respectivement. Au cours des dernières années, plus de 80% des débarquements ont été réalisés par les chalutiers et les senneurs. Pour les deux stocks, l'abondance était basse dans le milieu des années 1970 et au cours des dernières années. Les stocks étaient des plus abondants au début des années 1980. Les tendances des débarquements, de l'abondance et du recrutement sont relativement similaires entre les deux stocks. La production des deux stocks a été basse au cours des dernières années. Malgré les fluctuations dans le recrutement, les variations de l'abondance semblent être reliées principalement aux fluctuations du recrutement. Un indice de survie (rapport recrutement-biomasse parentale) indique que pour les deux stocks, des niveaux moins élevés de biomasse parentale ont donné lieu à un bon recrutement. Le nombre de recrues produites de la biomasse parentale élevée du début des années 1980 a été faible. Malgré que l'indice de survie faible des années 1980 correspond à une période plus froide (plus grande étendue de glace, température de l'eau plus froide), il n'existe pas de corrélation lorsqu'on examine les données sur la période entière. L'indice de survie était cependant faiblement relié à la décharge en eau douce dans le sud du Golfe. Tant que les facteurs influençant la survie ne seront pas mieux compris, des estimations directes de l'abondance des pré-recrues seront plus utiles pour prédire les trajectoires de ces stocks à court terme.

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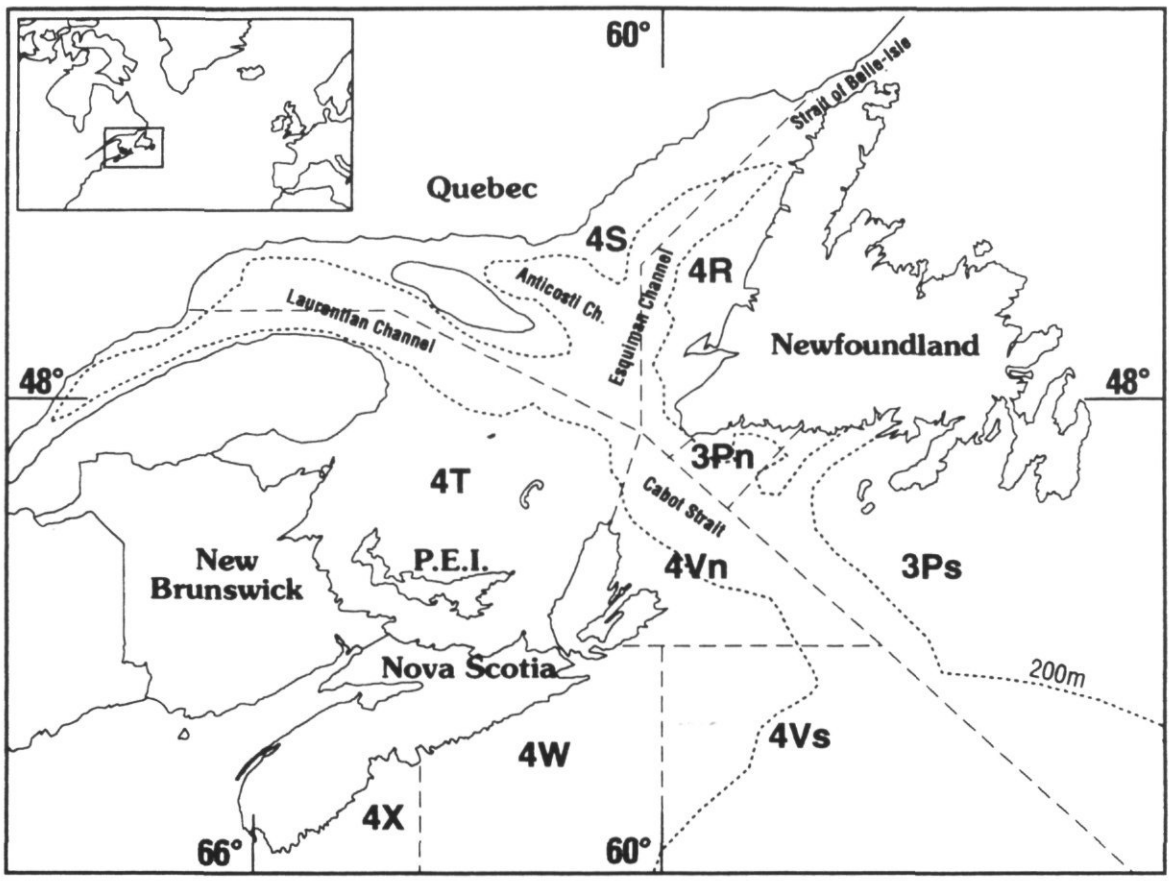


Figure 1. Map of the Gulf of St Lawrence showing some of the physical features and the Northwest Atlantic Fisheries Organization (NAFO) Divisions in the area.

Introduction

Located on the eastern coast of Canada, between 45° and 52°N, the Gulf of St Lawrence (Fig. 1) is a marginal sea of the Northwestern Atlantic. This area is divided into three Divisions of the Northwest Atlantic Fisheries Organization (NAFO): 4R and 4S in the north and 4T in the south. The area of Cabot Strait at the southern entrance to the Gulf of St Lawrence forms NAFO unit areas 3Pn and 4Vn.

The cod fisheries of the Gulf of St Lawrence exploit two different stocks of *Gadus morhua*: a northern stock and a southern stock, commonly referred to as the 3Pn, 4RS and the 4T-Vn (Jan.–April) cod stocks, respectively. Both stocks undergo an extensive annual migration (Halliday and Pinhorn, 1982). In summer, the southern stock is found in Division 4T while the northern stock is found in Divisions 4R and 4S. During the late fall, both stocks migrate outside the Gulf of St Lawrence to Cabot Strait, where they overwinter. It is thought that mixing of the water in the fall generates very cold waters from the surface down to over 150 m which contributes to the displacement of cod to deeper waters in winter (Fréchet, 1990). The northern Gulf cod stock moves to area 3Pn, while the southern stock migrates to 4Vn. The migrations are thought to extend farther south (areas 3Ps and 4Vs) from time to time. In the spring, as ice drifts out of the Gulf of St Lawrence, the two stocks return to their spawning and feeding grounds in the Gulf.

The northern and southern Gulf cod stocks are relatively well segregated. Numerous tagging studies show little mixing between the two (McCracken, 1958; Martin, 1962; Templeman, 1979). More recently, a study of 17 sites in the northern part of the Gulf showed that, with the exception of one site at 10%, less than 3% of the recaptures were made within the boundaries of the southern stock (Gascon *et al.*, 1990). Both stocks are slow-growing and late-maturing compared to others, such as the North Sea or the Georges Bank stocks.

The Gulf of St Lawrence has a surface of approximately 230 000 km^2, which makes it about the same size as the Persian Gulf or about 2.5 times smaller than the North Sea. The Gulf of St Lawrence is connected to the Atlantic Ocean by Cabot Strait to the south and by the Strait of Belle Isle to the north. It is bisected by the Laurentian Channel. The area south of the Laurentian Channel is relatively shallow and flat with depths seldom exceeding 75 m, while the area to the north is typified by two deep channels (Anticosti and Esquiman) with depths of 200 to 500 m. In the central southern Gulf and along the north coast in the northern Gulf, bedrock is at or near the surface (Loring and Nota, 1973).

One of the characteristics of the Gulf of St Lawrence is that it receives over half of its total freshwater input (~600 km^3 per year) from a single source; the St Lawrence River. This large discharge is a major driving element of water circulation in the area (Strain, 1988), particularly over the southern Gulf. The deeper waters of the Laurentian Channel and the northern Gulf are influenced by an inflow of the inshore branch of the Labrador Current through the Belle Isle and Cabot straits.

The area is subject to large annual variations in temperature. The Gulf of St Lawrence is covered by ice in winter. Ice formation starts in December–January, reaches its largest coverage by March, then recedes and has usually disappeared by May (June in the northernmost areas). As the ice cover expands from the northwest to the southeast, considerable mixing (upwelling, jets, etc.) occurs at the ice edge (Fréchet, 1990). A permanent feature of the Gulf of St Lawrence is a mass of cold water (<0°C) between 70 and 90 m. During summer, surface waters can reach 15–20°C. Salinity in the area ranges from about 27 to 35 ppm.

In terms of economic returns and employment, the crustacean fisheries [lobster (*Homarus americanus*), snow crab (*Chionoecetes opilio*), and shrimp (*Pandalus borealis*)] are the most important in the Gulf of St Lawrence. However, in terms of landings, the cod fisheries of the Gulf of St Lawrence are the most significant, averaging 130 000 t per year since 1960. Other commercial marine fisheries of importance include herring (*Clupea harengus*), redfish (*Sebastes* spp.) and various flatfish species. Chadwick and Sinclair (1991) concluded that fisheries production in the Gulf of St Lawrence was comparable to other coastal areas of similar size.

This article describes the cod fisheries in the Gulf of St Lawrence, their trends, the fluctuations in the abundance of the stocks that support them, and the variation in the environment to which they are exposed. Causes of fluctuations in these stocks in the last 20 years and the relationship to the environment are examined.

The cod fisheries of the Gulf of St Lawrence

The two cod stocks have been exploited by man, to some extent at least, since the 16th century voyage of the French explorer Jacques Cartier to the Gulf of St Lawrence. During that century, French fishermen regularly embarked on fishing expeditions to the Gulf of St Lawrence and adjacent areas (de la Morandière, 1962; de la Villemarqué, 1990). In this century, prior to the mid-1950s and early 1960s, landings statistics for these two cod stocks are less reliable because landings were reported by port of landing as opposed to area fished. Given the migratory nature of these stocks, the computation of these landings statistics requires that assumptions be made as to the fishing grounds. With the creation of the International Commission for the Northwest Atlantic Fisheries (ICNAF), the precursor of NAFO, in the early 1950s, and the progressive improvement in the understanding of the migrations of these stocks, reporting of landings statistics was refined for the needs of tracking abundance of stocks (Halliday and Pinhorn, 1990). As a result, reliable landing statistics for the northern stock are only available from about 1960 (Fréchet and Gagnon, 1993). Landings statistics for the southern Gulf stock were obtained from annual fisheries statistics bulletins for the period 1920–1949 (Anon., 1920–1949) and from Chouinard *et al.* (1992) and Sinclair (1993) since then. Statistics for the period 1920–1950 do not include French catches; however, there are no indications that these may have been substantial.

Although otter trawlers and other types of "mobile gears" were being used widely in the waters of the East Atlantic, the cod fisheries exploiting the Gulf of St Lawrence stocks were mostly being conducted by hook-and-line between 1920 and the late 1940s. This was due to a limit on the number of trawlers imposed when fixed-gear fishermen voiced concerns over the effect of trawling on fisheries resources (Parsons, 1993).

As for most other demersal fisheries in the Northwest Atlantic, management was largely done by setting minimum mesh size regulations until 1974, when ICNAF introduced total allowable catches (TACs). The general decline in groundfish resources prompted the declaration of extended jurisdiction by Canada in 1977 and the exclusion of all non-Canadian fleets from the fishery for these stocks, with the exception of France.

In recent years, the management schemes for these resources have become increasingly complex, with the TAC divided between the various fleets based on historical performance. A system of enterprise allocations [also called individual transferable quota (ITQ)] was implemented for some fleets in 1983 in the northern Gulf and in 1988 for the southern Gulf. Late in 1992, fleets

were required to submit conservation plans before they were allowed to fish.

Northern Gulf of St Lawrence

A description of the fishery in the 1950s in NAFO 4R and 4S is given in Wiles and May (1968). In the early 1960s, landings ranged up to 100 000 t, then fluctuated around 80 000 t per year (Fig. 2). Landings peaked at 105 000 t in 1970, then progressively declined to 60 000 t in 1975. Subsequently, landings increased to attain the high levels of the early 1960s in the period 1982–1984. Since then, landings have steadily declined and have been about 30 000 t in 1991 and 1992. Until 1977, the stock was exploited by Canada, France (metropolitan and Saint Pierre and Miquelon), Portugal, and Spain; only France was allowed to continue after extended jurisdiction. The stock is exploited by all adjacent Canadian provinces (Québec, the Maritime provinces and Newfoundland). Prior to 1977, approximately half of the landings were made by non-Canadian fleets; the proportion dropped and remained at less than 15% subsequently.

Two main gear sectors harvest the northern cod stock: the fixed (gillnets, long-lines, traps and hand-lines) and the mobile (otter trawls and seines). Landings from the

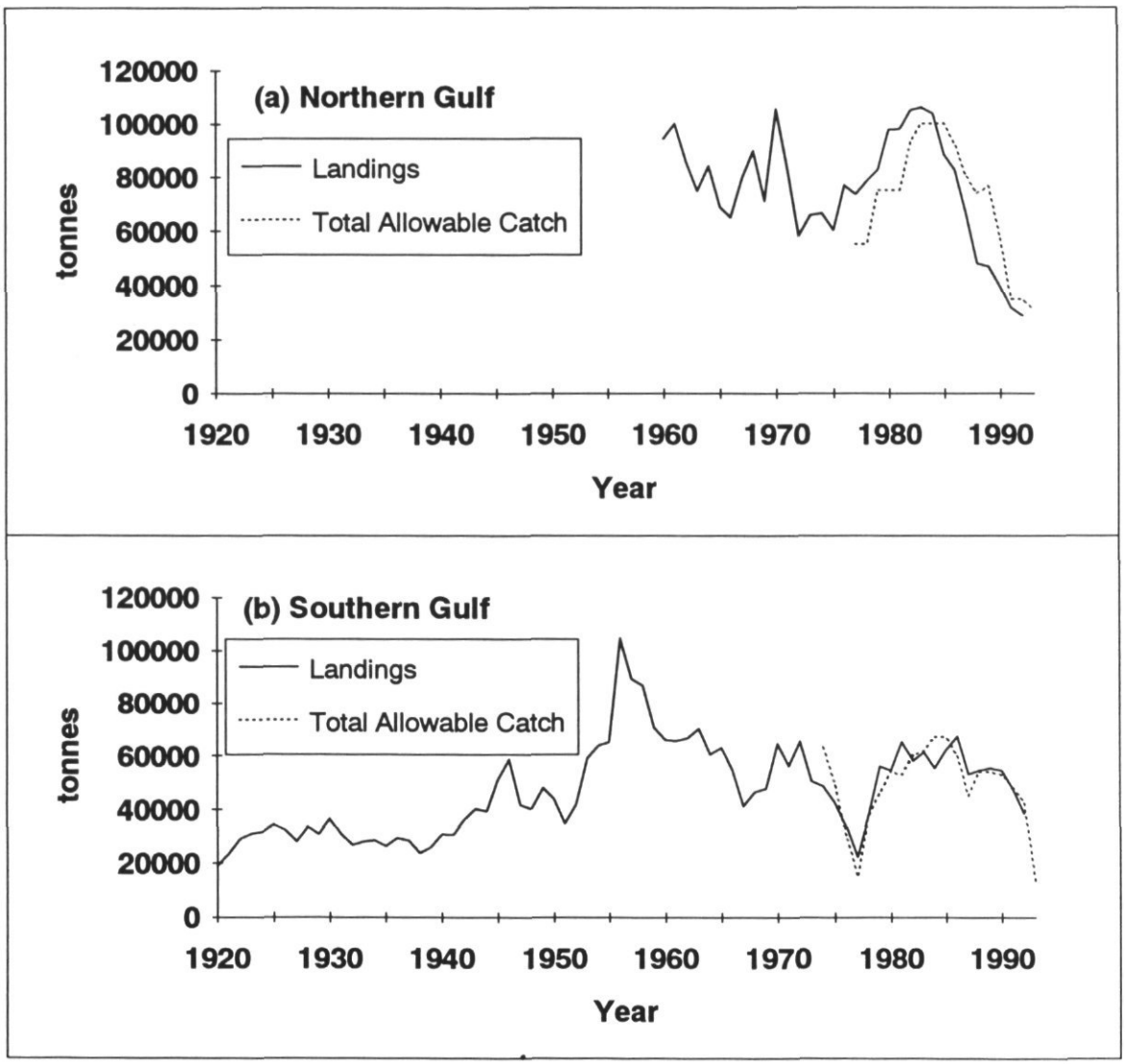


Figure 2. Landings and total allowable catch (TAC) for (a) the northern and (b) southern Gulf of St Lawrence cod stocks.

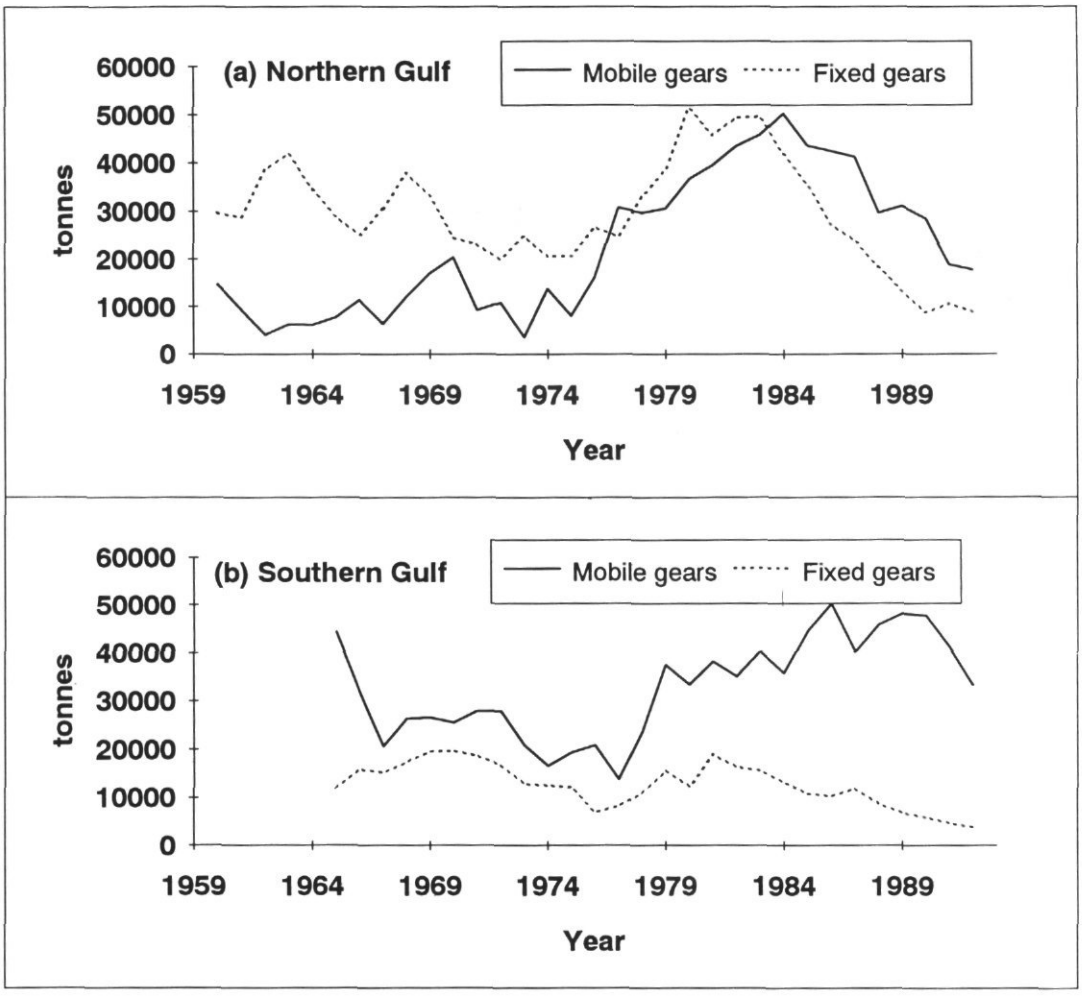


Figure 3. Landings of cod by gear type for (a) the northern and (b) southern cod stocks of the Gulf of St Lawrence. Mobile gears include otter trawls and seines, fixed gears include gillnets, hand-lines, long-lines, and traps.

fixed-gear sector have plummeted from 50 000 t to 9 000 t in the past decade (Fig. 3). Landings by gillnets and line gears accounted for over 80% of these landings. Landings by the mobile sector have also been reduced, through reduced TACs, from 62 000 t in 1984 to 20 000 t in 1992 (Fréchet and Gagnon, 1993).

The fishery is conducted year-round. In the winter, otter trawlers exploit the high concentrations of cod that are found in areas 3Pn and southern 4R. Catch rates are usually higher at that time of the year. The fishery is sometimes hampered by ice conditions. In recent years, fish concentrations have been found in much deeper waters than previously (Fréchet and Gagnon, 1991); in 1992, over 90% of the winter survey biomass was found in waters deeper than 360 m compared to less than 5% in the mid-1980s.

The summer fishery is prosecuted by a variety of gears with generally smaller vessels than in the winter fishery. In the northern reaches of the Gulf, the fishery often does not begin until mid to late June as ice leaves the area. Generally, over 70% of the landings are made between May and December. Fixed gears account for the majority of the catches from June to September. Rose and Leggett (1988) showed that catch rates of traps are particularly affected by winds that produce periodic upwelling.

Southern Gulf of St Lawrence

Between 1920 and 1945, landings from the southern Gulf stock varied between 20 000 and 50 000 t, averaging 31 000 t per year (Fig. 2). With the general expansion

in the fishery which occurred after 1945, landings increased and peaked at 104 000 t in 1956. The average yearly landings for 1946 to 1970 were twice those of the previous 25 years. Between 1960 and 1975 landings fluctuated between about 40 000 and 70 000 t, before declining to their historic low level of 22 000 t in 1977. Landings then increased to about 67 000 t by the mid-1980s. Since 1990, landings have declined and reached 39 000 t in 1992 (Sinclair, 1993). Landings have averaged over 50 000 t between 1971 and 1992.

Until the mid-1940s, the domestic fishery was almost entirely prosecuted with hook and line gears. Trawlers were introduced in the Gulf fishery in 1947, and in the early 1950s otter trawls became predominant. Fishing with gillnets started in the early 1960s (Halliday and Pinhorn, 1982). At about the same time, Danish and Scottish seines were introduced. Landings according to gear types are available since 1965. Since the early 1980s, catches using fixed gears (gillnets, long-lines, and hand-lines) have declined, attaining their lowest level ever in 1992 (Fig. 3). Many factors likely contribute to this decline, including smaller size-at-age of cod, a shift of some fishermen to the more efficient mobile gears and, in more recent years, the decline in the abundance of cod.

The winter fishery, which runs from January to April in 4Vn, is conducted primarily by larger trawlers (>30 m). In recent years, approximately 15% of the catch has been taken during the winter fishery. The fishery in NAFO 4T usually begins when most of the ice has left and cod are returning to the waters of the southern Gulf. This fishery is conducted by smaller vessels (10 to 20 m in overall length).

Concentrated fisheries with mobile gears occur in the spring and the fall in the eastern portion of the southern Gulf during the cod migration. Cod are found predominantly in the western portion of the southern Gulf during the months of June to September. Catchability is typically higher in the winter, spring, and fall. The fishery by fixed gears occurs primarily between June and October. This stock has been managed by quota since 1974. The TAC for 1993 was initially set at 13 000 t but the directed fishery was subsequently closed on 1 September 1993.

Trends in abundance, fishing mortality, recruitment, growth, and stock production

For these cod stocks, yearly assessment of the abundance of the populations has been conducted for several years, the most recent in May 1993 (Fréchet and Gagnon, 1993; Sinclair, 1993). Fishing mortality and abundance estimates are obtained from sequential population analysis (SPA) calibrated with annual groundfish surveys and, in the case of the southern Gulf of St Lawrence cod stock, otter trawl catch-rate-at-age. Natural mortality is set at a constant 0.2 over all age groups.

Northern Gulf of St Lawrence

Estimates of removals at age for this fishery are available only for the period since 1974. The assessment of the stock uses estimates of cod abundance at age from research vessel surveys conducted in January since 1978 to calibrate the SPA. The age aggregated index from the research survey is shown in Figure 4. Cod are recruited to the fishery at age 3.

The results of the assessment indicate that population abundance increased steadily from the mid-1970s to the early 1980s (Fig. 5). It then declined up to the late 1980s and appears to have stabilized in recent years. Total (age 3+) biomass has fallen from about 443 000 t in 1981 to 172 000 t in 1992, a reduction of 61% (Fig. 6). Adult (estimated as age 7+) biomass is estimated at 29 000 t in 1992, the lowest level in the period 1974–1992 (Fig. 7). Fishing mortality (ages 7+) in 1992 is estimated to be 0.51 and has ranged between 0.4 and 0.6 over the time period (Fig. 8). Fishing mortality appears to have been on the increase in recent years. In terms of recruitment (age 3), large year classes were produced in 1974 and 1975, and again in 1979 and 1987 (Fig. 9).

While the decline in population abundance is about 50%, the decline in biomass is over 60%. This is in part due to the lower growth rates observed during the 1980s. As an example of the changes seen, the average weight of a cod of age 7 has declined by about 40% since the mid-1970s (Fig. 10). Reasons for this decline are not well understood.

Two year classes comprised 55% of the removals in 1992. These are the 1986 and 1987 year classes at ages 6 and 5 respectively in 1992. They are preceded and followed by below-average year classes. Given that the estimates of recruitment and biomass in recent years are low, it is likely that recovery of the spawning-stock biomass to average levels observed previously could take several years.

Southern Gulf of St Lawrence

SPA was calibrated using a research vessel index of abundance derived from the September groundfish survey of the southern Gulf of St Lawrence and catch rates at age from the otter trawl fishery. For this stock, retrospective patterns (i.e. the tendency of current assessments to consistently overestimate stock abundance) have been apparent in previous stock analyses (Sinclair *et al.*, 1991). However, methods used in the assessment of the stock in 1993 were successful in eliminating this tendency (see Sinclair 1993 for further details) and these are considered more reliable.

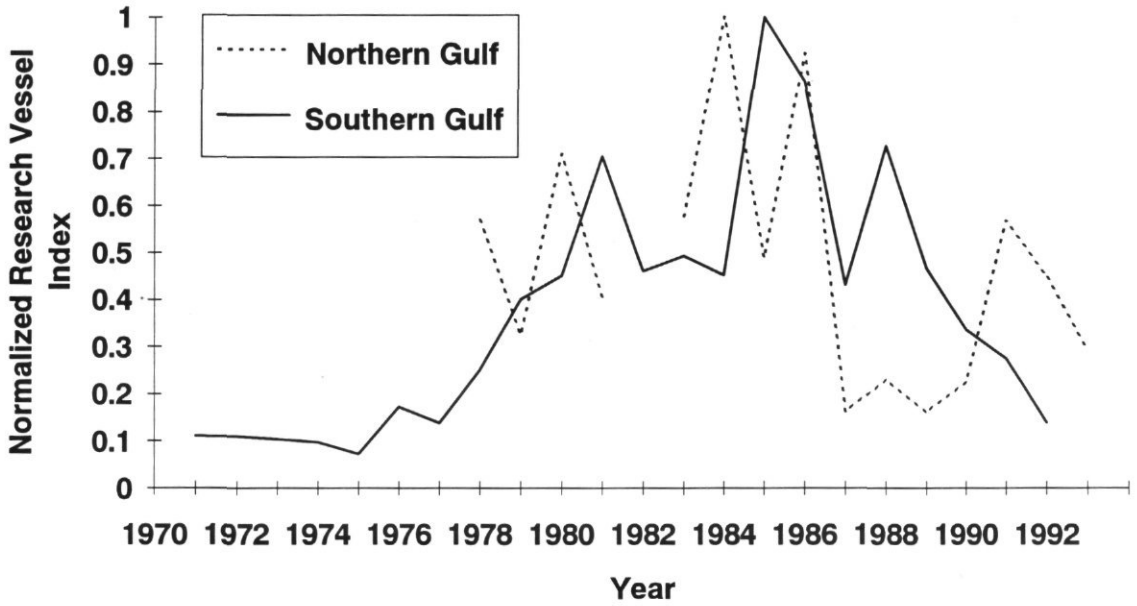


Figure 4. Normalized abundance indices derived from research vessel surveys in the Gulf of St Lawrence. Surveys are conducted in January in the northern Gulf and in September in the southern Gulf.

The research vessel survey abundance index (Chouinard *et al.*, 1992) (Fig. 4) shows that abundance was low in the mid-1970s, increased to the mid-1980s, and has been declining since 1985. Population abundance (Fig. 5) was high in the early 1950s. Given that average catches prior to 1950 were considerably lower, it is likely that the stock had been previously fished at a lower rate of exploitation, which would have resulted in a build-up of the stock. As the fishery expanded, abundance subsequently declined to reach its lowest level in 1975.

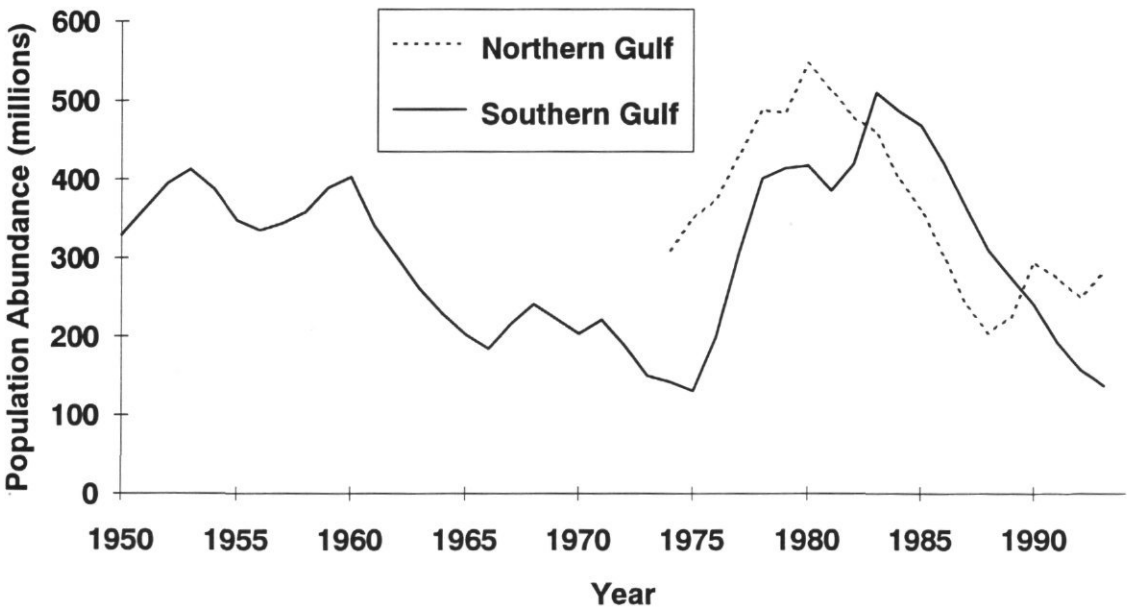


Figure 5. Trends in population abundance (millions) estimated using sequential population analysis (SPA) for the cod stocks of the Gulf of St Lawrence.

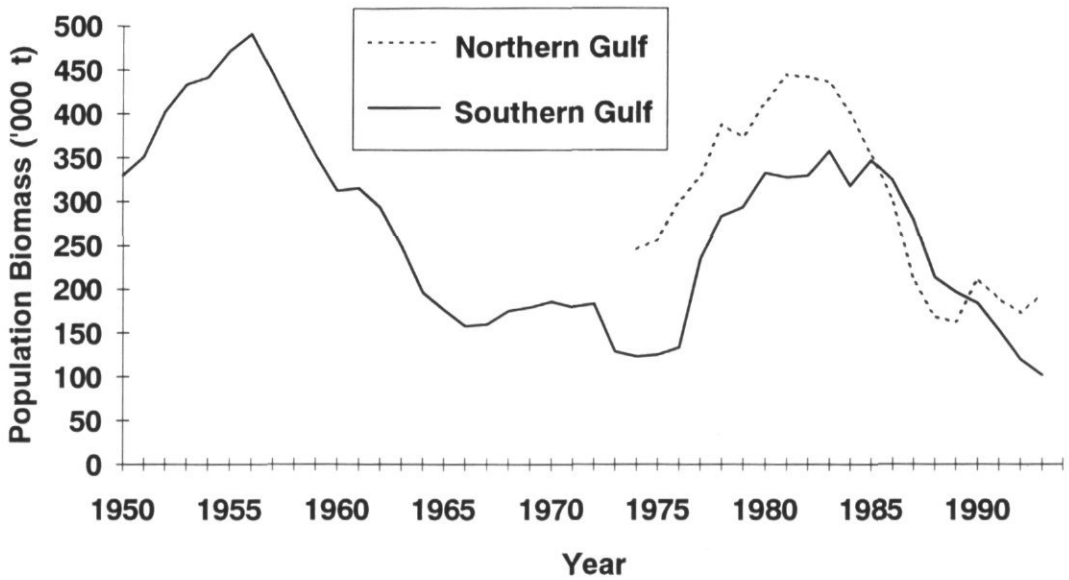


Figure 6. Trends in population biomass for the cod stocks of the Gulf of St Lawrence.

Population abundance increased dramatically to the mid-1980s and declined rapidly thereafter. Currently, population abundance is estimated to be at the low level observed in the mid-1970s.

The same trends can be seen for total biomass and spawning-stock biomass estimated by ages 5 and over (Figs 6 and 7). Total biomass is estimated to have been 491 000 t in 1956. Total biomass declined to 123 000 t in 1974 then increased up to the mid-1980s before declining thereafter. Total biomass is currently estimated to be about 100 000 t. Spawning biomass is also at the lowest level observed. Fishing mortality (ages 7+) was high

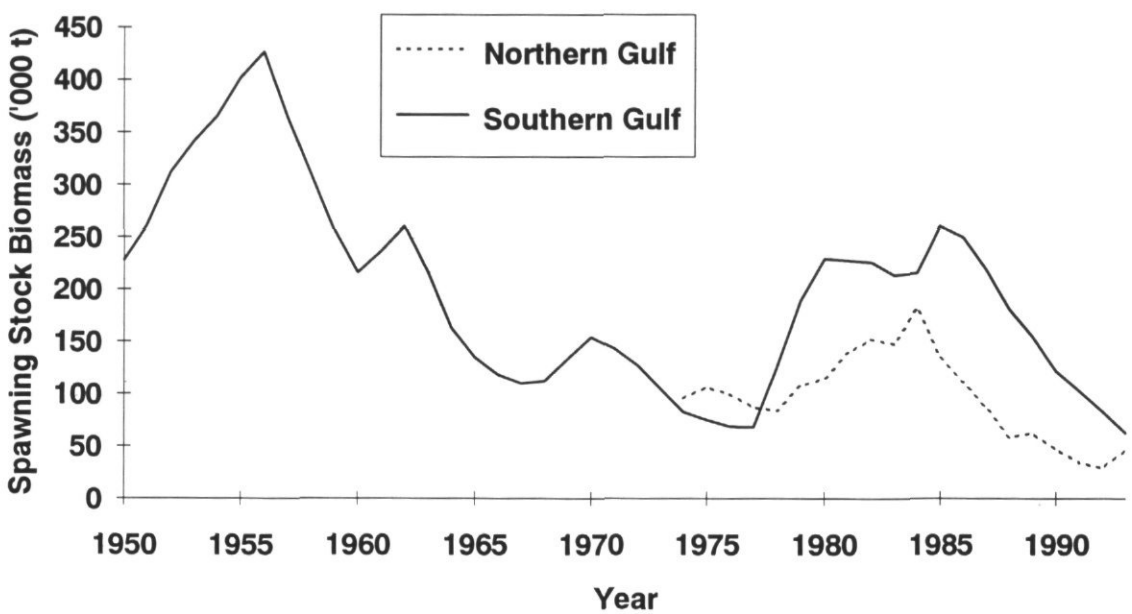


Figure 7. Trends in spawning-stock biomass (SSB) for the cod stocks of the Gulf of St Lawrence. SSB for the northern Gulf stock is estimated using the biomass of age 7 and older; the estimate for the southern Gulf stock is based on ages 5 and older.

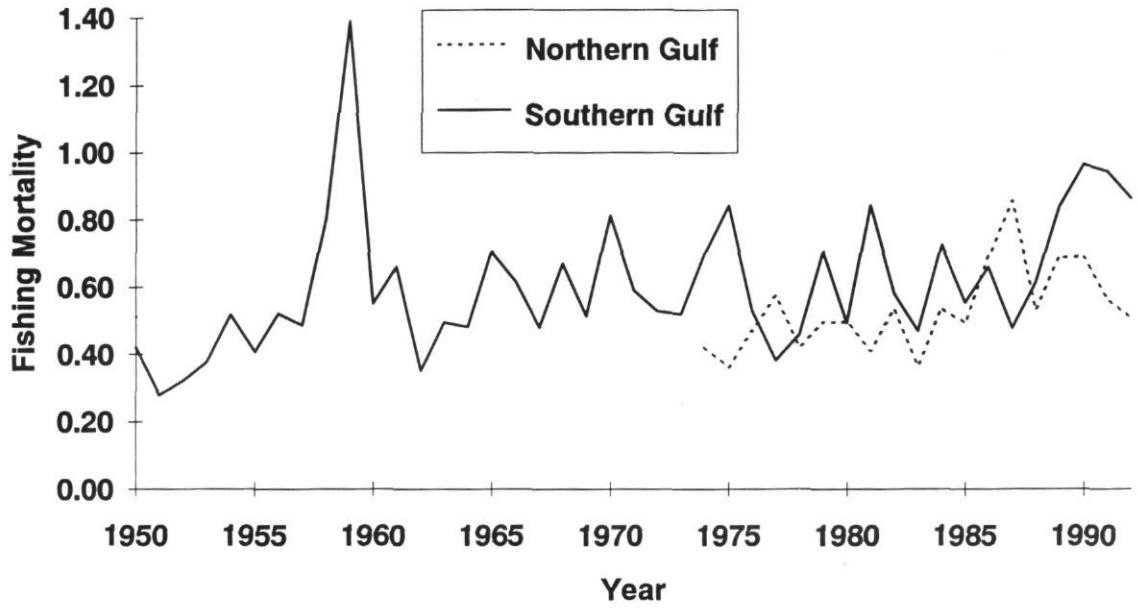


Figure 8. Fishing mortality (ages 7+) for the cod stocks of the Gulf of St Lawrence.

(>0.8) in 1958–1959 and in recent years (Fig. 8). For the remainder of the period, it varied between 0.4 and 0.8. Recruitment in the southern Gulf cod, estimated by age 3 abundance, has varied by a factor of five over the time period (Fig. 9). Large year classes were produced in 1956–1957, 1974–1975, and 1979–1980, and recruited to the fishery three years after. The abundance of year classes produced since 1980 has been continuously declining. The more recent year classes to have recruited to the fishery (1988–1989) appear to be particularly weak.

Of all the cod stocks in the Canadian zone, the change in size-at-age has been most pronounced for the

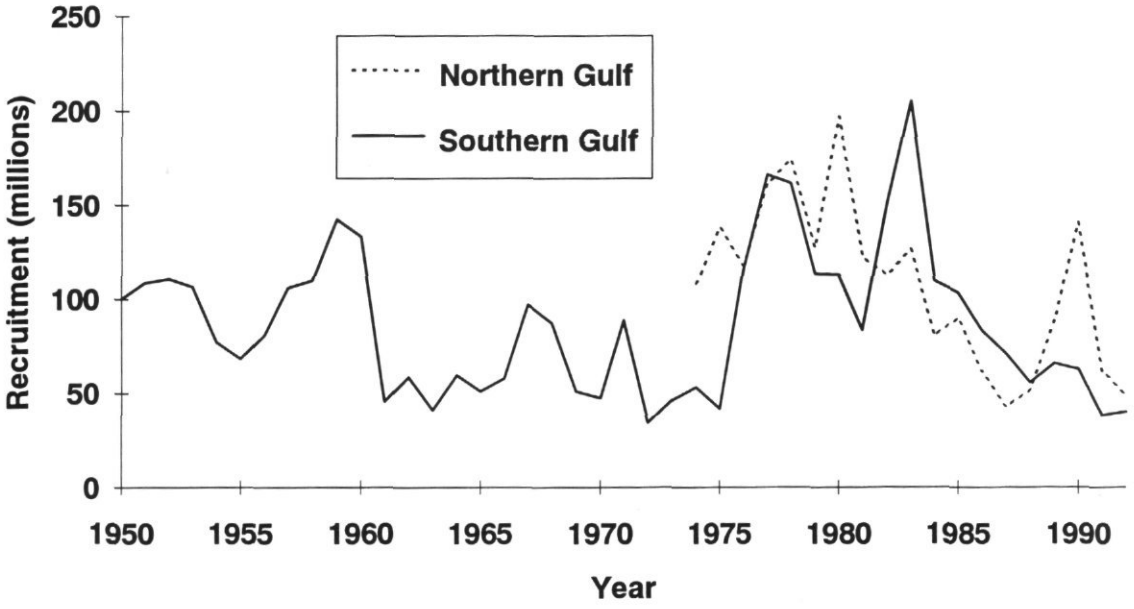


Figure 9. Estimates of recruitment (age 3) for the cod stocks of the Gulf of St Lawrence.

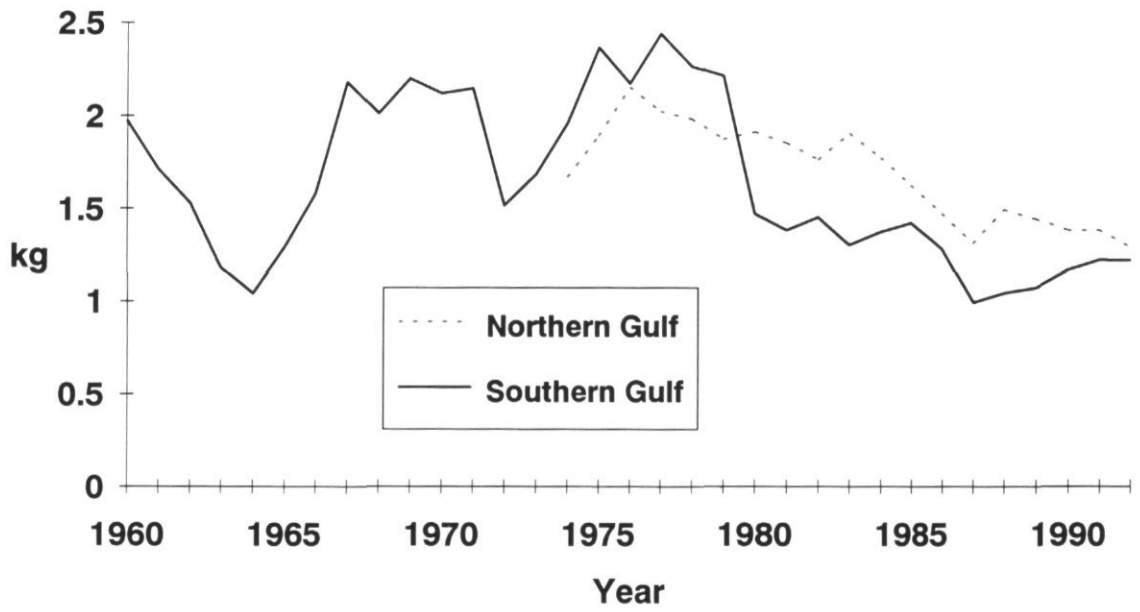


Figure 10. Average weight of a 7-year-old cod from the stocks of the Gulf of St Lawrence.

southern Gulf cod. The average weight of an age 7 cod has been 50% lower in recent years compared to the mid-1970s (Fig. 10). Similar to the northern cod stock, it is likely that recovery of the spawning-stock biomass could take a few years.

Stock production

The production of a stock can be partitioned into two parts; production due to recruitment and production due to growth during the year. The two components of production were calculated for the stocks using the method described by Rivard (1982), in which modified cohort analysis equations are used. The results (Fig. 11) show that production of the southern stock was high in the early 1950s and in the late 1970s and early 1980s. Production for the northern Gulf stock was also high in the late 1970s and early 1980s.

Trends in the environment

It is widely recognized that environmental conditions have an influence on the production and distribution of fish stocks. Cushing (1982) presents a review of many of the mechanisms involved. In this analysis, several indices of climatic conditions that may be relevant to cod stock fluctuations in the Gulf of St Lawrence were examined. The list presented is far from exhaustive. For example, time series of salinity, ice coverage, and other environmental variables were not readily available and were not examined.

North Atlantic Oscillation (NAO)

Local environmental conditions may ultimately be linked to global atmospheric circulation. In the North Atlantic, an important feature of atmospheric circulation is the North Atlantic Oscillation. Variation in this circulation pattern has been quantified as the difference in atmospheric pressure between a high-pressure system located in the Azores–Bermuda and a low-pressure system in the Iceland–Greenland area. The index is calculated by computing the mean difference in atmospheric pressure between Akureyri, Iceland, and Ponta Delgada, Azores. High NAO index values usually result in an intensification of winter westerly winds in the West Atlantic and hence colder conditions, while low index values are associated with warmer winter conditions. The NAO index shows low values from the early 1950s to 1964 and high values in the early 1970s, mid-1980s, and recently (Fig. 12, top panel).

Degree-days (DEGD) in the Gulf of St Lawrence

An index of temperature conditions in the Gulf of St Lawrence was calculated by taking the average of degree-days (Anon., 1992) from six nearshore weather stations (Gaspé, Sept-Iles, Charlo, Summerside, Iles-de-la-Madeleine, and Stephenville) in the Gulf of St Lawrence. These stations have been consistently monitored since at least 1962. The resulting index (Fig. 12, second panel) shows that conditions were generally warmer in the late-1960s and in the early 1980s. Cold

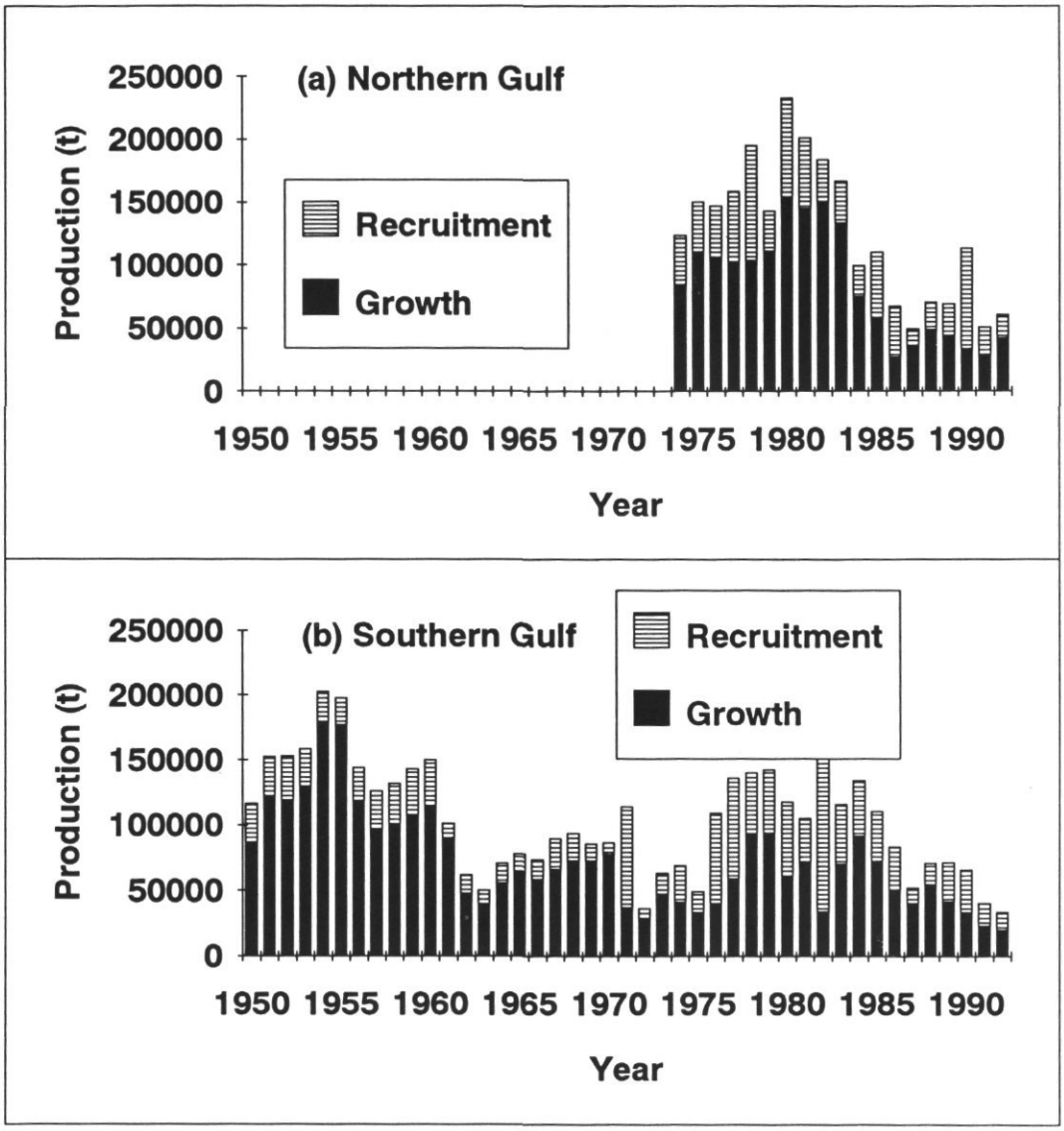


Figure 11. Growth and recruitment components of production for (a) the northern and (b) southern cod stocks of the Gulf of St Lawrence.

conditions were prevalent in the early 1970s and in some recent years.

Bottom temperatures in the Gulf of St Lawrence

Bottom temperatures from groundfish surveys that have been conducted in the Gulf of St Lawrence were also examined. In the northern Gulf, a survey conducted in January of each year since 1978 (with the exception of 1982) indicates that bottom temperatures were cooler in the early 1980s and in recent years (Fig. 12, third panel). In the southern Gulf, the survey has been conducted each September since 1971. Generally, bottom temperatures in the area at that time of the year were warm in the late 1970s.

Cabot Strait deep-water temperature

The changes in deep-water temperatures in Cabot Strait have been examined by Bugden (1991). The waters are thought to be a mixture of the Labrador Current and slope waters in essentially equal proportions. These waters have been shown to propagate upstream following a typical estuarine circulation pattern and reach the

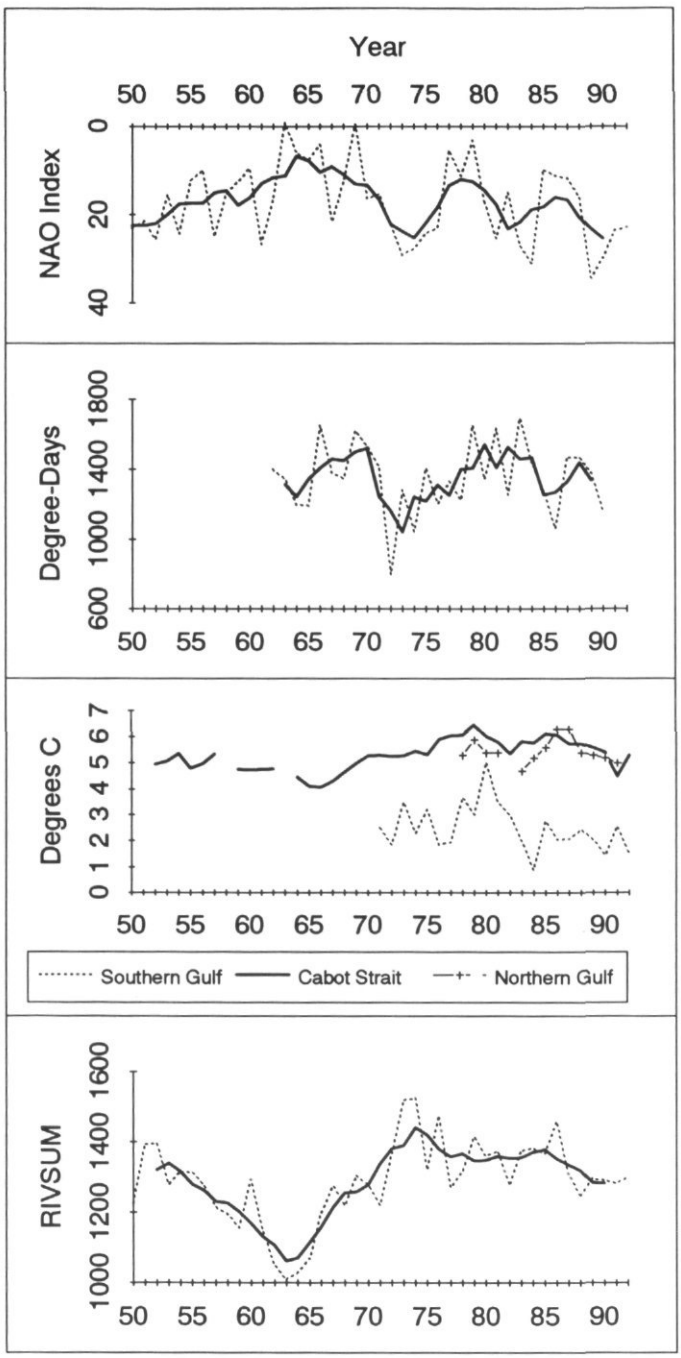


Figure 12. Plot of some environmental variables for the Gulf of St Lawrence. Top panel: Index of the North Atlantic Oscillation (dotted line) and running mean (solid line). Second panel: Mean degree-days of air temperature for six stations in the Gulf of St Lawrence (dotted line) and running mean (solid line). Third panel: Average midwater and bottom temperatures from research surveys conducted in the Gulf of St Lawrence (see text for details). Bottom panel: Index of freshwater discharge (hundreds of m^3/s) from the St Lawrence River (dotted line) and running mean (solid line).

St Lawrence estuary in approximately 2.5 years. The annual means of water temperatures at 200–300 m were calculated. Generally, the index shows that temperatures were low in the mid-1960s, before increasing to the early 1980s and then decreasing again (Fig. 12, third panel)

St Lawrence River Discharge (RIVSUM)

Sutcliffe (1973) found significant correlations between some fisheries resources landings and the freshwater discharge from the Gulf of St Lawrence. He hypothesized that freshwater discharge promoted nutrient enhancement of the top layer waters through mixing and entrainment processes. The index of river discharge used was the sum of monthly mean discharge from several gauging stations on the St Lawrence River (Lake Ontario, the Ottawa River, and the Saguenay River) and is referred to as RIVSUM. In the 1960s the index accounted for about 70% of the total discharge from the St Lawrence River in the estuary.

The RIVSUM index shows a progressive decline in river runoff from 1950 to the mid-1960s (Fig. 12, bottom panel). Discharge subsequently increased, attaining its highest level in the mid-1970s before declining slightly and fluctuating in the early 1980s. In 1989, the index was at the low levels of the early 1970s.

Causes of fluctuations: fishing or recruitment?

From a given level, the abundance of a fish population will fluctuate if the removals (fishing and natural mortality) do not equal the incoming recruitment. Mann (1993) concluded that, in many cases, fluctuations in the abundance of fish populations are due to large-scale oceanographic processes which affect year-class size rather than exploitation regimes. This hypothesis was provisionally examined for the two cod stocks of the Gulf of St Lawrence.

The influence of the variation in the exploitation rate (fishing mortality) and recruitment on population trends for the two stocks were investigated by conducting population simulations (Rivard, 1982) under two conditions. These were in effect stock predictions starting in the 1970s using different values of recruitment and fishing mortality. The population trends obtained from these projections were then compared with the estimated stock trends derived from the 1993 assessments of these stocks. A similar approach was used by Fréchet (1991) to examine the dynamics of the northern Gulf cod stock under various scenarios of exploitation.

Given an estimated initial population at age A and in year Y ($N_{A,Y}$), the population at age A + 1 and year Y + 1 were estimated using:

$$N_{A+1,Y+1} = N_{A,Y} \exp^{-(F_{A,Y}+M_{A,Y})}$$

where: $F_{A,Y}$ = fishing mortality at age A in year Y and $M_{A,Y}$ = natural mortality at age A in year Y. The numbers in the first age group were set equal to the recruits.

The periods examined were 1971–1992 for the southern Gulf of St Lawrence stock and 1974–1992 for the northern Gulf stock. From the results of the most recent assessment of these resources (Fréchet and Gagnon, 1993; Sinclair, 1993), the mean recruitment and the mean fishing mortalities over the time period for each age class and for each stock were calculated. These mean values were used in simulations using constant conditions of either recruitment or fishing mortality.

The estimated values of initial population, fishing mortality, and recruitment were those derived from SPA from the most recent stock assessments of these stocks (Fréchet and Gagnon, 1993; Sinclair, 1993). Starting with the initial population estimates at the beginning of these time periods (1971 for the southern Gulf and 1974 for the northern Gulf), population predictions were then conducted under two scenarios. In the first scenario, the estimated recruitment values from SPA and the mean fishing mortality at each age were used in the prediction. In the second scenario, the mean recruitment and the estimated fishing mortality from SPA were used. Natural mortality was set at 0.2.

The results (Fig. 13) were compared with the current estimates of population abundance for these stocks (i.e. those resulting from estimated fishing mortalities and recruitment values). They indicate that population abundance would have followed the same trends even if fishing mortality had remained constant over time, given the recruitment estimated. However, if we assume constant recruitment and use the estimated fishing mortality from SPA in the prediction, trends in population abundance do not match those estimated. This indicates that the year-to-year fluctuations in population abundance depend more on the variation in recruitment than on the variation in fishing pressure for these stocks. This is not to say that fishing had no impact on these resources, but rather that the *fluctuations* (as opposed to the actual level) in population abundance seen over the last 20 years or so have not been caused primarily by the variation in mortality at the exploited stage. However, in the case of the southern Gulf of St Lawrence (see bottom panel, Fig. 13), the recent increase in fishing mortality seems to have exacerbated the rate of decrease in population abundance.

The coefficient of variations of the estimated recruitment and total mortality values from SPA also provide an indication of which factor has more influence on the

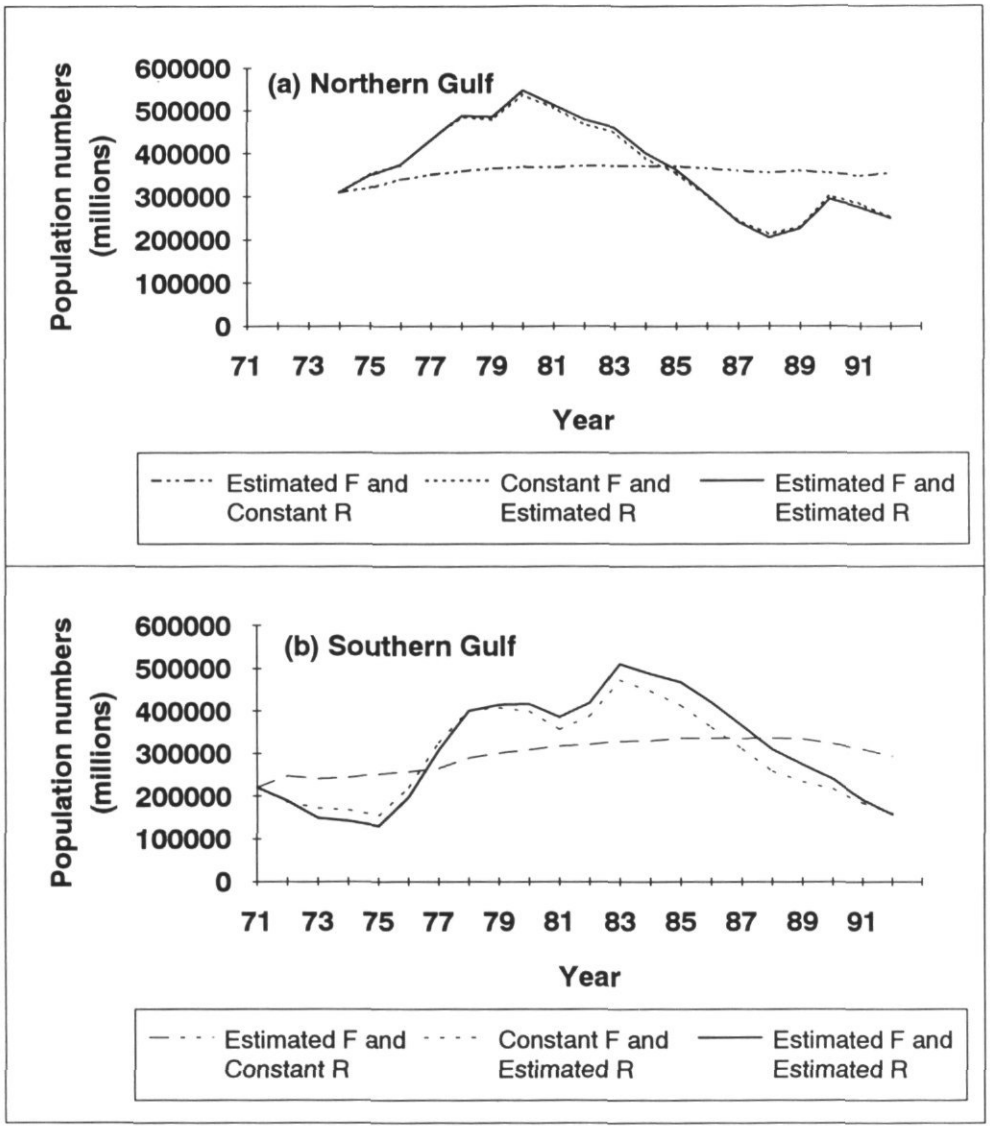


Figure 13. Results of simulations conducted with constant (i.e. average) and estimated (i.e. from SPA) values of recruitment (R) and fishing mortality (F) for (a) the northern and (b) southern cod stocks of the Gulf of St Lawrence. Starting population values were the population size estimated from SPA at the beginning of the time period and M was set at 0.2 (see text for details).

population trends. Recruitment tends to be more variable than the level of removals by the fishery (Table 1).

We conclude that in the case of these two stocks the fluctuations in population abundance have been largely caused by fluctuations in the recruitment. These fluctuations can be intensified by variation in fishing mortality.

Survival of pre-recruits and climatic conditions

As in the case of most other cod stocks, the stock–recruit relationships for the two cod stocks of the Gulf of St Lawrence do not conform with theoretical models of stock and recruitment (Fig. 14). It could, in fact, be argued that there is a negative relationship for the northern Gulf (Fréchet, 1991) or that we may have witnessed only the descending limb of a stock–recruitment relationship. As several authors have pointed out (Sætersdal and Loeng, 1987; Koslow *et al.*, 1987; Wyatt *et al.*, 1992), there are a number of environmental variables affecting the relationship. In this context, the notion of survival might reconcile the apparent lack of relationship between spawning stock and recruitment.

Iles (1973) suggested an index of survival of pre-

Table 1. The coefficients of variation of the estimated recruitment and total mortality values from SPA.

	Coefficient of variation (%)	
	Recruitment	Total mortality (ages 7+)
Northern Gulf (74–92)	41	17
Southern Gulf (71–92)	51	20

recruits by dividing the estimated recruitment (in this case, obtained from SPA) by the spawning stock biomass (SSB) which produced it. The SSB is seen as an index of the number of eggs produced, the recruitment in later years providing an index of how many survived. Pre-recruit survival for both stocks indicates that there was exceptional survival in the mid-1970s (Fig. 15). Survival during that period was about an order of magnitude higher than the lowest levels observed for the

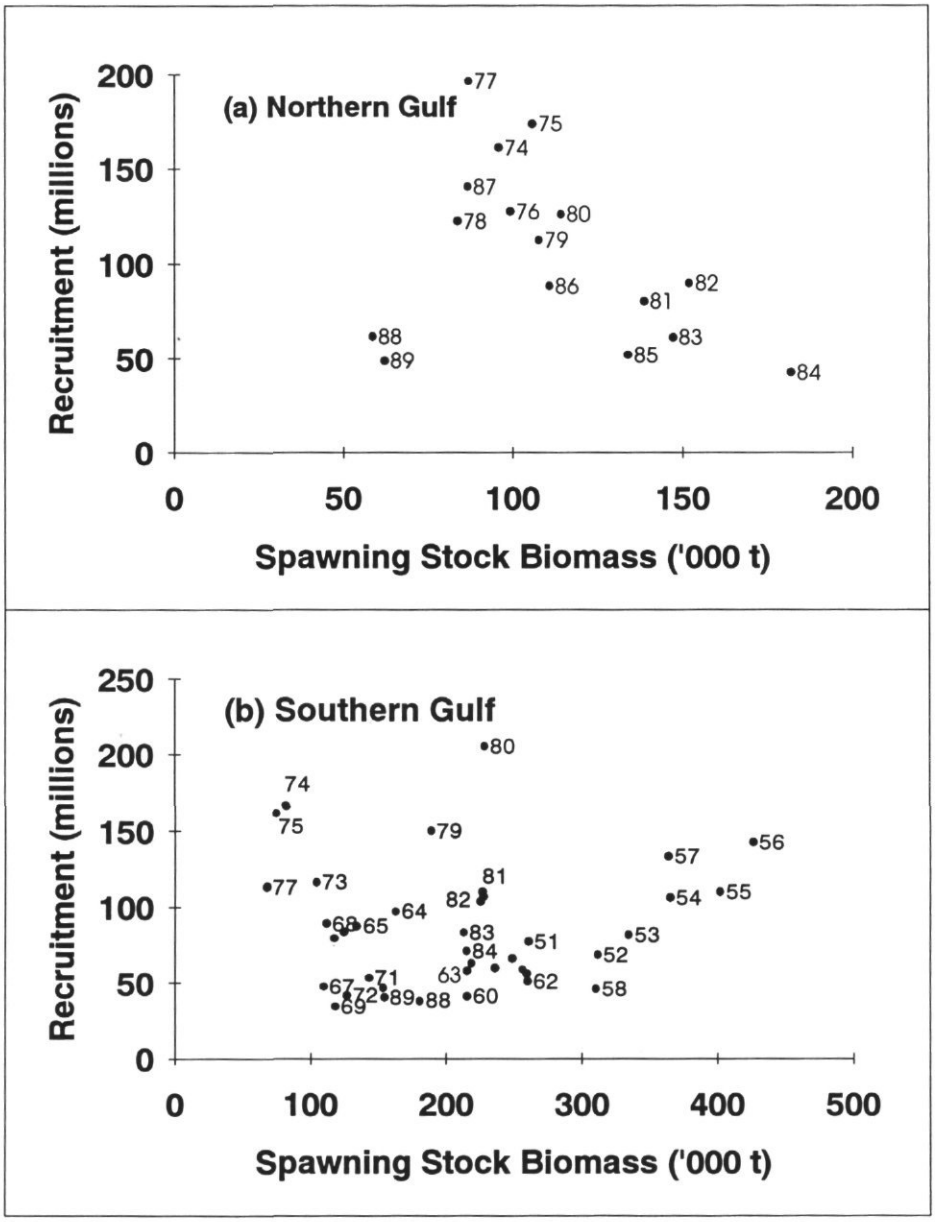


Figure 14. Plots of spawning-stock biomass and recruitment for (a) the northern and (b) southern cod stocks of the Gulf of St Lawrence.

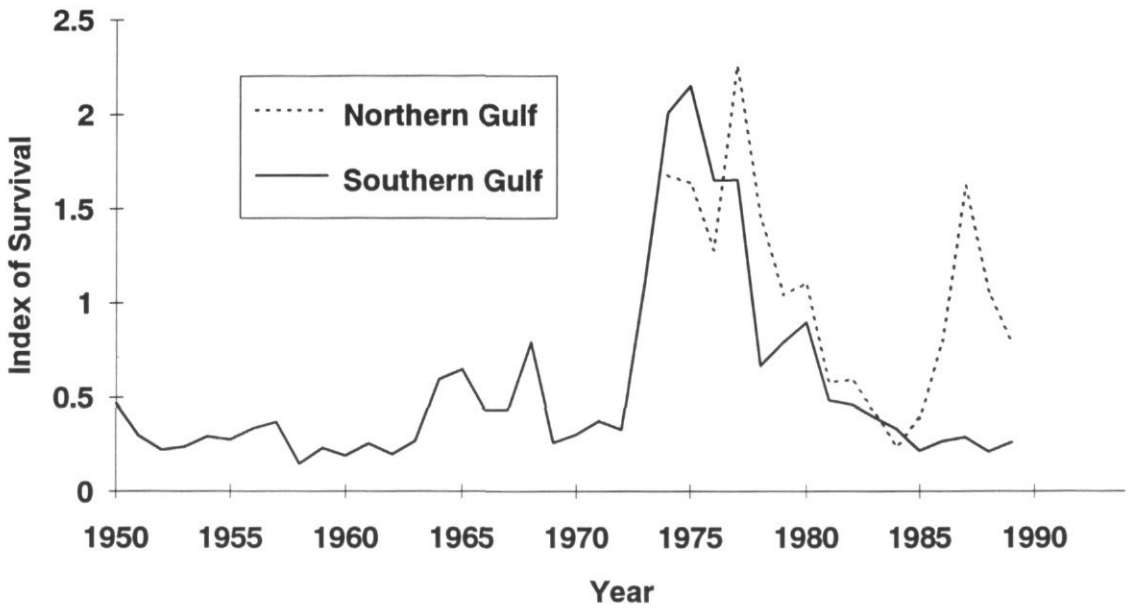


Figure 15. Index of survival (Recruitment/SSB) for the cod stocks of the southern Gulf of St Lawrence.

stocks. The year classes in recent years produced by large biomasses have had lower survival.

Pearson correlation coefficients between this index of survival and the environmental variables RIVSUM, NAO, and degree-days (during the birth year) were calculated for the southern Gulf stock. Other environmental variables were not examined, as it is hypothesized that survival would be influenced by conditions in the near-surface during the first year of life. For the northern Gulf stock, RIVSUM was not used as general

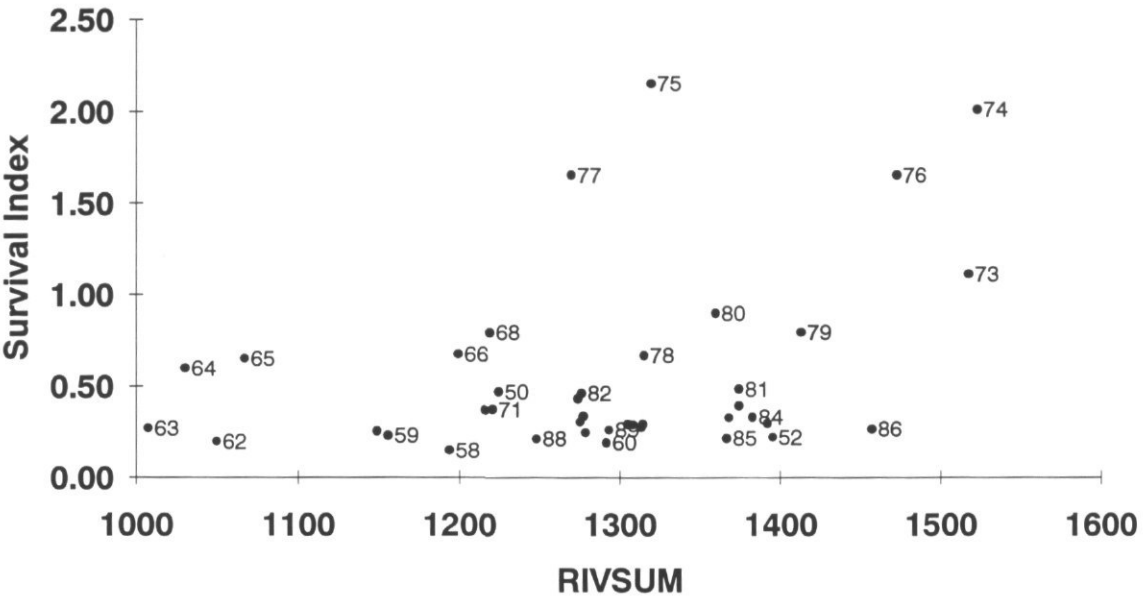


Figure 16. Plot of the index of discharge from the St Lawrence River (RIVSUM) and the index of survival for the southern Gulf of St Lawrence cod stock.

circulation patterns indicate that the outflow from the St Lawrence River is predominantly on the southern Gulf.

Results (see Table 2) indicated that the index of survival is weakly correlated with freshwater discharge but not with degree-days for the southern Gulf stock. A plot of the data (Fig. 16) shows that there are probably other factors at play as there have been some low survival rates associated with above average discharges; however, very high survival was only achieved when freshwater runoff was above average.

Discussion and conclusion

Trends in landings in the cod fisheries of the Gulf of St Lawrence were relatively similar. Generally, they show the same trends seen in the adult population biomass. Since 1974, the management objective has been to exploit the stocks at a constant target fishing mortality (F_{MAX} then $F_{0.1}$) (Parsons, 1993). Despite the fact that the targets were not achieved, estimated fishing mortality was maintained at a relatively stable level and it is not surprising to see trends in landings to be synchronous with exploitable biomass. However, for the southern Gulf stock, the trends in landings prior to 1974 also follow trends in biomass quite closely, despite the fact that the fishery was less regulated. Fishing mortality gradually increased between 1950 and the early 1970s but growth also increased between the early 1960s and early 1970s, with the result that trends in landings followed the trends in biomass.

The two cod stocks exhibit relative synchrony in their stock status trends. Generally, the mid-1970s and recent years were periods of low abundance for both stocks, while abundance was high in the mid-1980s as a result of the large year classes that were produced in the late-1970s and early 1980s.

Our results show that, for these two stocks, population abundance fluctuations were largely determined by short-term variations in the recruitment as opposed to those in fishing mortality. Almost certainly, if fishing mortality had been lower on average, population abundance would have been higher. Nevertheless, it would likely have fluctuated in response to change in recruitment levels, albeit at a higher level. Our analysis did not include feedback from an undefined underlying stock–recruitment relationship. However, given that fishing mortality did not fluctuate much over the time period, the impact on the results would probably be minimal.

Table 2. Results of correlation analyses of the index of survival for the northern and southern Gulf of St Lawrence cod stocks and selected environmental variables.

	r	p	n
Northern Gulf			
NAO	−0.35	0.17	17
DEGD	−0.25	0.34	17
Southern Gulf			
NAO	0.12	0.45	40
DEGD	−0.20	0.30	29
RIVSUM	0.36	0.02	40

Koslow *et al.* (1987) showed that there were significant correlations between recruitment of several cod stocks in the Northwest Atlantic. Cohen *et al.* (1991) indicated that the correlations were usually strongest between neighbouring stocks. Given that similar trends in abundance are also seen for most other cod stocks in the Canadian Atlantic, with the exception of Georges Bank and Bay of Fundy stocks (Sinclair, 1993), it would appear that fluctuations in abundance may be related to fluctuations in recruitment as opposed to fluctuations in fishing mortality for most of these as well.

The impact of physical forcing has long been thought to have a major impact on the recruitment of fish stocks (Cushing, 1982). The indices of temperature examined indicate some similarities. For example, the values of the NAO index roughly correspond with periods of lower and higher degree-days in the Gulf of St Lawrence. As expected, bottom temperatures, which are influenced by factors such as the degree of stratification or inflow of cold waters from the Atlantic, do not match the trends well.

The problems with correlations of environmental variables and fish stock recruitment have been highlighted by several authors (Walters and Collie, 1988; Cohen *et al.*, 1991). Statistical theory states that if numerous correlations are done, some are bound to be significant. As Mann (1993) points out, more often than not the relationships eventually cease to hold, probably because a series of other factors with different levels of importance intervened. Correlations can nevertheless be useful to establish hypotheses that can be tested with the proper experimental design.

The correlations of the index of survival and the environment examined here do not include all the possible effects, such as other environmental variables (salinity, etc.) and predator–prey relationships. For example, Lett (1980) hypothesized interactions of cod and mackerel in the southern Gulf.

In our analyses, the only significant correlation found was for the index of survival for the southern Gulf stock and the freshwater discharge of the Gulf of St Lawrence. Therriault and Levasseur (1986) have shown that the primary productivity of the St Lawrence estuary was influenced by freshwater discharge. Thórdardóttir (1986) described a similar effect in the Icelandic coastal current. Skreslet (1976) found that the survival of juven-

ile Arcto-Norwegian cod hatched on the north coast of Norway was positively correlated with freshwater discharge on the southwest coast of Norway the previous year. Bugden *et al.* (1982) previously examined the effect of the Gulf of St Lawrence freshwater runoff on year-class variability of cod in the Gulf of St Lawrence, concluding that the effect was weak. The relationship found here is not strong either; in some years, high discharge did not lead to higher survival; however, high survival was only observed when freshwater discharge was above normal. This probably implies that other factors are at play in the mechanism(s) involved or that the freshwater discharge is simply a proxy for some other condition, such as the degree of mixing of nutrients or even primary and/or secondary production.

Several predictions of global warming have been prepared for Canada (Kemp, 1991). One prediction, which relates to freshwater discharge, is that the flow from the Great Lakes basin to the St Lawrence would be reduced by about 20% (Sanderson, 1987). The relationship between the index of survival for cod in the southern Gulf of St Lawrence and the discharge from the St Lawrence is admittedly weak. However, this may mean that under the same other conditions that prevailed in the mid-1970s, higher survival than average could be less likely.

Although the recruitment component of production appears to be affected, the growth component may not be affected in a similar way or by the same variable(s). For the southern Gulf of St Lawrence, Hanson and Chouinard (1992) have shown that changes in size-at-age are consistent with size-selective fishing mortality. Density effects have also been suggested with smaller size-at-age observed at high population abundance (Paloheimo and Kohler, 1968; Chouinard and Hanson, unpublished data). For example, the year classes produced in the late 1960s and early 1970s, which are estimated to be small, attained an average weight of about 2.5 kg at age 7, the largest observed in the time series. Conversely, cod produced in 1980, the largest year class on record, barely reached a weight of 1 kg in 1987. Density has also been associated with changes in distribution (Swain and Wade, 1993). At high densities, the geographic range of southern Gulf of St Lawrence cod increased. Changes in the bathymetric distribution patterns related to density have also been observed (Swain, 1993). At high densities, cod were found in deeper waters.

There is evidence that climatic fluctuations can also affect migration and distribution of cod stocks. For the Gulf of St Lawrence stocks, Fréchet (1990) showed that concentrations of overwintering cod from the northern Gulf stock are found at the marginal ice zone. The results of the study showed that cod were virtually absent within the ice field. The increase in ice coverage seen since 1990 was therefore likely responsible for the extended migration of the southern Gulf stock into area 4Vs in recent years (Hanson *et al.*, 1991). It is also possible that a similar extension of the migration of the northern Gulf stock happened as well.

Up until recently, Canadian stock assessments have focused their efforts on estimating fishing mortality and abundance as opposed to trying to predict the size of incoming year classes. Our analysis shows that efforts to better estimate both current and incoming recruitment may be more helpful in predicting stock trends, providing that some control on fishing effort remains in place. As for the mechanisms that determine the abundance of the year classes, these are no doubt complex and, in addition, the relative importance of the various factors may be changing with changes in the environment.

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Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod

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Taggart, C. T., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J., Murphy, E., Myers, R., Rose, G., and Shelton, P. 1994. Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. – ICES mar. Sci. Symp., 198: 140–157.

Total landings of cod in the Newfoundland region (NAFO Divisions 2GHJ, 3KLMNO, and Subdivision 3Ps) increased from $\sim 1 \times 10^5$ metric tonnes (t) in 1800 to $\sim 4 \times 10^5$ t in 1950. Landings then increased to $>1 \times 10^6$ t in 1968 and then declined to $<2 \times 10^5$ t by 1978. Landings again increased to 3.5×10^5 t in the 1980s and after 1988 dropped to $<1 \times 10^5$ t. By 1993 the cod fishery throughout the majority of the region was closed. Northern cod (2J+3KL) spawner population estimates follow a temporal pattern similar to landings; current levels are at a record minimum of $<1 \times 10^8$ and have been paralleled by a collapse in the size and age structure of the stock. Under the prevailing levels of fishing mortality, recruitment per spawner was below replacement from 1983 onwards, paralleling the stock decline. Recruitment determination is consistent with a parent stock-recruitment relationship. Widespread distributions of age 5+ cod, typically seen in the 1980s, became more aggregated toward the offshore, culminating in very few major aggregations along the shelf break in 1992. Winter–spring spawning throughout the region is protracted (3–4 months) and may be more frequent in inshore regions and on banks than has been previously perceived. The overall physiological condition of northern cod in more northerly regions has been decreasing since 1988, and only in the most recent years have capelin been virtually absent from the stomachs of cod in northerly regions. Lengths at 50% maturity have been declining since the early 1980s, particularly in northerly regions. Fishing mortality for northern cod was consistently >0.4 in the mid-1970s. The reduction of F to <0.4 during 1977 to 1980 was paralleled and followed by increases in the abundance of the spawner population. Slowly increasing fishing mortalities after 1980 accelerated after 1987. The combined effects of fishing mortality on spawning population size and reduction in length and age reduced fecundity contributions of older individuals. A recent examination of a salinity–recruitment relationship shows that with the addition of spawning-stock biomass estimates, recruitment estimates can be well modelled. A series of years characterized by better than average environmental conditions will likely be required to provide the good recruitment necessary to rebuild the stock size and length/age structure.

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Introduction

The critical status of Atlantic cod (*Gadus morhua* L.) in the Newfoundland and Labrador region of the Northwest Atlantic, particularly northern cod in the Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J+3KL, was recognized in the late 1970s (Kirby, 1982), again in the mid-1980s following a severe decline in the inshore fishery (Alverson, 1987), and more recently in 1989 (Harris, 1990). Since then, cod stock levels have become so low that Canadian commercial cod fishing is now banned throughout most of the region (Divisions 2J+3KLNO and Subdivision 3Ps) and long-term pros-

pects for rebuilding the northern cod stock are such that "recovery of the spawning stock biomass is unlikely before the year 2000 at the earliest" (Anon., 1993, p.16). At the same time a considerable effort has been mounted to examine more closely the nature of catch statistics, fishing effort, population size, distribution and structure, spawning and recruitment, feeding, growth, maturity, and condition, etc., as well as variations in the climate and the physical environment. The majority of these efforts, which have primarily focused on the "northern cod" of NAFO Divisions 2J+3KL, are ongoing, and some of those results are presented elsewhere in this ICES Cod and Climate Change Symposium volume.

The goal of this article is to compile from these sources some of the more important aspects of the findings in order to provide a timely, though primarily descriptive, overview of the cod stocks, their biology and surrounding environment in the Newfoundland region, focusing mainly on northern cod over the last 10 to 20 years. In doing so, we hope to provide for general and future insights to analytical comparisons with the other Atlantic cod stocks and to provide a general background for the more specific and analytical studies on cod from the Newfoundland region that are contained within this volume.

Landings, population estimates and distribution

Landings

Atlantic cod have been exploited in the Newfoundland region (NAFO Divisions 2GHJ, 3KLMNO and Subdivision 3Ps) since the late 1400s. Total reported commercial landings by all Canadian and Newfoundland fleets and gear increased from about 1×10^5 metric tonnes (t) in 1800 to around 4×10^5 t in 1950 (Fig. 1). Subsequent to 1950, and with the extension of long-distance foreign fleets (primarily European and Soviet) into the Northwest Atlantic, total reported landings increased dramatically to $>1 \times 10^6$ t in 1968 and then declined just as sharply to $<2 \times 10^5$ t by 1978, a trend which helped stimulate the introduction of total allowable catch (TAC) limits in 1974 and the extension of Canada's economic management zone to 200 miles in 1977 (Fig. 1). In the mid-1980s, landings increased to $\sim 3.5 \times 10^5$ t, paralleling the introduction and increased exploitation by the Canadian offshore trawler fleet. After 1988 landings dropped sharply to $<1 \times 10^5$ t in 1992, partly a result of the early closure of parts of the Canadian offshore cod fishery, and later the inshore fishery. Later in 1992 Canada closed all commercial cod fishing within the Canadian economic management zone throughout 2J+3KL (northern cod). The closure has since expanded to include Divisions 3NO and Subdivision 3Ps. Exploitation by foreign fleets outside the Canadian economic management zone (the "nose" and "tail" of the Grand Bank and Division 3M – Flemish Cap) is under NAFO jurisdiction, and although not limited by the Canadian closure, NAFO has subsequently endorsed the cessation of commercial cod fishing on the "nose" and "tail" of the Grand Banks, but not on the Flemish Cap (Division 3M).

Since 1950, Newfoundland and Labrador cod stocks have been managed more-or-less as stock "components" according to the NAFO Divisions, i.e. 2GH (northern Labrador cod), 2J+3KL (northern cod), 3NO (southern Grand Bank cod), and 3Ps cod. More recently (since 1987) TAC management for northern cod (2J+3KL) has reflected a one-third allocation among each of the Divisions (2J, 3K, and 3L) for the offshore fishery, although the stock is assessed as a unit. Divisional landing statistics show a high degree of variation within and among Divisions (Fig. 2). Landings were highest in all Divisions during the 1960s (reflecting foreign exploitation), though relatively low ($\sim 5 \times 10^4$ t) and stable in the most southern region (3Ps) and in the most northern region (2GH), with the exception in the latter of increased exploitation (again primarily foreign) during 1965 to 1970 (Fig. 2). The highest landings have been consistently and conspicuously derived from the "northern" cod stocks in 2J+3KL, particularly the southern Labrador banks (2J) and the northern Grand Bank (3L) throughout the 1960s and early 1970s (Fig. 2).

Population estimates

Sequential population analysis (SPA) estimates of spawners (ages 6+ in this section of the paper) in the Newfoundland region from the mid-1950s to 1993 follow a temporal pattern similar to that seen in the total landings, with the maximum estimates of $>1 \times 10^9$ in 2J+3KL in the early 1960s declining by one order of magnitude to $\sim 1 \times 10^8$ in 1977 (Fig. 3). Subsequent increases to $>3 \times 10^8$ in 1987 in 2J+3KL were soon followed by a sharp decrease to a record minimum of less than 1×10^8 in 1993 (Fig. 3). The temporal pattern seen in the age 6+ population estimates is also apparent, though less pronounced, in the historically much smaller (always $<1 \times 10^8$) 3NO and 3Ps estimates (Fig. 3).

SPA recruitment estimates of age 3 cod also show a pattern similar to that seen in both the landings and spawner population estimates (Fig. 3). The general correlation ($r^2=0.54$) between spawner and recruit estimates for 2J+3KL cod is indicative of a stock–recruit relationship (see Myers *et al.*, 1993a) and is further addressed below.

The reduction in population size of 2J+3KL cod has been paralleled in recent years by a reduction in the average size and age of the population. The interquartile

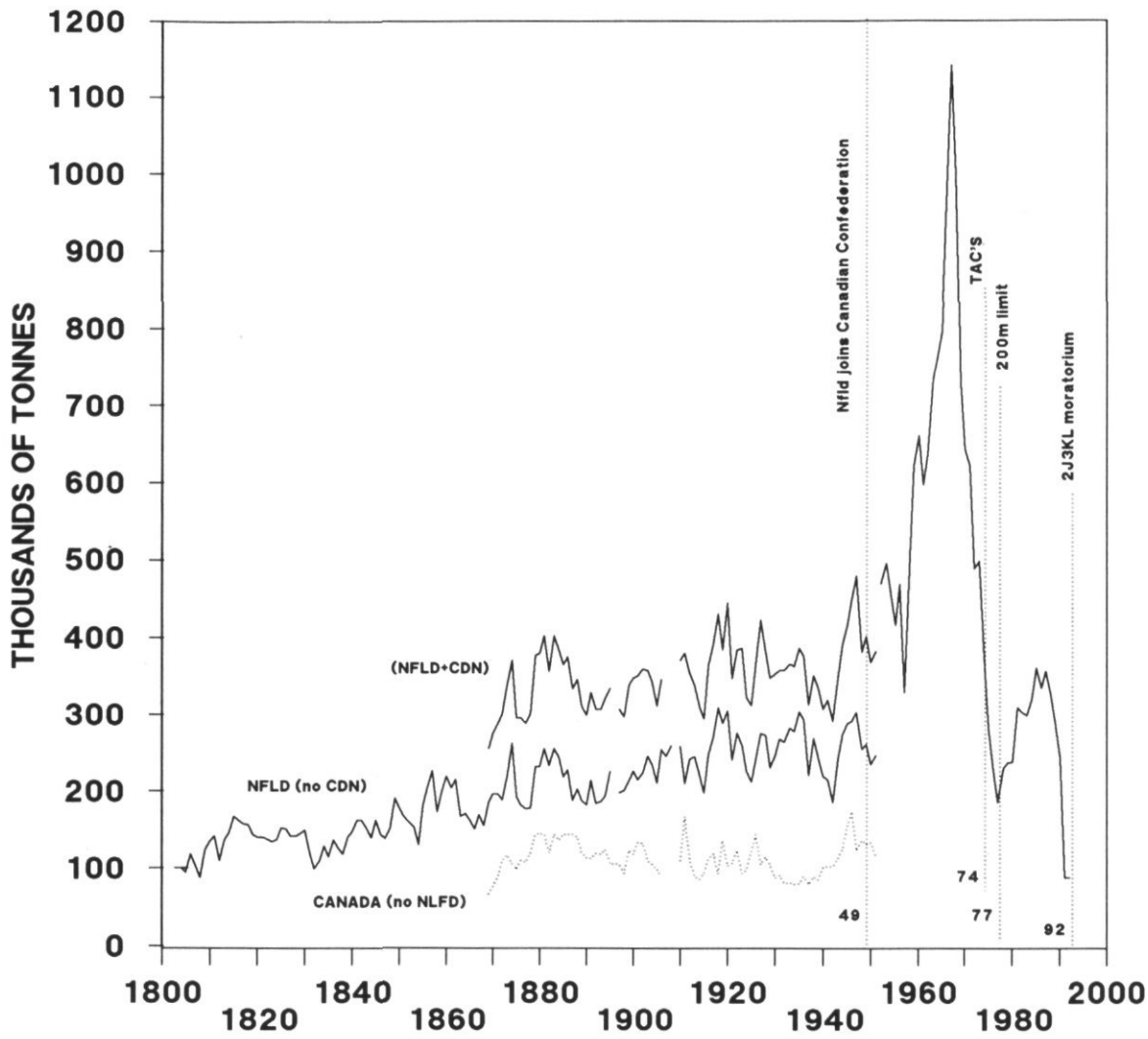


Figure 1. Total reported commercial landings (t) of cod in the Newfoundland region (NAFO Divisions 2GHJ, 3KLMNO, and Subdivision 3Ps) since 1800 for all gear sectors. Reported landings to 1950 for pre-confederation Newfoundland (NFLD-no CDN) include NAFO Areas 2 and 3 only and exclude Canadian and foreign landings. Reported landings to 1950 for Canada (Canada-no NFLD) include only NAFO Area 3 and exclude Newfoundland and foreign landings. Total reported landings subsequent to 1950 include all Canadian and foreign fleets and gear in NAFO Areas 2 and 3. Major management changes are noted in 1950 (following Newfoundland joining Canadian Confederation in 1949), 1974 (introduction of Total Allowable Catches), 1977 (extension of Canadian economic management zone to 200 miles), 1992 (Canadian moratorium on domestic commercial catch in 2J+3KL). Data are derived from ICNAF (1959–1978) and NAFO (1978+) Statistical Bulletins and Anon 1981. Post-1989 data are considered provisional.

length ranges of cod in migrating aggregations declined from 45–57 cm in June 1990 to 42–48 cm in June 1992 (Bishop *et al.*, 1993; Rose, 1993). The average age in 1993, derived from research vessel (RV) survey data, was ~4 years and was bounded by a relatively narrow age distribution (Fig. 4).

Adult distributions

Abundance distributions of cod in the Newfoundland and Labrador region, derived from annual RV surveys in the early 1980s, can be considered "typical" (see Bishop *et al.*, 1993 for greater temporal detail) and show

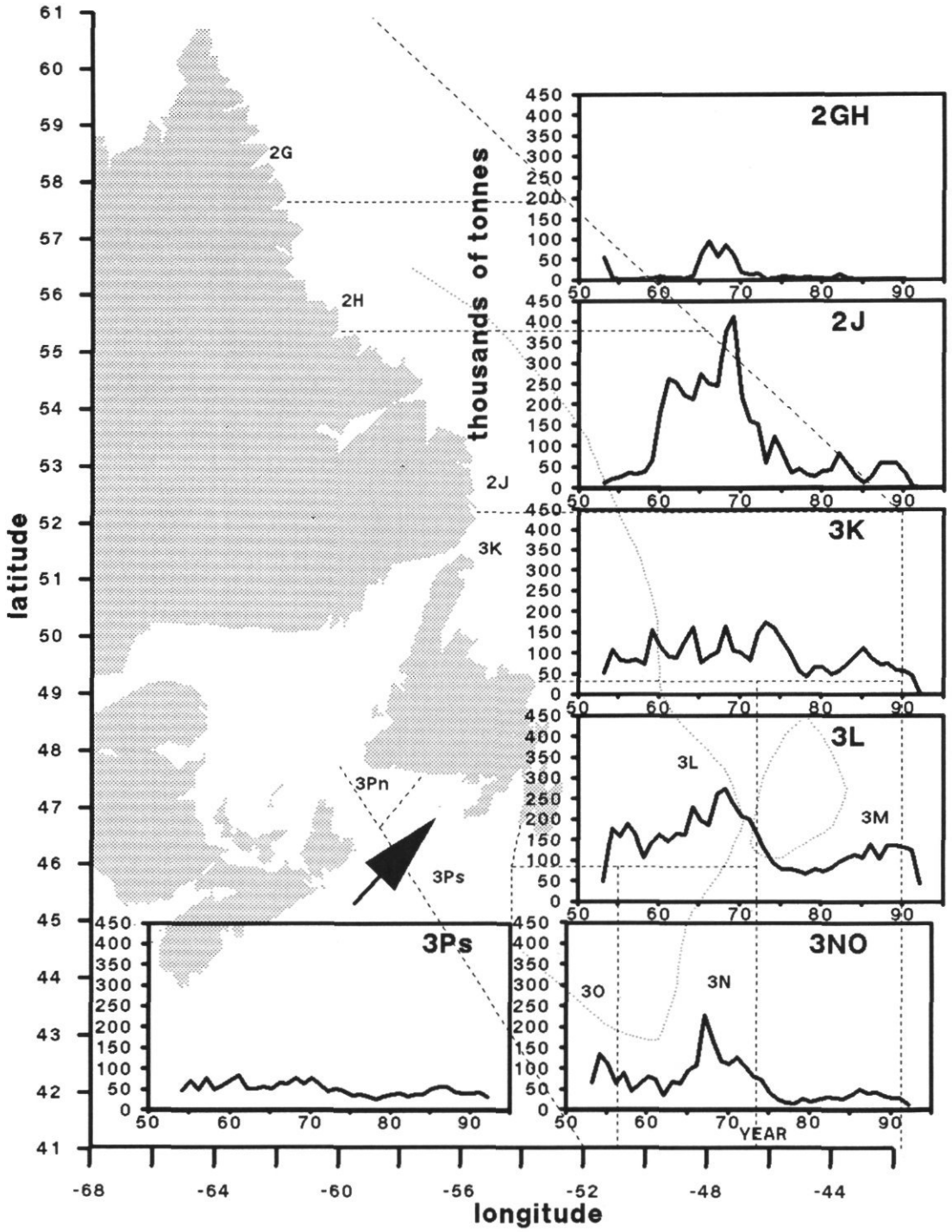


Figure 2. Total reported commercial landings (t) by all fleets and all gear (foreign and Canadian) of cod for the period 1953 to 1992 in the Newfoundland and Labrador region of the Northwest Atlantic by NAFO Division. Times series are overlaid on the Divisional chart (- - - -), which also shows the 1000 m isobath outlining the shelf break and the Flemish Cap (. . . . .). Data are from Anon. (1981), ICNAF (1959–1978) and NAFO (1978+) Statistical Bulletins. Post–1989 data are considered provisional.

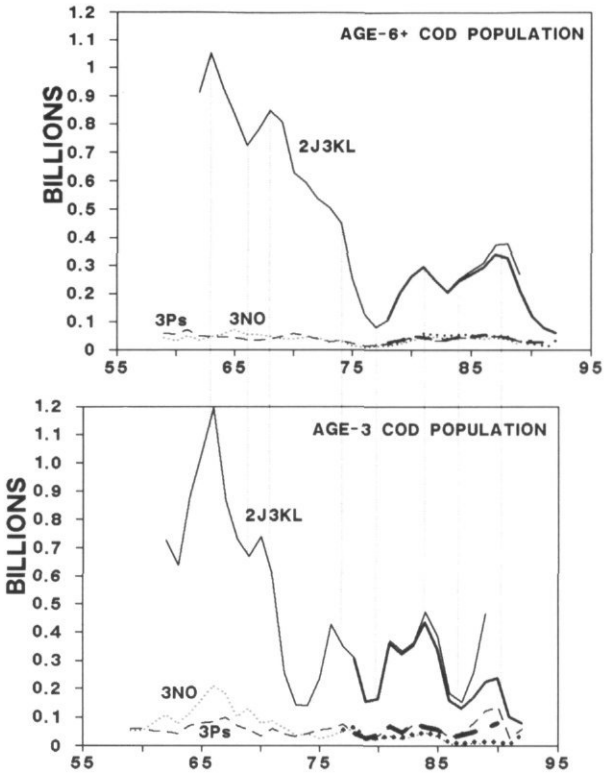


Figure 3. Population assessment estimates of age 6+ spawners and age-3 recruits for Newfoundland cod in NAFO Divisions 2J3KL, 3NO, and 3Ps for the period 1958 to 1993. Note the illustrations are offset by 3 years to align the age-3 estimates with the spawner population at year of birth. Fine-traced estimates are derived from the 1990 and 1991 sequential population estimates (after Baird *et al.*, 1990 and Bishop *et al.*, 1991) which included Canadian research vessel survey estimates, commercial catch rate information, and the French research survey data for 3Ps. Post-1977 estimates traced in bold are from 1993 sequential population estimates calculated using research vessel survey estimates only (after Bishop *et al.*, 1993).

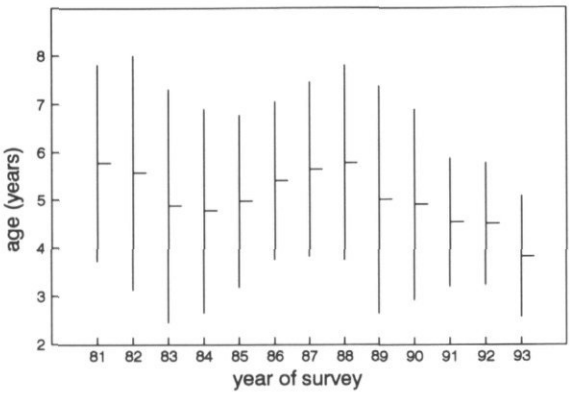


Figure 4. The average age (years ± 1 s.d.) of cod in NAFO Divisions 2J+3KL for the period 1981 to 1993 calculated from autumn research vessel survey catch data weighted by survey stratum area.

frequent, widespread catches of age 5+ cod ranging from 10 to 100 per 1/2 h standard tow (Fig. 5). During the late 1980s and early 1990s catches became progressively more contagious, and relative to the earlier period high catches were more frequent in a southerly direction and were closer to the offshore shelf break. This progression culminated in 1992 with severely reduced survey catch rates in the majority of sets (≪10 per 1/2 h tow) throughout the region, except for one large aggregation along the shelf break at the border between 3K and 3L and two smaller aggregations near the shelf break in Subdivision 3Ps (Fig. 6). An examination of some of these distributional changes and associated variations in water temperature is provided in Rose *et al.* (1994).

Juvenile distributions.

Investigations of the distributions of demersal juvenile cod during the period 1981 to 1992 (Anderson, 1993) show that age 1+ juveniles are concentrated primarily along the coastal regions of northern Newfoundland and Labrador and further offshore on the Grand Banks (Fig. 7). This pattern is, in part, consistent with distributions of 0-group pelagic juveniles, at least for the years 1991 and 1992, when the 0-group was primarily concentrated in the inshore regions (Anderson and Dalley, 1993). The nearshore concentrations appear to be a recent pattern and not consistent with historical observations which show 0-group pelagic juveniles widely distributed over the shelf region (Anderson *et al.*, in press). Nevertheless, with increasing age, juveniles during the period 1981 to 1992 were found progressively further offshore on the shelf (Fig. 7), a pattern strikingly similar to that seen for the older age groups during the 1980s (Fig. 5) and consistent with the observation that by age 4 the juveniles are beginning to adopt the distributional and migratory behaviour of the mature age classes (Rose, 1993).

Spawning, egg, and larval distributions

Myers *et al.* (1993b) have concluded that cod spawning throughout the 2GHJ and 3KL Divisions is protracted (3–4 months); generally beginning and ending earlier in the north (Jan–Jun) and later and more protracted (Feb–Sep) in the south. Spawning in the more southerly Divisions of 3NO and 3Ps reaches its maximum in Apr–May and there is no significant latitudinal trend in the average spawning time (Myers *et al.*, 1993b).

Historically, cod eggs and early stage larvae in the

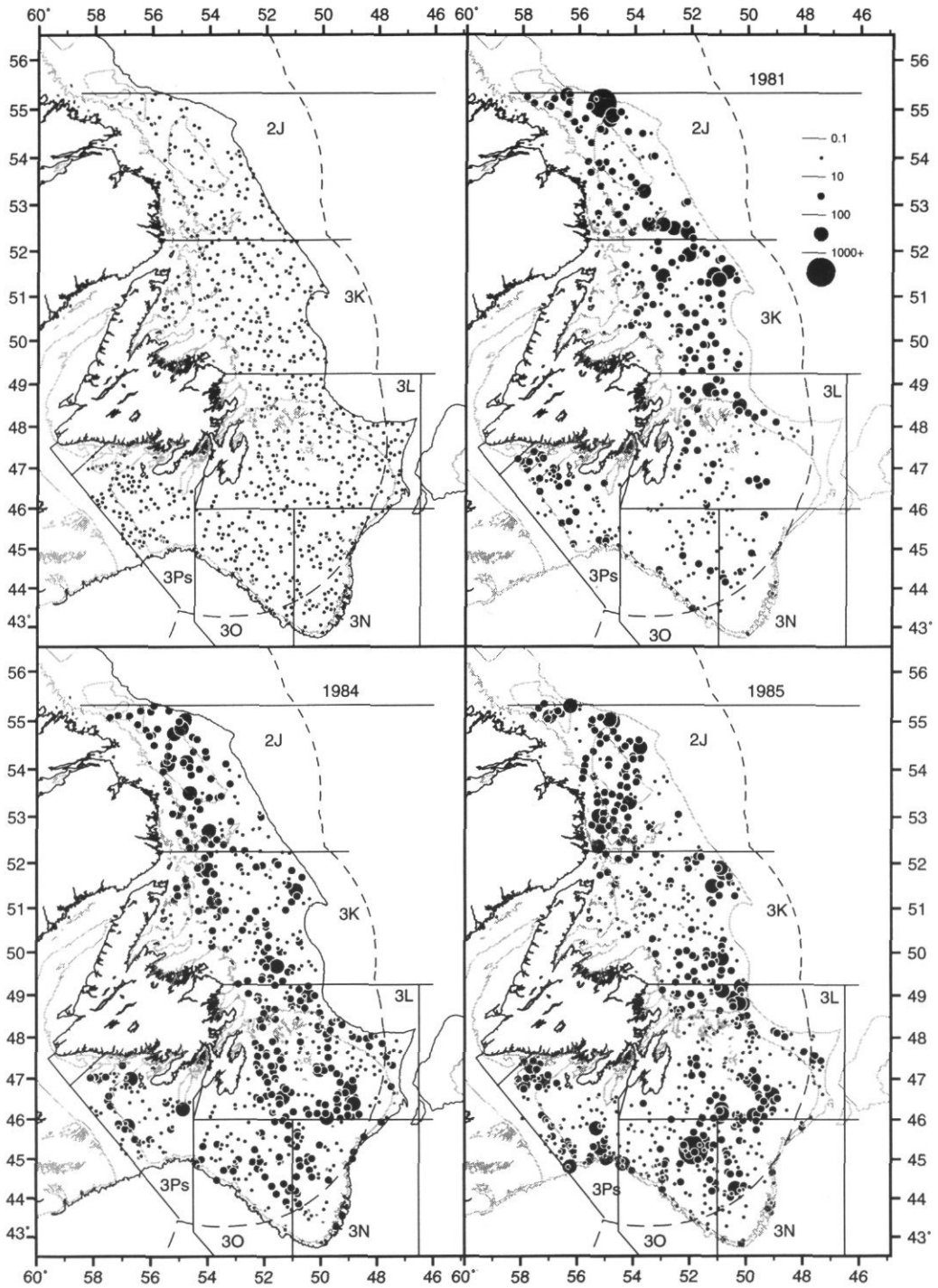


Figure 5. Research survey $\log_{10}$-scaled abundance (number per 1/2 h tow) distributions of age-5+ cod in NAFO Divisions 2J+3KL (Sep. to Nov. of year), Subdivision 3Ps (Feb. of year+1), and 3NO (April of year+1) during the period 1982 to 1984 (after Bishop *et al.*, 1993). Note: only non-zero catches are plotted. Set concentration for a typical annual survey is illustrated in the upper left panel.

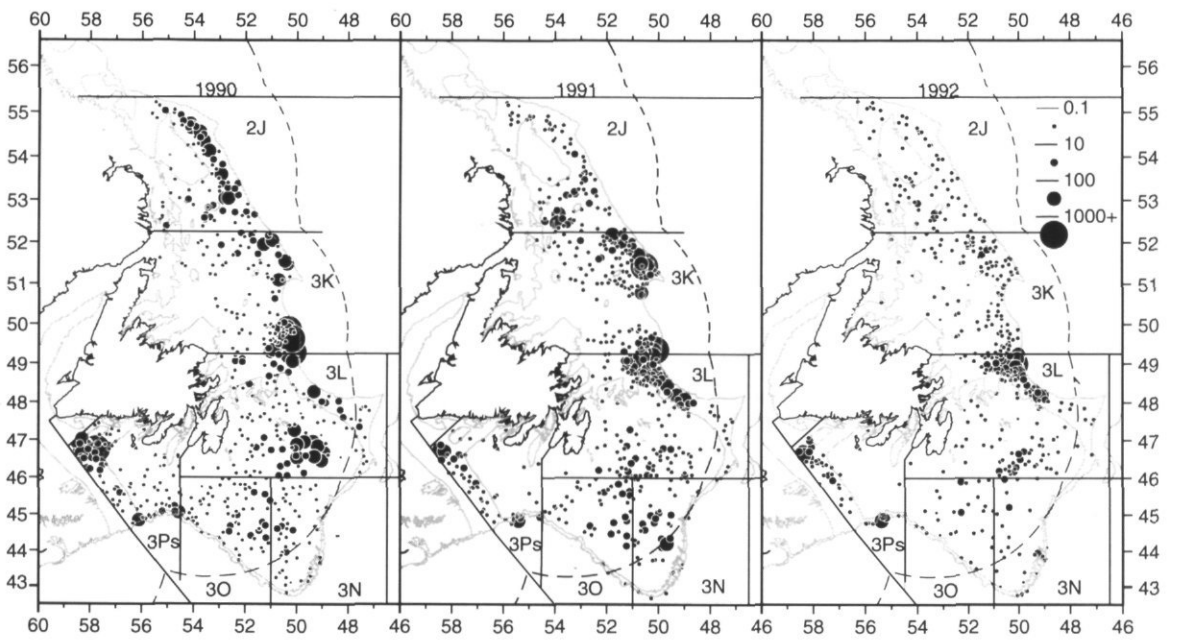


Figure 6. Research survey $\log_{10}$-scaled abundance (number per 1/2 h tow) distributions of age-5+ cod in NAFO Divisions 2J+3KLNO (Sep. to Nov. of year) and Division 3Ps (Feb. of year+1) during the period 1990 to 1992 (after Bishop *et al.*, 1993). Note: only non-zero catches are plotted. Set concentration for a typical annual survey is illustrated in the upper left panel of Figure 5.

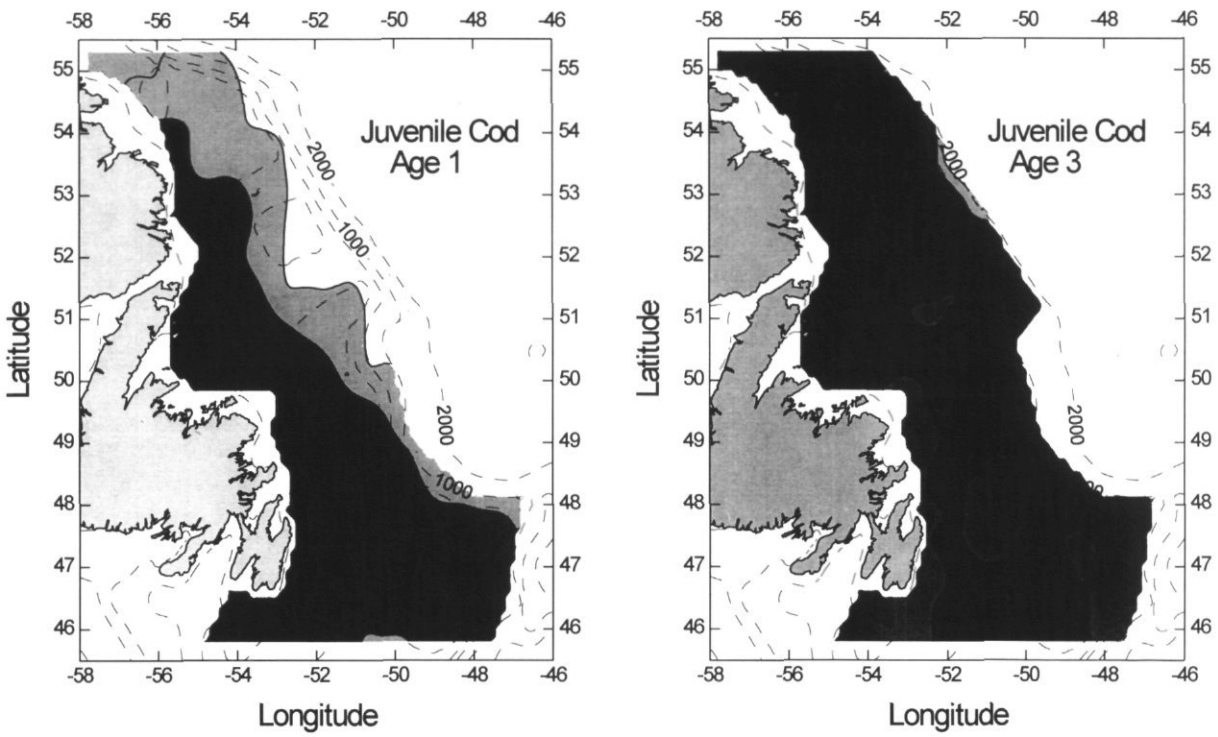


Figure 7. Catch probability isopleths of Age 1 and Age 3 demersal cod from juvenile cod research surveys over the shaded region during the period 1981 to 1992. For Age 1 the grey scale grades from <0.2 to >0.2<0.3 and to >0.3. For Age 3 the grey scale grades from <0.3 to >0.3<0.5 to >0.5<0.7 and to >0.7. After Anderson (1993).

offshore have been concentrated on and along the shelf break of the Labrador Shelf and Grand Banks, particularly in the more northern regions (Serebryakov 1965, 1968). Data compiled by Fitzpatrick and Miller (1979) suggested spawning was concentrated along the shelf break of Hamilton, Belle Isle and Funk Island Banks in 2J+3K, the southern shelf break of the Flemish Cap (3M), the southwest and southeast shelf break of the Grand Banks (3NO), and the shelf break of St Pierre Bank in Division 3Ps (Fig. 8). However, recent analysis by Hutchings *et al.* (1993) of cod maturity data collected during the period 1946–1992 suggest that spawning may be more prevalent in inshore regions, along western (landward) edges of offshore banks, as well as the interior of the Grand Bank (Fig. 8), spawning on the shelf, in northern Division 3L, has been documented in 1991 and 1992 (Rose, 1993).

Stock health

Body condition indices

The overall average body condition index (Kf = gutted weight × length^{-3}) of age 3 to 11 cod in Divisions 2J+3KL during the period 1979 to 1992 is 0.77, and older individuals (age 9+) are generally in better than average condition relative to the younger age classes (Fig. 9). However, the youngest age group (ages 3–5) in (3L) is often at or below average condition, whereas the same age group in the more northerly (2J) region is generally above average, except most recently (Fig. 9). It is apparent from these data that the average condition in all age groups in 2J and 3K has been decreasing since 1988 (see also Bishop and Baird, 1993).

It is possible that the body condition index (Fig. 9) may be size-dependent, as shown by general increases in condition with age (and therefore generally with length) in all three divisions. Thus, we calculated the liver condition index (Kl = liver weight × gutted weight^{-1}) for four different length groups (27–35, 45–53, 63–71, and 90–98 cm) of 2J+3KL cod as opposed to the age groups. Some aspects of the patterns observed in Kf among Divisions and age groups are generally reflected in the liver condition index (Fig. 10). The overall age Kl for the period 1979 to 1992 for the length groups considered is 0.066 and the larger length classes are generally in better condition than the smaller length classes. As seen in the Kf condition index, the larger length classes in the more northerly Divisions (2J+3K) are in above average condition, except in the most recent years in Division 2J, where a decreasing trend, starting in 1989, is apparent. Although similar short-term trends were apparent in previous years, the recent trend in 2J is toward record low levels. In contrast, the three smallest length classes in the most southerly region (3L) have been consistently below the overall average Kl, except subsequent to 1988, when the Kl's show monotonic increases that appear to be approaching record high levels in all the length classes considered (Fig. 10).

Three different processes may explain the observed variation in condition indices. The first, and perhaps simplist, is that generally "good" condition cod have moved from more northerly regions (2J) to more southerly regions (3L), thereby influencing the apparent recent increases in condition in 3L. This explanation is consistent with the observed changes in the survey-based distribution of cod seen in the most recent years (Fig. 6). However, if this was the only process, a similar change would be expected in the condition of 3K fish and this is not readily apparent.

A second possible explanation is that both conditional indices (Kf and Kl), each derived from seasonally fixed annual survey samples, have recently become progressively aliased with respect to normal seasonal cycles in cod physiology that are dependent on temperature and feeding success. Jangaard *et al.* (1967) have shown that the oil content (and a variety of lipid constituents) in cod livers on the Scotian Shelf has a pronounced seasonal cycle that peaks in late autumn and early winter following seasonal increases in temperature and feeding. This seasonal cycling is consistent with that shown for liver weights in Norwegian cod (Eliassen and Vahl, 1982). Condition indices compiled from several years of data for Division 3L on the Grand Bank show that Kl cycles around the overall average Kl of 0.066 estimated above (Fig. 11). Because temperature patterns, expressed as physiological degree-days, have become progressively shifted in recent years in the Newfoundland region, particularly in northward regions where anomalously cold environmental conditions exist (see below), it is reasonable to hypothesize that the normal physiological cycle, as expressed in condition factors, has shifted. Thus a time series of annual estimates can result in apparent anomalous trends, because the sampling for the indices has not been adjusted for the physiological shift. The potential for this effect may be further compounded by the fact that survey data for condition indices are collected at different times (spread over 1 to 3 months) among the different regions during the Autumn survey period.

A third explanation for the variation in condition factors may be found in feeding performance as estimated from partial fullness (capelin and other prey) indices for cod (Fig. 12). Although the data have not been standardized for sampling effort (see Lilly, 1993, 1994), it is apparent that in the most recent years (1991 and 1992) capelin have been virtually absent from the stomachs of cod collected in Division 2J, consistent with the recent declines in Kf and Kl. These findings are also consistent with the virtual absence of capelin in Division

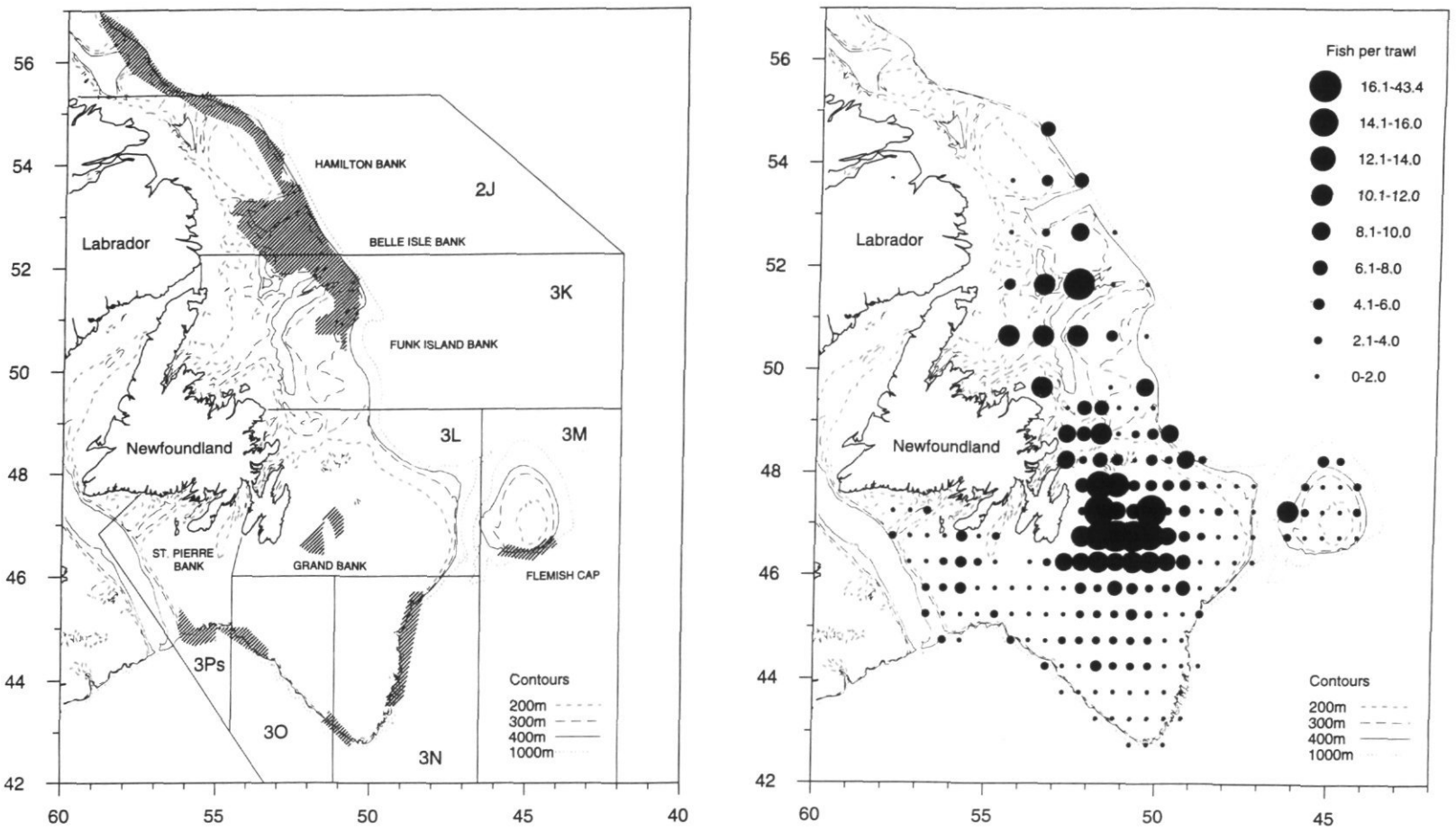


Figure 8. Distributions of cod spawning areas in the Newfoundland region based on spawning maturity data compiled by Fitzpatrick and Miller (1979) as shown by hatching in the left panel, and as compiled by Hutchings *et al.* (1993) as shown by numbers of fish per trawl in spawning condition in the right panel. After Hutchings *et al.* (1993).

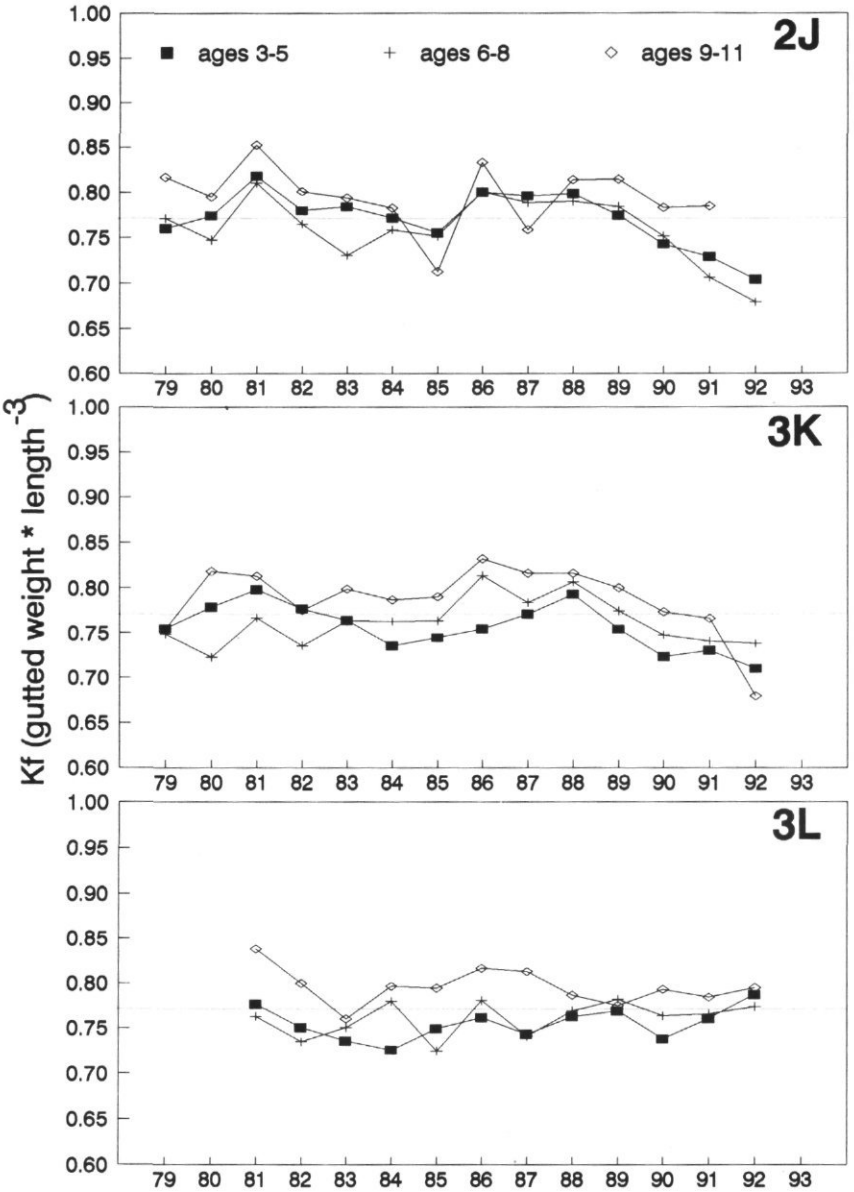


Figure 9. Average body condition indices (Kf = gutted weight × length^{-3}) for cod in NAFO Divisions 2J, 3K, and 3L averaged over three different age groups (3–5, 6–8, 9–11) sampled during autumn research surveys over the period 1979 to 1992. The dotted line at 0.77 reflects the overall (all ages, all Divisions, all times) average condition. Data from Bishop and Baird (1993).

2J in recent years, at least during the autumn capelin research surveys (Miller and Lilly, 1991; Miller, 1993). In contrast, stomach fullness indices for cod in Division 3L in 1990 through 1992 are the highest on record and show a greater proportion of capelin than for any previous estimate (Fig. 12), a pattern that is also consistent with the apparent recent increases in Kl in Division 3L. Finally, fullness indices for Division 3K have been consistently at or above average since 1986, a pattern that is not reflected in the Kf and Kl estimates. However, it is unclear at this time how the changing geographic distributions of cod and their prey through time may be influencing the fullness indices (see Lilly, 1994).

Length and age of maturity

Lengths at 50% maturity in both female and male cod throughout Divisions 2J+3KL have been trending

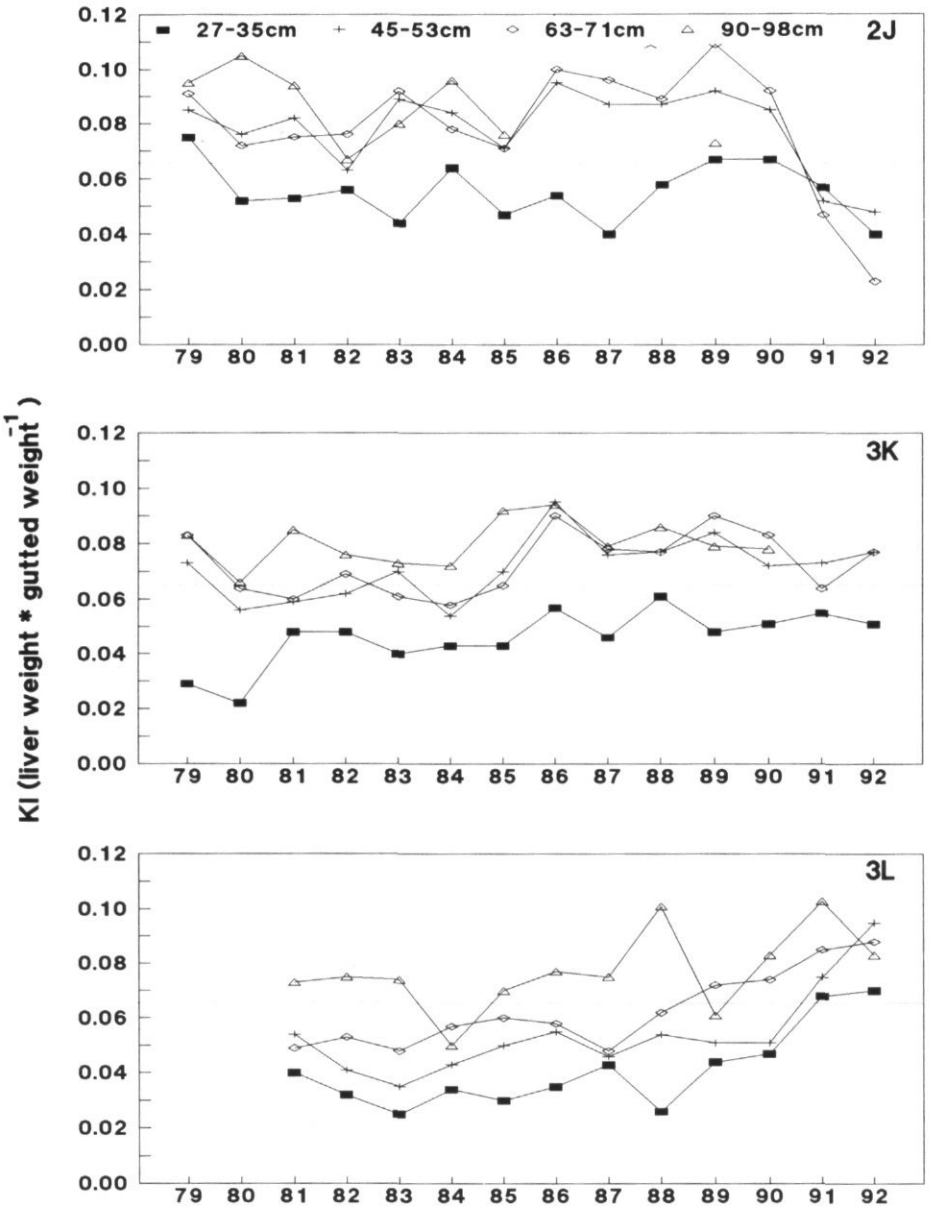


Figure 10. Average liver condition indices (KI = liver weight × gutted weight^{-1}) for cod in NAFO Divisions 2J, 3K, and 3L averaged over four different length groups (27–35 cm, 45–53 cm, 63–71 cm, and 90–98 cm) sampled during autumn research surveys over the period 1979 to 1992. The dotted line at 0.066 reflects the overall average KI for the length groups (all Divisions, all times).

downward since the early 1980s (Fig. 13a, b). The declining trend is most pronounced and least variable in 2J fish (slowest growing), while more variable and less pronounced in the more southerly and faster growing 3L fish. The overall declines calculated from the combined ogives amount to ~ 10 cm in the females (Fig. 13a) and ~8.5 cm in the males (Fig. 13b). Decreases in length at maturity are consistent with size selective exploitation. Changes in the average age at 50% maturity of female and male cod from the same Divisions over the same period (Fig. 13c) did not show a downward trend until the late 1980s; females and males are now showing the youngest ages at 50% maturity (age 5.4 and age 4 respectively) in the 1979 to 1993 record. Model-based

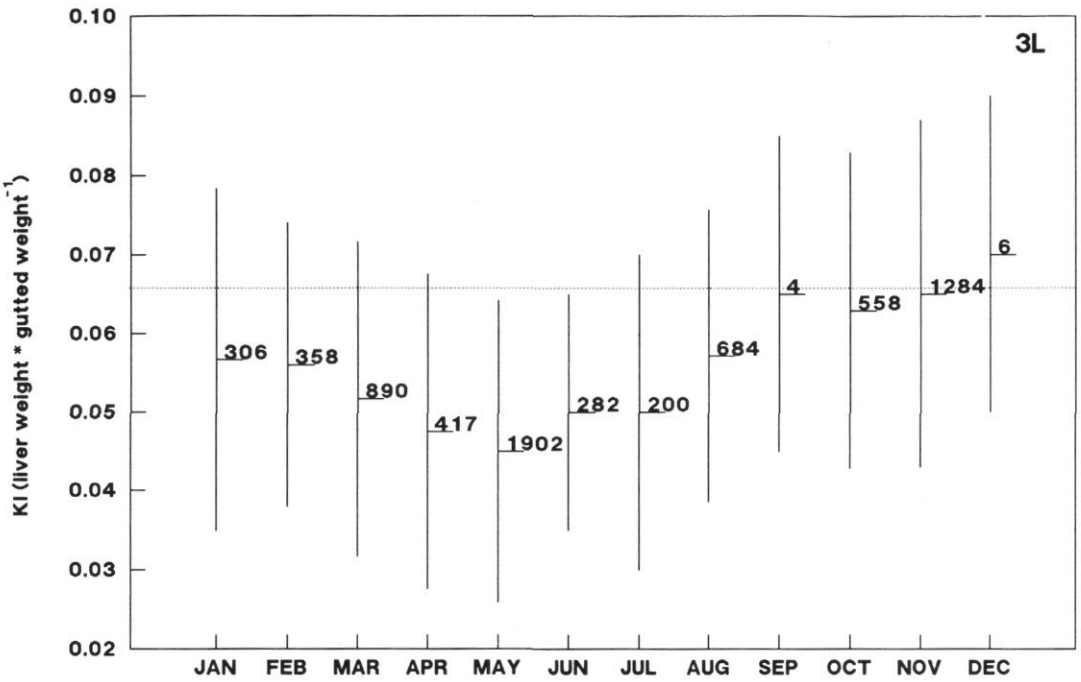


Figure 11. The seasonal cycle in the average (±1 s.d.) of annual monthly averages (when available) of the cod liver condition index (KI = liver weight × gutted weight^{-1}) for NAFO Division 3L compiled for the period 1978–1992. The sample size for each monthly average is highly variable and is noted beside each. Note: not all years are represented for all months. The dotted line at 0.066 reflects the overall average KI for the Divisional length groups shown in Figure 10.

estimates of maturity at age also show a trend in increasing proportions mature for cod aged 5, 6, and 7 years since 1986 (Shelton and Morgan, 1993a, b, in press).

Fishing mortality and spawner biomass replacement

Fishing mortality estimates (F) for cod in Divisions 2J+3KL examined recently by Shelton and Morgan (1993a, b, in press), derived from SPA estimates in Bishop *et al.* (1993), were consistently >0.35 in the mid-1970s, at times exceeding 1.0 in the older (9–11) age classes (Fig. 14a). High Fs occurred during the precipitous decline in landings (Figs. 1, 2), and in estimates of the size of the spawner population and age 3 recruitment (Fig. 3). During the 1977 to 1980 period, following the extension of Canada's economic management zone to 200 miles in 1977 (see Fig. 1), there was a reduction in F to below 0.4 in all age classes (Fig. 14a). This period of reduced exploitation was paralleled by increases in the size of the spawner population and subsequent recruitment from 1978 to 1982 (Fig. 3). However, from 1980 to 1991 (after which severe catch restrictions and fishing closures began) there was a consistent increasing trend in fishing mortality (Fig. 14a) with a particularly marked increase during the final stage of the precipitous decline in landings (Figs. 1, 2). It must be noted that the SPA population and fishing mortality estimates are derived under the assumption of a fixed natural mortality. Nevertheless, despite the reduced F estimates in the late 1970s and early 1980s (Fig. 14a), landings in 2J showed a limited increase to a recent (post-1977) maximum in 1984 (Fig. 2). Increased landings were more pronounced in 3K to a recent maximum in 1985, and in 3L to recent maxima in 1985 and 1988 (Fig. 2). Increased landings were associated with increasing fishing mortalities after 1980 (see also Hutchings and Myers, in press).

The combined effects of fishing mortality on the spawning population size of northern cod, and the resulting reduction in length and age structure of the populations, has reduced the fecundity contributions of the older (larger, more fecund) individuals and can have a dramatic influence on recruitment (Hutchings and Myers, 1993). Changes in weights and proportions mature at age have acted in concert with changes in fishing mortality to influence the amount of recruitment required to replace the spawner stock (Shelton and Morgan, 1993a, b, in press). Calculations of recruitment per spawner show that annual values were below replacement levels in the mid-1970s, rose briefly above replace-

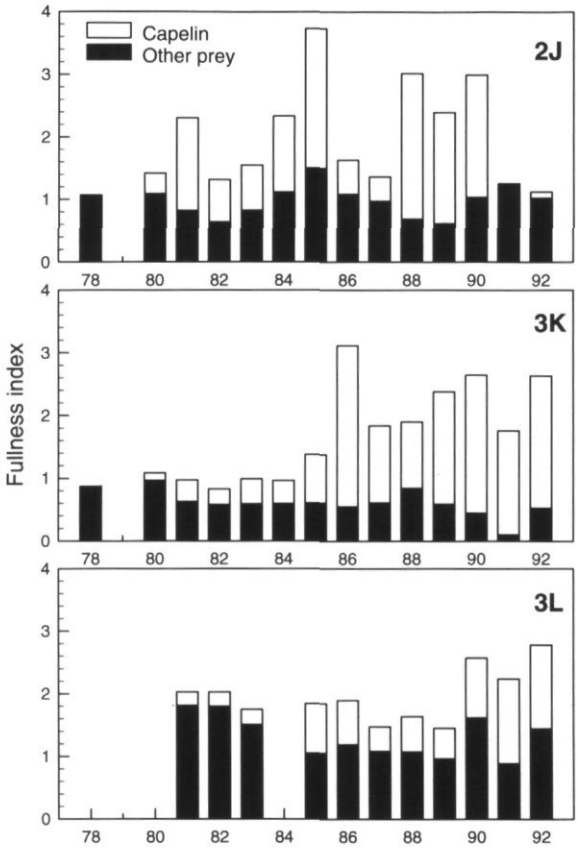


Figure 12. Average fullness index for cod stomachs partitioned into capelin and "other" prey species sampled during Autumn over the period 1978 to 1992 in NAFO Divisions 2J, 3K, and 3L. Zero (baseline) indices indicate no data available. From Lilly (1993, 1994).

ment levels in the late-1970s and early 1980s, and remained below replacement levels from 1983 onward (Fig. 14b), paralleling the stock decline. Even when the effect of fishing mortality is removed from the calculations of replacement, the combined effect of changes in weights and proportions mature at age cause the level of recruitment required to meet spawner biomass replacement to increase steadily from 1980 onward (Fig. 14b). Values of recruit per spawner for the apparently poor year classes of 1988 and 1989 (see Fig. 3) were very close to the replacement level, i.e., the level of recruitment below which the population can go extinct even in the absence of fishing. Thus, despite the apparent increased size of the spawner population in 1987 (Fig. 3), the required replacement recruitment remained high, recruitment per spawner has remained low and parallels recent and continuing declines in length and age of maturity and some indices of condition.

Recruitment and the environment

Recruitment in northern cod has been at, or near, record minima subsequent to the formation of the 1982 year class (age 3 in 1985, Fig. 3). Although the size of the spawning stock plays a role in determining recruitment (Myers *et al.*, 1993a), recruitment appears to have been negatively influenced by extreme environmental conditions (anomalously cold) since 1983, with a brief respite in 1986 and 1987, as indicated by a variety of strongly correlated oceanic and atmospheric indices (Fig. 15 and see Colbourne *et al.*, 1994). Of the 36 correlations possible among 9 different environmental variables, including various measures of the wind and pressure fields (Fig. 15), ice conditions, water temperatures throughout the water column, and the volume and extent of the cold intermediate layer overlying the Newfoundland and Labrador shelf regions (Fig. 15), a full 28 (78%) are each independently significant at $\alpha = 0.05$ (Table 1). Correction for the simultaneous correlations requires $p < 0.0013$ and thus 44% remain significant. The Labrador air temperature and the Winter–Spring ice-extent anomalies are significantly correlated with most of the other indices (Table 1) and perhaps represent the best measures of the overall environmental conditions in the Newfoundland and Labrador region. It was only during 1986 and 1987 that there was a marginal increase in recruitment of northern cod (Fig. 3), similar to the increases seen in the period 1978 to 1982 when environmental conditions were also warmer than average (Fig. 15). Thus it appears that recruitment variability in the recent past is determined, in part, by environmental conditions. The persistence of the extremely cold conditions suggests that future recruitment, at least for northern cod, will not reach the levels estimated in the 1960s (Fig. 3b), particularly given the limited size of the spawner population.

Recruitment levels in northern cod may also be determined by the distributional pattern of the spawners (at least offshore) and ocean climate variations. For example, deYoung and Rose (1993) have hypothesized that northerly distributions of spawners are necessary for relatively high recruitment levels, and will likely occur during relatively warm periods (see Rose *et al.*, 1994). However, the relationship between water temperature and recruitment is unclear (see deYoung and Rose (1993) and Hutchings and Myers (in press)), and although Helbig *et al.* (1992) have suggested that other factors, such as storm tracks, may have a significant impact on egg and larval drift and subsequent settlement distributions and recruitment, these same authors conclude that no convincing relationship has been demonstrated between recruitment in northern cod and the available climatic indices.

Of the various environmental indices available, early

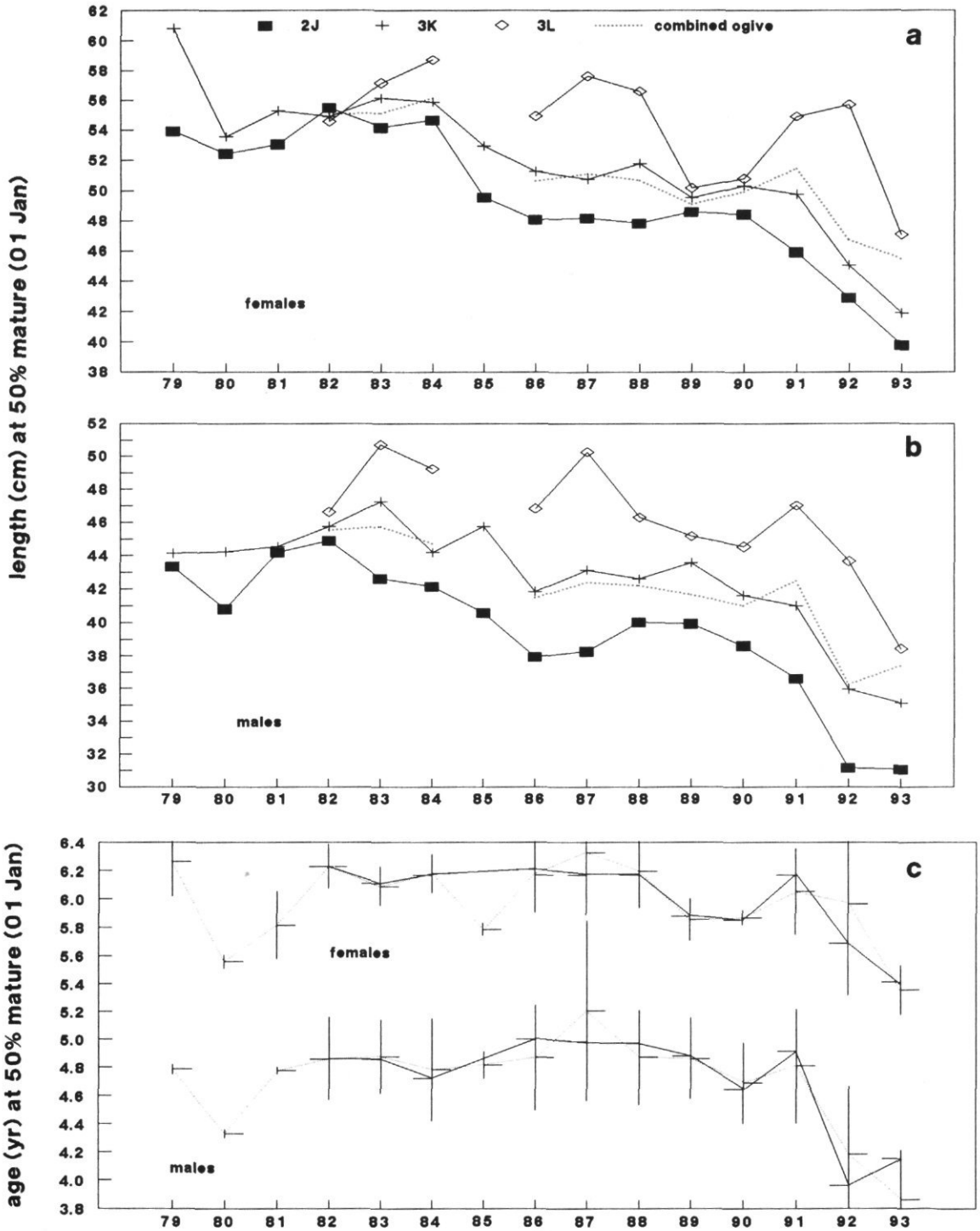


Figure 13. Average length (cm) at 50% mature estimates for cod females (a) and males (b) in NAFO Divisions 2J, 3K, and 3L, and (c) average age (years ± 1 s.d.) at 50% mature for females and males combined for all three Divisions during the period 1979 to 1993. Estimates of the combined ogives are shown with the dotted line. Data from Morgan *et al.* (1993).

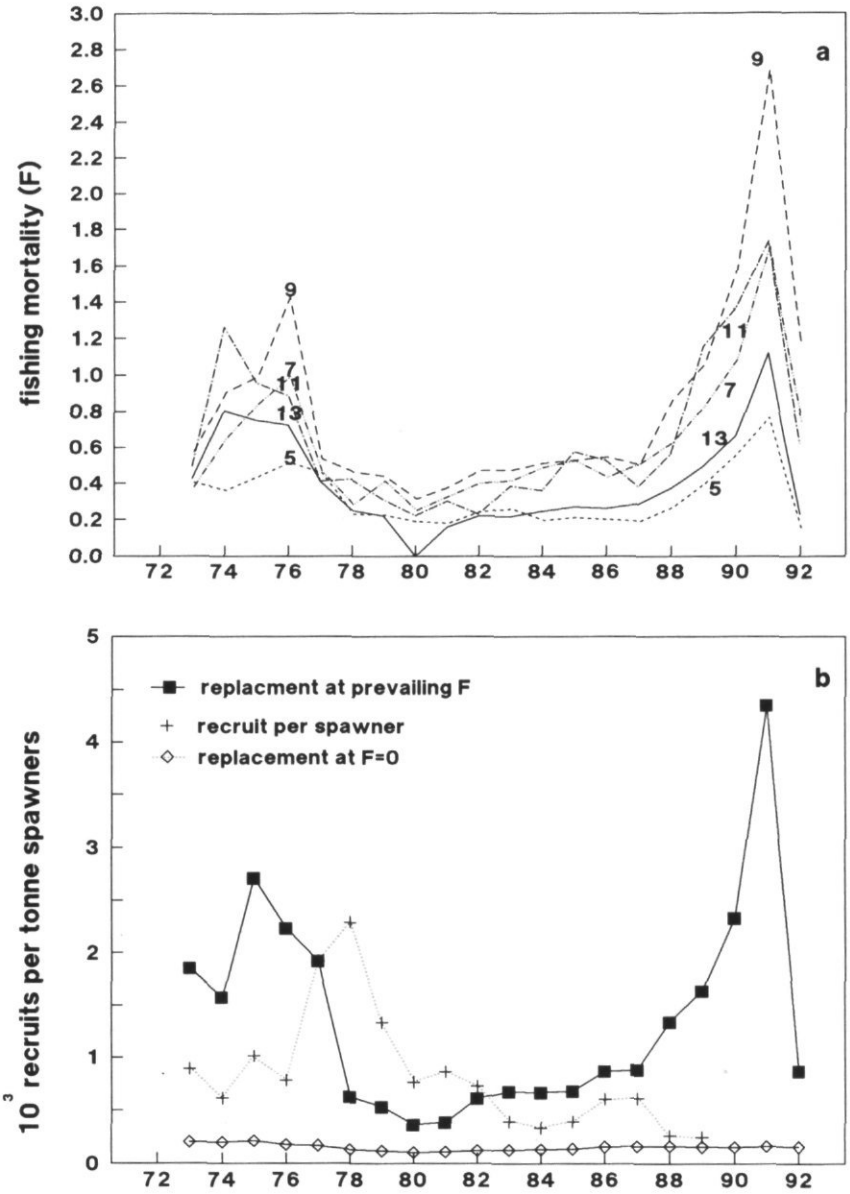


Figure 14. (a) Estimates of fishing mortality (F) for ages 5, 7, 9, and 13 in NAFO Divisions 2J+3KL for the period 1972 to 1992, and (b) annual values of recruitment (10^3 individual) per spawner (t) and spawner biomass replacement levels calculated at the prevailing fishing mortality (F) and at F = 0 over the period 1972 to 1992. After Shelton and Morgan (1993a,b, in press), and data from Bishop *et al.* (1993).

work by Sutcliffe *et al.* (1983) showed that variations in northern cod recruitment could be explained by variations in depth-averaged (0–50 m), summer salinity measurements at Station 27 in Division 3L. A recent examination of the salinity–recruitment relationship by Myers *et al.* (1993a) has generally confirmed those initial findings and shows that the salinity variations can reproduce recruitment fluctuations during the period 1962 to 1988, although the mechanism(s) accounting for the modelled relationship remains elusive. Although the salinity-based model was able to capture the fluctuations in recruitment variations, it was unable to capture the long-term trend from high recruitment (and high-spawning biomass) in the 1960s to low recruitment (and low-spawning biomass) in the 1970s and 1980s. With the addition of spawning-stock biomass estimates to the

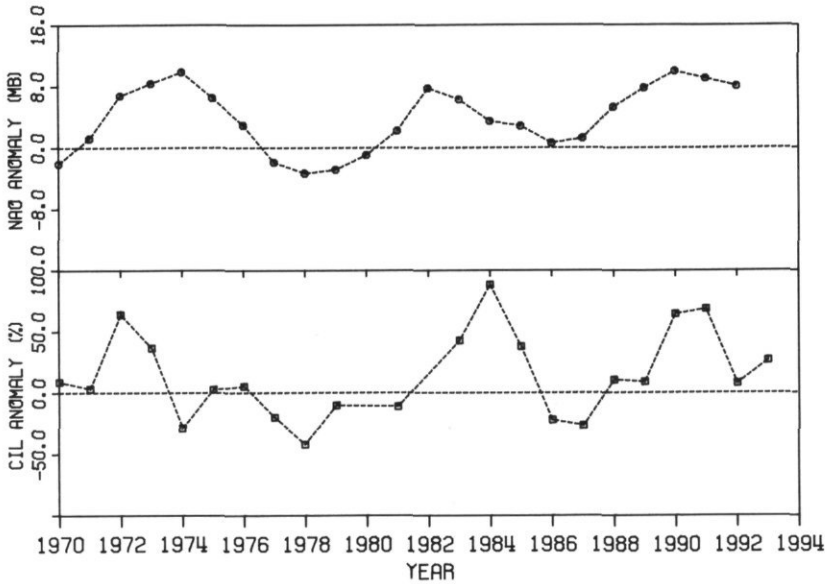


Figure 15. Time series of atmospheric pressure differentials using the annual North Atlantic Oscillation (NOA) anomaly index (positive values infer poor environmental conditions), and the percentage difference from the average cross-sectional area of water <0.0°C in the cold intermediate layer (CIL) of the Newfoundland Shelf (NAFO Divisions 3K+3L). After Colbourne *et al.* (1994).

Table 1. Correlation matrix of coefficients of determination and significance values for annual estimates of oceanic and atmospheric variables (1970 to 1993) in the Northwest Atlantic region of Newfoundland. CIL ( ) refers to the cross-sectional area of the −1, 0, and 1 degree isotherms of the cold intermediate layer in summer on the continental shelf; NAO ANOM is the North Atlantic oscillation (pressure differential) annomaly relative to the 1951–1980 average; CIL(MIN) CORE-T is the minimum summer core temperature of the cold intermediate layer; NW WIND FREQ is the frequency of winter NW winds measured in Labrador; AIR-T ANOM is the Labrador air temperature anomaly referenced to the 1960 to 1985 average; SELF ICE ANOM is the winter and spring areal ice cover relatived to a 25-year average; and STN-27 BT is the bottom temperature anomaly at Station 27 referenced to the 1946–1993 average. Shaded values are significant at a = 0.05. See Colbourne *et al.* (1994) for greater detail.

	CIL(0) AREA SUMMER	CIL(−1) AREA SUMMER	CIL(1) AREA SUMMER	NAO ANOM 51−80	CIL(MIN) CORE−T SUMMER	NW WIND FREQ LAB.	AIR−T ANOM LAB.	SHELF ICE ANOM NFLD
CIL(−1) AREA	0.884 0.000							
CIL(1) AREA	0.965 0.000	0.787 0.000						
NAO ANOM	0.515 0.017	0.538 0.012	0.411 0.064					
CIL(MIN) CORE−T	−0.582 0.005	−0.680 0.001	−0.515 0.014	−0.332 0.142				
NW WIND FREQ	0.263 0.263	0.311 0.183	0.192 0.418	0.746 0.000	−0.253 0.281			
AIR−T ANOM	−0.647 0.003	−0.628 0.004	−0.564 0.012	−0.847 0.000	0.571 0.011	−0.784 0.000		
NFLD ICE ANOM	0.780 0.000	0.743 0.000	0.764 0.000	0.720 0.000	−0.716 0.001	0.528 0.017	−0.852 0.000	
STN−27 BT	−0.438 0.042	−0.520 0.013	−0.409 0.059	−0.662 0.001	0.235 0.292	−0.492 0.020	0.699 0.000	−0.851 0.000

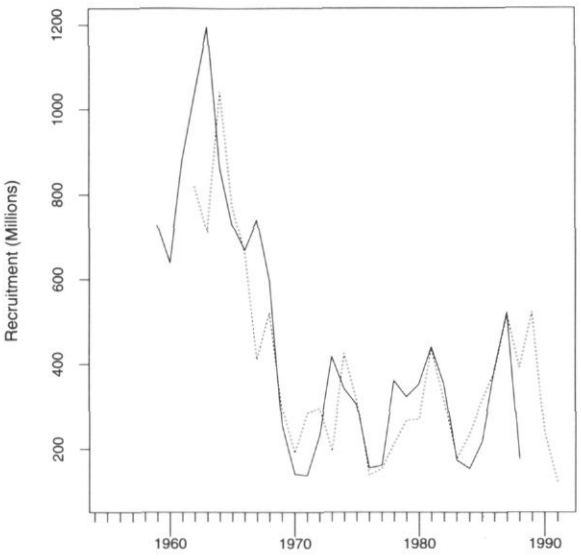


Figure 16. Time series of survey-based estimates of recruitment (solid line) and modelled recruitment (dotted line) using annual 0–50 m summer salinity averages at Station 27 (NAFO Division 3L) and annual survey-based spawning stock biomass estimates. After Myers *et al.* (1993a).

model (Myers *et al.*, 1993a), the long-term trend and short-term fluctuations in northern cod could be reproduced (Fig. 16), reflecting both the stock size and environmental influences on recruitment. Model predictions indicate recruitment will be at a record low in 1991, simply reaffirming the quotation in our introduction that "recovery of the spawning stock biomass is unlikely before the year 2000 at the earliest" (Anon., 1993, p.16).

Conclusions

It is apparent from the variety of information presented that intense fishing, particularly on northern cod in Divisions 2J+3KL in the 1960s reduced the Newfoundland stocks to a point where long-term average recruitment was reduced by ~50%, partly in response to decling spawning stock size, but also as expressed through the equally precipitous decrease in the fecundity contribution by older age groups as the size and age structure was compressed.

Although the estimated spawner biomass increased in the late 1970s, changes in weights and proportions mature at age, together with increasing fishing mortality, imply that from the early 1980s onward an ever-increasing amount of recruitment per spawner was required to exceed replacement and permit population growth. In addition, poor environmental conditions have apparently had an additive effect in further limiting potential recruitment.

Persistence of poor environmental conditions into the 1990s will likely continue to influence the distribution and physiological conditions of adults. This may have further negative effects on fecundity and recruitment. However, the Canadian moratorium on cod fishing should help to protect the remaining stock. Continuance of a poor environment may also limit recruitment, even if the most recent recruitment serves to increase the spawner population. The above suggests that a series of better than average environmental years is needed if the chances for a series of good recruitment years rebuilding the stock size and length/age structure are to be increased. The long-term record suggests that this may only occur: (1) if fishing pressure remains at or near zero; (2) if the size of the spawner population increases significantly (at least to some level exceeding that of 1987); (3) if the lengths at 50% maturity rebound to the early 1980 levels; and (4) if the current, offshore distributional patterns of the adults changes to resemble the distributions seen in the 1980s.

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Fluctuations in the occurrence of cod in Greenland waters and their possible causes

Erik Buch, Svend Aage Horsted, and Holger Hovgård

Buch, E., Horsted, S. Aa., and Hovgård, H. 1994. Fluctuations in the occurrence of cod in Greenland waters and their possible causes. – ICES mar. Sci. Symp., 198: 158–174.

In historical time cod has probably always been present in Greenland waters, but its abundance and spatial distribution have varied greatly as a result of variations in the marine environment. The general warming of the northern hemisphere around 1920 evidently led to the establishment of a self-sustaining and very abundant West Greenland cod stock which through the 1930s to 1960s produced good year classes at relatively short intervals. It is, however, clear that an important contribution to the fisheries at West Greenland stems from cod spawned at Iceland. A third component of the cod stock at West Greenland is composed of local inshore stocks in some fjords. The warm period came to an end in the late 1960s. The subsequent period has shown three extremely cold periods explained by different geophysical events. The West Greenland cod stock has not produced any good year classes since the 1960s. All important year classes since then have been of Icelandic origin. The latest of these, those of 1984 and 1985, sustained reasonable fishing during 1988–1990, but evidently left West Greenland waters thereafter. At present, cod is as sparse in the West Greenland offshore area as it was at the beginning of this century. The inshore local stocks seem to be surviving and may still support limited local fisheries.

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Introduction

At West Greenland, cod occurs at one of its northern limits and both abundance and spatial distribution have shown considerable changes in historical time. The large variations are reflected in the annual yield, which has varied by a factor of one hundred within the present century. The climate at West Greenland has also undergone very marked changes, and in a very general sense periods with higher water temperature coincide with periods of high cod abundance. The changes in overall cod abundance, however, are difficult to relate to climate, as three different stock components are involved: local stocks in fjords, offshore cod from spawning at Greenland, and cod of Icelandic origin.

It is the objective of the present paper to describe the climate changes in Greenland, the stock structure, and the development of the stock and fisheries. Emphasis is placed on the present century, for which statistical information is available, but some historical information from the preceding centuries has been included. Statistical divisions and names of localities and cities mentioned in the text are shown on the map (Fig. 1).

Marine environment – climate

The marine climate off West Greenland has undergone dramatic changes during the last century. Figure 2 shows the classical picture by Smed (1980) of the interannual variability of the surface temperature in the West Greenland area, and the follow-up observations from Fylla Bank by Buch (1993a). The Fylla Bank data material constitutes the longest and most complete time series from the West Greenland standard hydrographical sections. Comparison with data from various West Greenland sections reveals similar trends (Buch, 1984). Although the data material behind the two graphs in the

figure is different, the graphs give the same general picture of surface temperature variability for the period of overlap (1950–1975). From a climatic point of view a number of interesting events are reflected in these figures.

A strong and rapid increase in temperature (1.5–2°C) started around 1920. Temperatures remained high until the late 1960s when the first of three extremely cold periods was observed. The following two cold periods were seen in the early 1980s and the early 1990s. In between the cold periods, temperature improved but never reached the levels of the 1920–1970 period.

Interannual variability in the temperature conditions of the upper ocean layer can be explained by the following processes.

Ocean circulation

The physical oceanography along the West Greenland fishing banks is governed almost entirely by the inflow of water masses from other parts of the North Atlantic (Fig. 3). In the present context, distinction is made between only two water regimes along West Greenland. A more detailed analysis and description of the water-mass distribution can be found in Buch (1990), where the water masses are classified by their temperature and salinity characteristics.

The surface layer (0–150 m) is dominated by cold, relatively fresh Polar Water carried to the area by the East Greenland Current, while the underlying layer (150–800 m) consists totally of water originating from the warm, salty North Atlantic Current (Buch, 1990, 1993b). Mixing and heat diffusion between the two layers are important factors which among other things are dependent on the flow intensity.

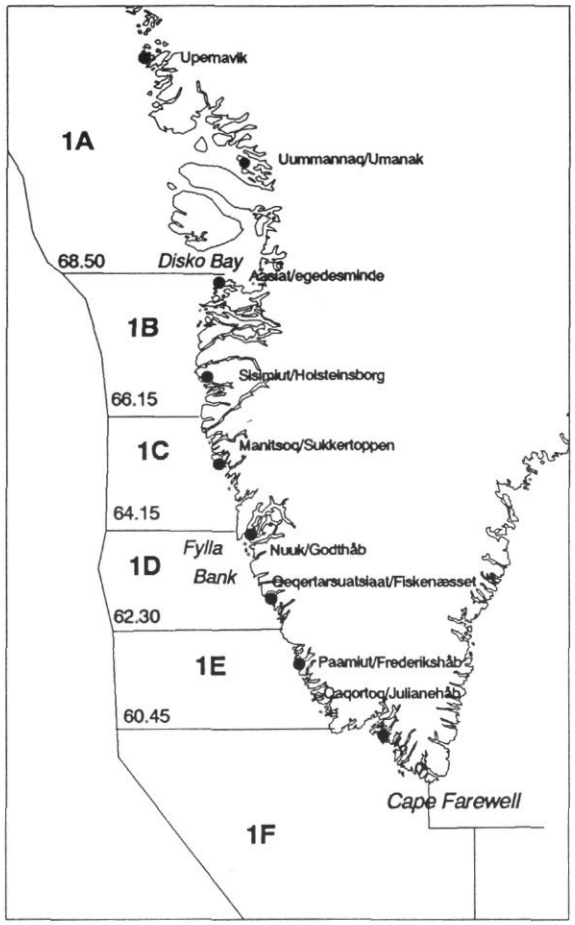


Figure 1. Map of part of Greenland with NAFO statistical divisions and names in Greenlandic and Danish of cities and settlements mentioned in the text.

Intensity of inflow to the West Greenland area

Since the West Greenland area is influenced by inflow of water from both a cold and a warm current component, the relative strength between the two will obviously affect the temperature conditions in the area. The two currents also have a distinct seasonal variability, the East Greenland Current being strongest during spring and early summer while the Atlantic component attains maximum strength in late autumn and winter. The temperatures given in Figure 2 reflect spring–summer conditions, i.e. the period of maximum inflow of Polar Water. Years with a strong East Greenland Current will tend to show up as cold ones and vice versa.

The cold period around 1970 was explained by Dickson *et al.* (1975) by this process. Formation of an abnormal atmospheric high pressure over Greenland and low pressure over northern Norway resulted in a high frequency of northerly winds in the area between Greenland and Norway, whereby great amounts of cold water and ice were carried out of the Arctic Ocean and advected towards Iceland and West Greenland by the East Greenland Current.

The inflow of Polar Water to the West Greenland area may be predicted, since a high correlation between the areal extent of sea ice in the Greenland Sea in December (reflecting the intensity of the outflow of cold water from the Arctic Ocean) and the Fylla Bank temperature the following June has been demonstrated (Sloth and Buch, 1988).

Air–sea interaction in the West Greenland area

Local exchange of heat between ocean and atmosphere is everywhere a process of great climatic importance. Recent research has documented that variations in the air pressure gradient between the Subtropical High near

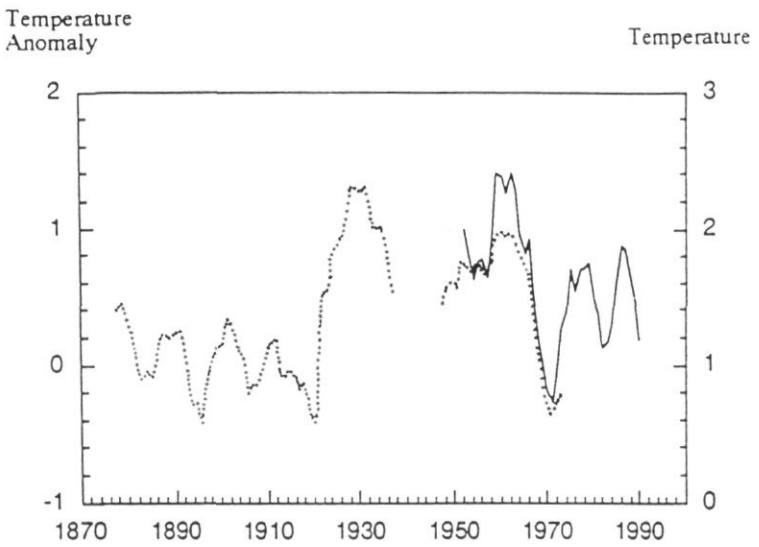


Figure 2. Sea-surface temperature variability at West Greenland (1876–1992). Dotted line: sea-surface mean temperature anomalies off West Greenland (base 1876–1915); (five-year running mean) (after Smed, 1980). Full line: mean temperature in 0–40 m depth on the top of Fylla Bank (five-year running mean).

the Azores and the Subpolar Low near Iceland – the so-called North Atlantic Oscillation (NAO) index – has a great impact on air temperatures over Greenland and Europe (Van Loon and Rogers, 1978; Rogers and Van Loon, 1979; Rogers, 1985). A greater than normal difference in the air pressure between the Azores and Iceland results in strong westerlies, whereby heat is carried to Europe while Greenland experiences cold conditions. The opposite is the case when the air pressure difference is below normal. Correlation analysis between ocean temperatures at Fylla Bank and the monthly mean air temperatures observed at the Nuuk meteorological station reveals high correlation (0.63–0.70) between the sea and the atmospheric temperatures (Stein and Buch, 1991; Buch and Nielsen, 1990).

The two recent cold periods observed off West Greenland can be explained by the process of local air–sea interaction (see Rosenørn *et al.*, 1985 and Buch, 1993a). On both occasions a cold Arctic air mass was situated over the Davis Strait with its centre close to Aasiaat (Egedesminde). Particularly during winter, extreme negative temperature anomalies in the atmosphere were observed, whereby the ocean surface layer cooled so effectively that sea ice formed in areas usually free of ice. The presence of sea ice damps the heating of the ocean surface layer the following spring and summer, since great amounts of heat energy are used to melt the ice, so a cold winter will naturally have a negative impact on the following seasons.

It can therefore be concluded that the environmental conditions in the surface layer off West Greenland are ruled primarily by local air–sea interaction and by the intensity of the inflow of cold Arctic water, which also may be related to air–sea interaction effects in the Arctic Ocean–Greenland Sea area. The interannual variability of these processes is ruled by the large-scale air pressure distribution over the northern North Atlantic.

The rise in temperature at the beginning of this century was a phenomenon registered throughout the northern hemisphere (Kelly, 1984), while the cold conditions experienced during the last two to three decades, including three extremely cold periods, is a phenomenon characteristic of the western North Atlantic and specifically of the Davis Strait. The climatic change in the late 1960s can be interpreted as changes in the atmospheric pressure distribution over the North Atlantic resulting in different wind patterns and associated changes of the ocean currents.

Stock structure of the cod at West Greenland

The cod at West Greenland is recruited from three different spawning stocks: (i) inshore spawners, (ii) offshore spawners around southern Greenland, and (iii) Icelandic cod. Inshore spawning is observed in a range of fjords in central West Greenland (64–67°N.lat.) (Jensen and Hansen, 1931; Hansen 1949). Little or no spawning takes place in areas to the north and south (Hansen 1949 etc; Hovgård and Wieland, unpubl.). The best information on the inshore spawning is from the Godthåb

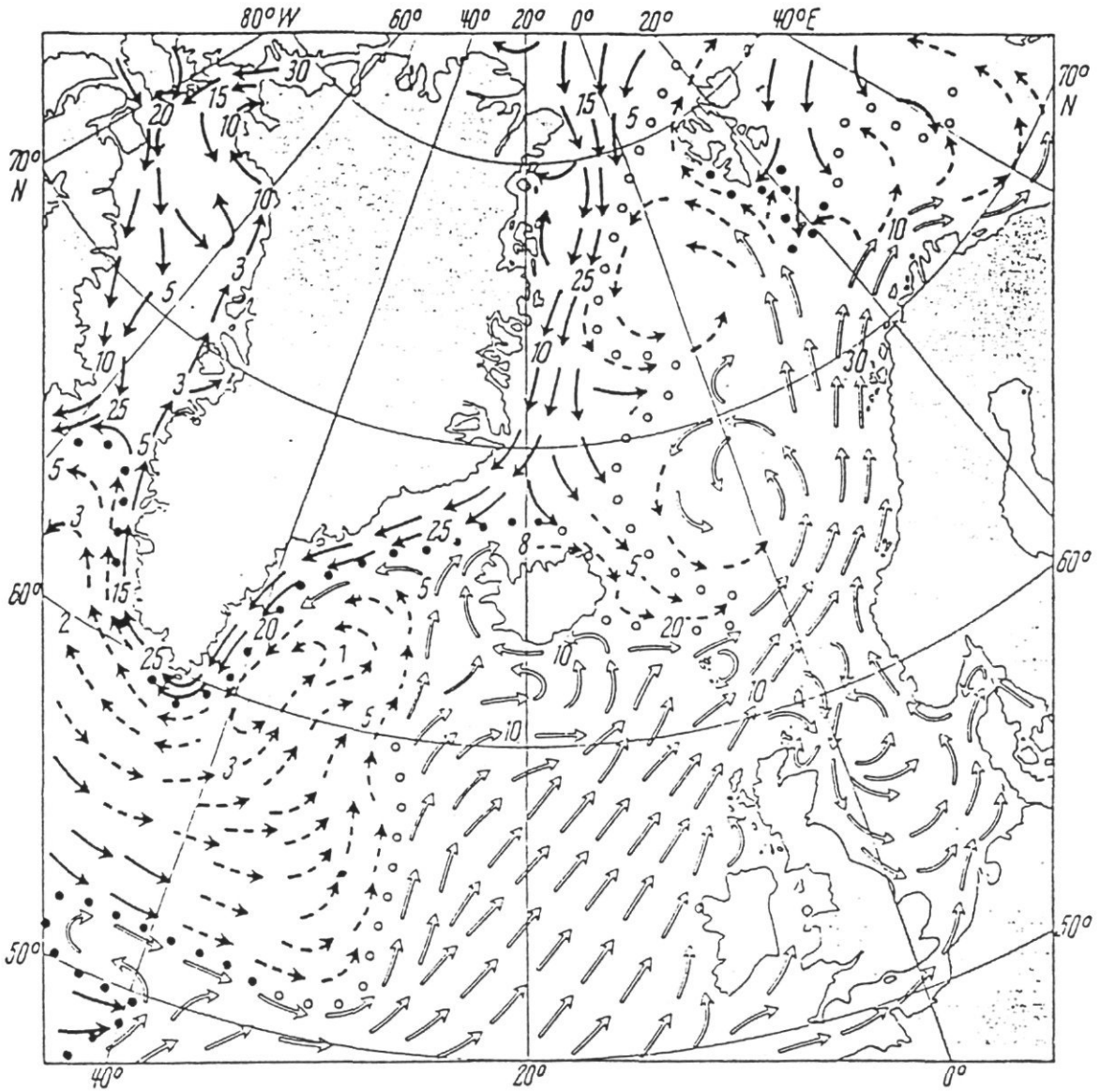


Figure 3. Surface currents in the northern part of the Atlantic Ocean (after Dietrich, 1957). White open arrows: Atlantic water. Full line arrows: Polar water. Broken line arrows: mixed water. Circles and black dots: Polar front. The numbers give the current speed in cm sec^{-1}.

Fjord (64°N.lat.), which has been extensively covered by egg surveys (Smidt, 1979) The main spawning area is located in a shallow fjord branch in the innermost part of the fjord. Egg density declines gradually from 60 000 per haul at the spawning area to reach low values (less than 100) at the entrance of the fjord (Hovgård and Wieland, unpubl.).

The offshore spawning area was well covered by the NORWESTLANT surveys in 1963 (Hansen, 1968), when large densities of eggs were found in a broad belt around southern Greenland, with the highest densities off Southeast Greenland (Fig. 4). A similar distribution was found by a USSR survey in spring 1962 (Serebryakov, 1967). Surveys in other years covering only West Greenland confirm that eggs are found in a belt parallel to the southwestern coast (Hovgård and Wieland, unpubl).

In May–June 1963, almost no larvae were seen at East and South Greenland (see Fig. 4) and by July–August few larvae were found south of 64°N.lat. at West Greenland. A large number of surveys conducted off West

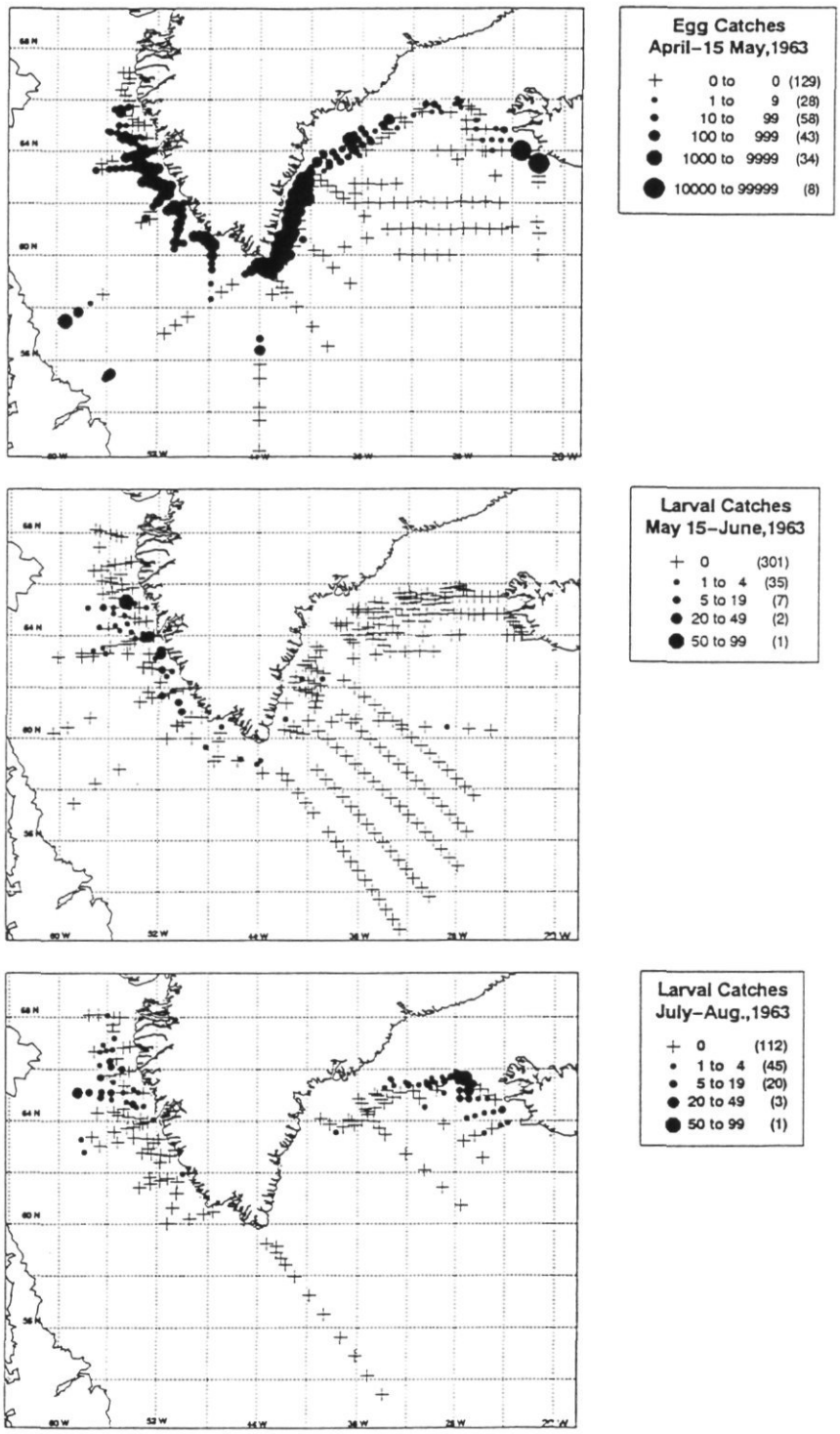


Figure 4. Catches of cod eggs and larvae per 30 min stramin net (2 m diameter) hauls in the NORWESTLANT surveys in 1963. Catches of eggs off Southeast Greenland converted from Hensen net catches by Hovgård and Wieland (MS submitted to NAFO).

Greenland in July in other years show very similar larval distributions (Hovgård and Wieland, unpubl.). Harden Jones (1968) assumes that the settling area of these cod is in the more northern part of West Greenland, which was described as a nursery area by Horsted (1967). The size distribution of larvae taken in the surveys supports this view. In June, larval size ranges from 3 to 17 mm and in July from 4 to 36 mm (Hovgård and Wieland, unpubl.). The size at settling at the bottom at Greenland is not known, but for the Barents Sea – the area most resembling Greenland – settling size is given as 60–100 mm (Sundby and Godö, in prep.) with a pelagic phase extending up to six months (Bergstad *et al.*, 1987).

Spawning at Iceland takes place off the southwestern coast from the end of March to the beginning of May (Jónsson, 1982). Pelagic surveys, conducted in August since 1970, show that 0-group cod are found predominantly north and west of Iceland (Helgason and Sveinbjörnsson, 1987). However, in 1973, 1984, and 1985, high numbers of cod were observed between Iceland and Greenland. Cod larvae have been observed earlier in this area by Schmidt (1909), Tåning (1943), and during the NORWESTLANT survey in 1963 (see Fig. 4). Recent surveys indicate that such cod from Iceland settle in southeast and southwest Greenland. Furthermore, Hovgård and Messtorff (1987) noted that young haddock (this fish is relatively rare at Greenland, but is spawning at Iceland) with the same ages as the drifting cod had settled in East Greenland and at the southernmost part of West Greenland.

If the Harden Jones (1968) migration hypothesis is correct, then one could use tag/recapture data to reveal stock structure, assuming that a cod tagged at Greenland and caught at Iceland was born at Iceland and returned to its parent spawning area. Since the first tagging in 1924 it has been known that cod migrates from Greenland to Iceland. Tagging from 1924 to 1939 showed that 71% of returns from tagging south of 62°30′N.lat. were from Iceland. From more northern tagging, 19% were returned from Iceland (Hansen, 1949). Since 1945, tagging experiments at Greenland have shown the same pattern, although the proportion of returns from Iceland has been much lower. Only 1–4% of the returns from tagging north of 62°30′N.lat. (NAFO Division 1ABCD) are from Iceland compared with 23% and 17% for the two southernmost divisions at West Greenland and 51% from East Greenland (Hovgård, 1991). Norwegian tagging, 1953–1956, conducted north of 66°N.lat. similarly showed that only 3% of the returns were from Iceland (Rasmussen, 1959). Regarding cod tagged in the fjords, data from the best-covered area (the Godthåb Fjord) show that 82–86% of the recaptures are taken within the fjord, suggesting that these populations are relatively stationary (Hansen, 1949; Hovgård and Christensen, 1990).

The stock mixture is also revealed by the spatial distribution of year classes. Hansen (1949) showed that the abundance of cod at West Greenland varies as a result of wide fluctuations in the strength of the year classes, some of which had a mainly northern distribution and others mainly a southern one. Meyer (1957) and Rasmussen (1957 and 1959) observed the same phenomenon and explained such variation in year-class distribution by the parental origin of the year classes, speaking about a "true West Greenland stock" and a stock component of East Greenland or Icelandic origin.

Occurrence of cod and cod fisheries at West Greenland in the 17th–19th centuries

The occurrence of cod in Greenland waters has been episodic in character. Jensen (1925), Bendixen (1930), Jensen and Hansen (1931), and Hansen (1949) reviewed the history of the Greenlanders' cod fisheries.

In so far as occurrence of cod in the nineteenth century is concerned the above-mentioned authors refer to the classic descriptions of Rink (1852 and 1857) that cod were plentiful in two periods in the first part of the nineteenth century. Rink was told of a period before 1820 when cod were present in great numbers in the Disko Bay area and in southernmost Greenland (Julianehåb district) during the years 1819–1821. The other (better documented) period occurred in the last half of the 1840s, when up to 10 British vessels were fishing on the West Greenland fishing banks and cod were numerous at several inshore places. This period seems to have come to an abrupt end just after 1851, when cod was absent or occurred at only scattered inshore locations on the West Greenland coast until the beginning of the present century.

A wider study of the literature and archives, however, does show occurrences of cod at Greenland to be more variable. Major sources for information are Gad's History of Greenland (Gad 1967, 1969, and 1976) and some notes from his studies of archives for the period 1757–1808 (these notes are filed in the Greenland Fisheries Research Institute).

There is evidence of the occurrence of cod offshore (Fylla Bank) in the mid-seventeenth century (Dannell's expedition 1653), and the Dutch whaler captain L. Feykes Haan (1719–1720) reported cod at the beginning of the eighteenth century (Bobé, 1915).

There are several reports of the occurrence of cod in the coastal area between Frederikshåb (NAFO Division 1E) and Holsteinsborg (Division 1B) between 1749 and 1783. The settlement of Fiskenæsset (NAFO Division 1D) was founded in 1754, and this site is the one most frequently mentioned when occurrence and abundance

of cod at West Greenland are described up to about 1910. In 1777, some vessels reported large quantities of halibut and large cod (5–6 kg) in the offshore area between Godthåb (Division 1D) and Sukkertoppen (Division 1C), but offshore fishing was abandoned by the official Trade Company. (For names and divisions see map, Fig. 1.).

For a short period around 1790 there seems to be no specific information on occurrence of cod. However, in 1796, it was reported from Egedesminde that production of salted cod was poor that year, probably indicating that it was better some years prior and close to 1796 (Gad, 1969).

During the period 1799–1807, cod occurred in fishable quantities in the Disko Bay area (Division 1A), and in the same period Fiskenæsset again had some years of good fishing. There are records in 1810 and 1823 of offshore cod concentrations (Jensen, 1950), confirming Rink's notes (1852) of a cod period around 1820. There is also a number of records of cod and cod fishing at Fiskenæsset in the period between that period and Rink's second period (late 1840s) (Sveistrup and Dalgaard, 1945). During the latter period, British vessels were fishing cod offshore during 1847 to 1851 (Rink, 1857). 1848 was a good year (20 000 to 30 000 fish per vessel). Catches decreased in 1849, were lower again in 1850, and British fishing came to an end after a very poor 1851 season. Danish experiments in the same period also failed after 1850.

Jensen and Hansen (1931) state that cod was absent at West Greenland from about 1850 to 1908–1909. However, this seems a rather categoric statement. Jensen (1925) says that the production of cod at Fiskenæsset was abandoned in 1865, higher priority being given to sealing. He further states that cod liver was again bought at Fiskenæsset in 1881, but also that fishing there failed in 1884–1886 and again in 1903–1905.

From the above-mentioned pieces of evidence it may be concluded that cod occurred commonly at West Greenland throughout the period between 1750 and 1850, with low abundance around 1790. It was not unknown there before then, but the present study does not indicate whether or not cod were scarce between Haan's observations about 1715 (Bobé, 1915) and observations by Geelmuyden in 1749 (Gad, 1969), nor is it yet possible to conclude anything for the period between Dannell's observations in 1653 (Gad, 1967) and those in the eighteenth century mentioned above.

During the period 1750–1850 the distribution and abundance seem to have fluctuated a great deal. There was a fairly wide distribution around 1800, including the Disko Bay area, and probably also high abundance at that time. The abundance also seems to have been high in the last half of the 1840s. Rink's characterization still seems pertinent. "It would be too long-winded to relate how fishing at the various localities has varied from year to year. Evidently, cod show up every year, sometimes here, sometimes there from Julianehaab up to Holsteinsborg, between the islands and skerries and in the fjords, and there are localities where it never or seldom fails to appear, amongst these by far Fiskenæsset" (Rink, 1857, p. 218, author's translation).

In summary, Figure 5 shows years or periods for which evidence of occurrence of cod or the lack of cod at West Greenland during the period 1650–1910 was found in the present study. The figure also shows the climatic variation during that period as revealed by heavy oxygen isotope analyses of a deep core from the Greenland ice cap (Dansgaard *et al.*, 1970). The figure does not indicate a correlation between occurrence of cod and the warm periods for the years shown, except for the warm period which started around 1920.

The West Greenland cod stock in the twentieth century

In 1906, the Faroese skipper Napoleon Andreasen carried out cod fishing experiments from two vessels. In spite of what seems a considerable and professional effort, virtually no cod, only a number of halibut, were caught offshore. In the fjords at Holsteinsborg, around 1800 specimens of cod were taken, but much too little to make Andreasen recommend foreign cod fishing at Greenland, rather to warn against such experiments (Andreasen, 1906 and logbooks of the two vessels).

At the time of the "Tjalfe" expeditions in 1908–1909, cod were still seldom seen offshore but they were observed at a number of places inshore and seem to have increased at Fiskenæsset (Jensen, 1909a). However, the most remarkable observation was probably the occurrence of cod in southernmost Greenland, especially in the sounds at Cape Farewell. Although Greenlanders told Jensen that this latter occurrence was a regular phenomenon in autumn (Jensen, 1909b), the abundance seems to have been high in 1909 and may be regarded as the first sign of the enhancement of the cod stock at West Greenland which became evident in the next decade, as described by Jensen and Hansen (1931).

As from 1911, the buying and preparation of cod for export was organized at a few inshore places where the "Tjalfe" expeditions had found the abundance of cod of sufficient proportions to warrant commercial fishing (Fiskenæsset and fjords at Holsteinsborg). From 1917, cod gradually spread northwards along the coast, reaching Godthåb in 1922, Holsteinsborg in 1927, Egedesminde in 1929, and Umanak in 1931. In the late 1930s it extended as far north as the Upernavik District (Hansen, 1949; Jensen, 1939).

Offshore, cod was found on Fylla Bank in 1921 (Jen-

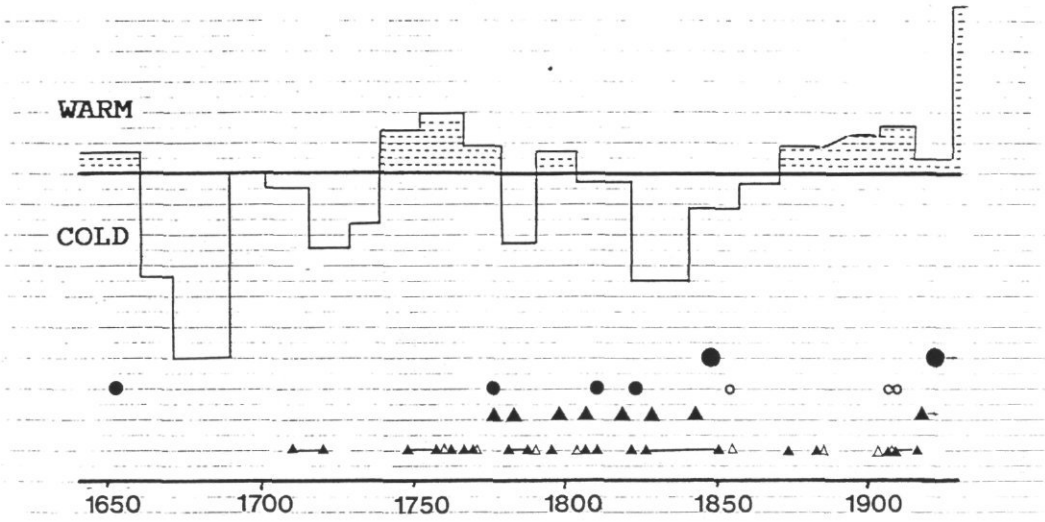


Figure 5. Upper part: climatic variation (relative air temperature) as revealed by heavy oxygen isotope analyses of a deep ice core from Camp Century on the Greenland ice cap (redrafted extract of a figure by Dansgaard *et al.*, 1970). Lower part: observations of occurrence of cod at West Greenland. Large black dots: evidence of relatively high offshore abundance. Small black dots: evidence of some offshore abundance. Open circles: no offshore cod observed. Large black triangles: Evidence of relatively high inshore abundance. Small black triangles: evidence of some inshore abundance. Open triangles: inshore fishing failing on traditionally good fishing grounds. Lines connecting symbols: period over which the symbols apply.

sen and Hansen, 1931). In 1924, Tåning discovered cod in quantities on Fylla Bank in June (Jensen and Hansen, 1931) and in August of the same year Hjort found cod on Fylla Bank and on Little Hellefiske Bank (Hjort and Ruud, 1929). Offshore fishing by foreign vessels then started and increased rapidly.

The fluctuations in the West Greenland cod stock in this century can be illustrated in various ways:

fisheries statistics, available for Greenland since 1911 and for the international offshore fisheries since their start in 1924 through the ICES and ICNAF/NAFO statistical publications

analytical assessments, especially Virtual Population Analyses (VPA) here back to 1924

direct biomass and abundance estimates through trawl surveys carried out since 1982, and

variation in the spatial distribution reflected by catch distribution and the results of trawl surveys.

Fluctuations in catches

Annual catches of cod at West Greenland by nation are generally readily available. However, in some cases, especially for the years before the mid-1950s, estimates have to be made; for instance, when some catches were reported for the whole Northwest or even for the whole North Atlantic without a breakdown on subareas such as West Greenland. For instance, Portuguese catches of up to 100 000 t annually in the Northwest Atlantic, as reported in ICNAF *Statistical Bulletin*, are not broken down by gear, nor by subarea, until 1947, and for trawlers not by subarea until 1952. Data in this paper are based on the statistics published by ICNAF/NAFO and ICES, and on tables from relevant working groups of these organizations. A paper updating catch statistics for Greenland waters, including proposals for the allocation of such unallocated catches, is stored with the NAFO Secretariat (Horsted, 1994).

The fluctuations in catches are illustrated in Figure 6. Until 1968, the Greenland part of the catch can be considered inshore. The non-Greenlandic part is almost entirely offshore. Foreign fishing (except by Portugal) was stopped during World War II but expanded rapidly thereafter, culminating in 1962 when the total international catch was about 460 000 t. The rapid increase during the 1950s was due to increased effort. A dramatic decline started after 1968 when catches in 1969 and 1970 were both halved compared with the preceding year's catch. A further decline took place in 1973. There was very little foreign fishing activity during 1984–1987, some fishing in 1988–1990 (on the 1984 year class), but thereafter virtually no foreign cod fishing has been registered at West Greenland. Greenland's own catches have dropped to a level of 6000 t in 1992, all taken inshore.

Fishing has been regulated by TACs and quotas since 1974. Although the regulations may have had some

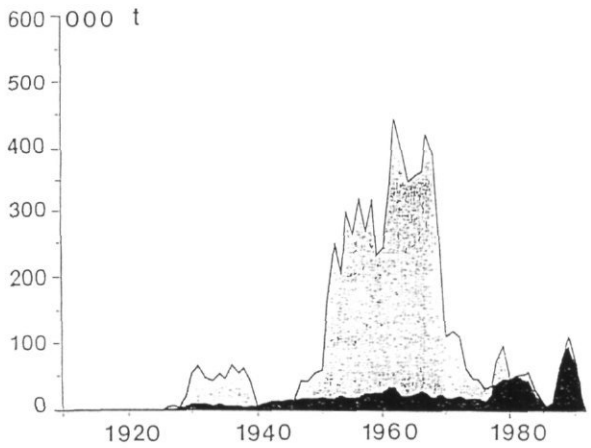


Figure 6. Catches (nominal landings) of cod at West Greenland (1911–1992) by Greenlanders (black signature) and by others (grey signature).

influence on catches, this is thought to be less than the influence that the environment has had on stock fluctuations.

Analytical stock assessments

VPAs have been used extensively in annual stock assessments back to 1963 (Horsted *et al.*, 1983). Moreover, Schumacher (1971) covered the period 1956–1969. In the present work we have attempted to carry the analysis back to 1924. Catch by numbers and weight-at-age data for the period since 1956 were taken from Schumacher (1971) and Horsted *et al.* (1983). For years previous to that, the catch-at-age was estimated from Greenland information (Hansen (1949) for the period 1924–1947, Hansen (unpubl. material) for the period 1948–1955), and this age composition was then raised to match the total international catch. Maturity data given in Horsted *et al.* (1983) were averaged and used as a common maturity ogive for the entire period. Terminal F values for the last year were derived by Extended Survivor Analyses (XSA) using German trawl survey catches available since 1982.

Fishing mortality was below 0.1 for many years before the 1950s, making the VPA stock sizes sensitive to the choice of terminal F. To avoid an overestimate of the stock size the terminal-F values were not allowed to drop below 0.08. This value is based on catch curves (age 9 to 14) from the period 1930 to 1939, when catches, and presumably effort, were relatively stable. It should also be noted that no attempts have been made to correct for the migration from Greenland to Iceland. Simulation suggests that as long as the Icelandic component (i.e., cod returning to Iceland to spawn) is confined to 50% of the total stock, the errors in recruitment and fishing mortality are at most 10%.

According to the VPA, average recruitment (at age 3) in the period 1924 to 1934 was about 76 million fish with the year classes 1922, 1924, and 1926 being around 200 million and the remaining less than 50 million (Fig. 7). In the following four decades the recruitment was exceptional – the average for the years 1935 to 1966 was 225 million fish, with a minimum recruitment of 76 million fish. Since 1966, recruitment has again been low, with a 1967–1989 average of 61 million fish. Moreover, this average is very dependent on the 1973 and 1984 year classes that were of Icelandic origin.

Stock biomass peaked at 4 million tonnes in 1950 (Fig. 7) due to the good recruitment and low effort in the 1940s. A large international fishery developed off West Greenland during the following years, producing an average yield in excess of 300 000 t between 1950 and 1970 (Fig. 6). During the same period F increased from 0.1 to 0.6 (Fig. 7), resulting in a reduction in stock biomass to less than 1 million tonnes. However, the catches decreased dramatically at the end of the 1960s – from 394 000 t in 1968 to 114 000 t in 1970. The year classes of 1961 to 1963 all showed up in large quantities as age 7 fish in Iceland (Schopka, 1991); this decline may thus, at least partly, be attributed to a spawning migration out of the Greenland area.

In the recent two decades annual catches have been poor and dependent on the emergence of single strong year classes, such as those of 1973 and 1984, which gave rise to a booming fishery in 1988–1989 before suddenly disappearing during 1990.

Trawl surveys

Stratified-random bottom-trawl surveys off West Greenland have been conducted in late autumn since 1982 by research vessels from the Federal Republic of Germany. Cod biomass and abundance estimates for the total survey area (not including areas inside the 3 nautical mile limit) are given in Table 1.

As early as in 1982, the biomass was very low compared with the values it must have had during the 1950s–1960s, when catches were well above the biomass observed in 1982, but it continued to decrease to a low of 25 000 t in 1984. The recruitment of the good 1984 year class is reflected in the abrupt increase in 1987. However, this effect lasted for only three years. Thereafter, the biomass declined abruptly (by about 90%) from 1989 to 1990 with a further decline through 1991–1992 to a figure which indicates a stock size similar to that seen at the beginning of the cod epoch of this century.

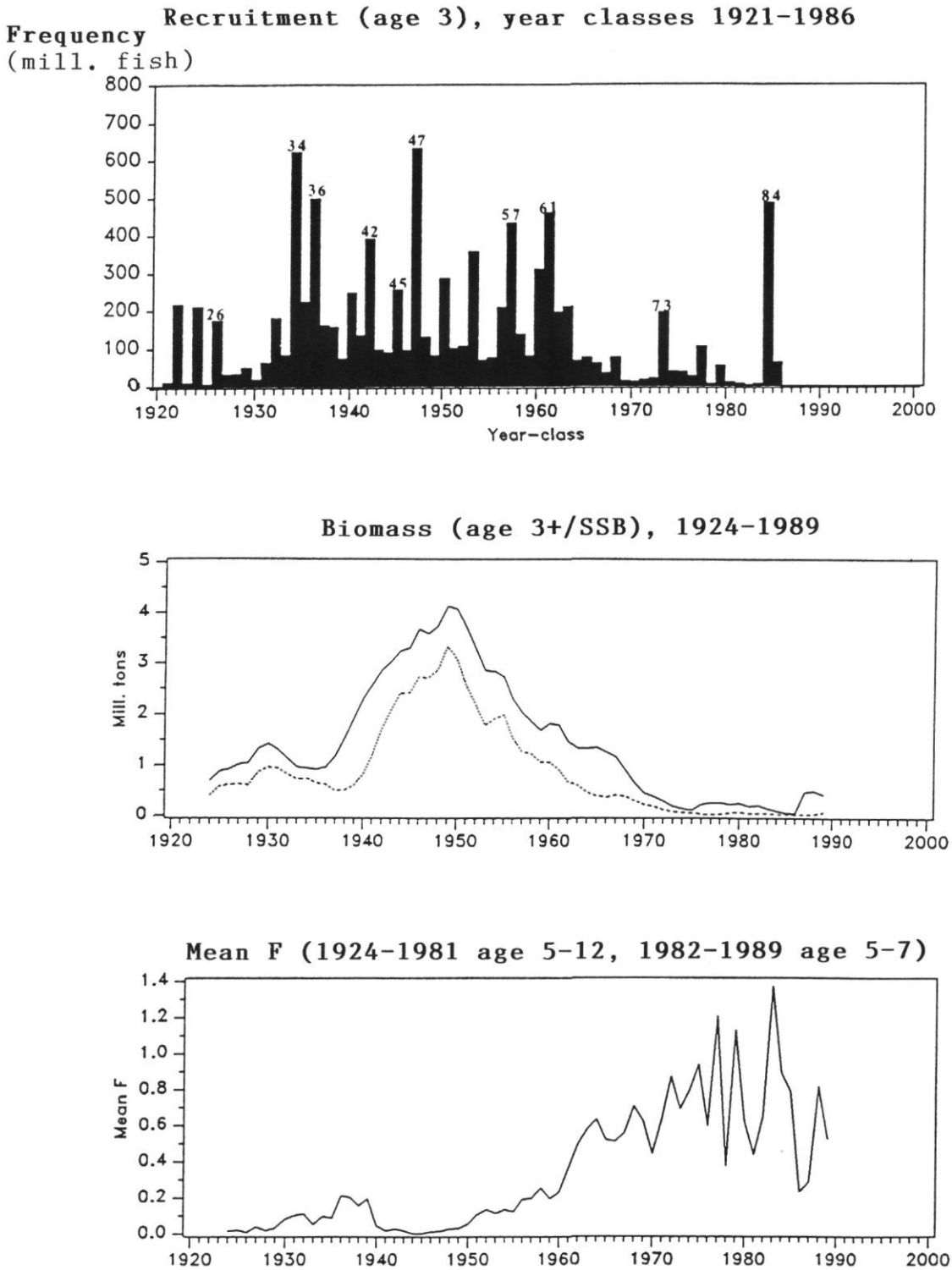


Figure 7. Results of VPA in terms of recruitment, biomass and spawning biomass, and mean fishing mortality coefficient.

Variation in the spatial distribution

Throughout the period in this century when cod was common at West Greenland, its spatial distribution has varied much offshore as well as inshore. The northward advancement of the stock has been referred to by Jensen (1939) and Hansen (1949) (see pp. 161–163).

Throughout the 1950s–1960s cod was commonly caught in all statistical divisions offshore as well as inshore, although catches in each division as well as the proportional catch between divisions fluctuated from year to year. Part of the variation between divisions can be ascribed to the tendency of various fleets to prefer certain fishing grounds, for instance the Portuguese dory fleet preferred fishing banks in Divisions 1B and 1D, while British trawlers traditionally fished in Division 1F. However, the origin of the various year classes influences the picture. The 1963 year class, described as being of East Greenland origin (Meyer, 1969a), no doubt contributed to keeping relatively high catch levels in Divisions 1C–1F in the late 1960s, while catches decreased dramatically in Division 1B.

From the late 1960s the trend in offshore catch and stock distribution was a southward displacement. Since 1968, with the exception of the catch in 1980, the offshore catch in Division 1B has thus been below 5% of the total offshore catch, whereas in its best year (1962) this division accounted for 29% of the total offshore catch and in its relatively most important year (1959) 36% of the offshore catch was taken there (Fig. 8).

The southward stock displacement in recent years, resulting primarily from the migration of the 1984 year class, is also illustrated by the results of the German trawl surveys carried out since 1982 (Table 1).

The distribution of the inshore catches has also varied (Fig. 9). The southern divisions (1E–1F) showed high catches around 1980 and again in 1989. The peak in 1980 was due almost entirely to the 1973 year class (of Icelandic origin), while that in 1989 was due to the 1984 and 1985 year classes, of which at least the former seems to have been of Icelandic origin. Contrary to the offshore situation, the inshore catches in 1991 were relatively high in Division 1B, where a local 1986 year class seems to play a major role.

Discussion

At present, the abundance of cod at West Greenland is at a very low level, with the 1992 catches the lowest experienced since 1925. Trawl surveys conducted during 1990–1992 in the offshore area show cod biomass less than 1000 t, with the 1986 to 1991 year classes being hardly detectable and with no offshore fishing since spring 1991. Inshore gillnet surveys confirm that viable stocks exist in central southwest Greenland, but a catch of only 5600 t in 1992 indicates that they are barely able to sustain the local trap fishery at higher levels. A similar situation was found in the mid-1980s, but owing to the recruitment of the 1984 and 1985 year classes a good fishery developed for a few years. However, when considering that these year classes were of Icelandic origin, as was the 1973 year class, it could be said that the true cod period off West Greenland came to an end by about 1970.

The present stock situation is very similar to that prevailing at the start of this century, when both Napoleon Andreasen and Adolf Jensen found small concentrations of cod inshore and almost none offshore. Information from the two preceding centuries does not allow precise guesses of stock sizes, but it seems well documented that cod were never absent in that period, especially in inshore areas. The short periods of good offshore concentrations seen in the nineteenth century may well have been caused by a single large year class being of Icelandic origin. The regularly observed occurrence of cod in the sounds at Cape Farewell, reported by Adolf Jensen in 1909, further suggests a drift of eggs and larvae from Iceland, since recent surveys in that area find cod only of year classes known to be of Icelandic origin. However, in the period between the 1920s and the 1960s the Greenland cod stock experienced an exceptional development, with catches in the best years matching those of Iceland, the Barents Sea, or the Grand Bank.

The northern hemisphere underwent significant climatic changes around 1920, resulting in a general rise in temperature. In Greenland, this was seen in both air temperature (Dansgaard, 1985) and in the sea (Fig. 2). By the end of the 1960s the climate again changed on a large scale (see pages 159–160) this time resulting in cooling in Greenland.

Various scientists working in the Greenland area have associated the changes in cod abundance and distribution with the concurrent changes in the environment. In a classic publication, Jensen (1939) showed that a number of boreal marine species, cod an outstanding example, extended their area of distribution to the north in the 1920s–1930s while some Arctic species, e.g., *Gadus ogac*, retreated northwards. Annual hydrographical observations on standard sections off West Greenland have also been commonly used to predict relative year-class strength. The June temperature over Fylla Bank was especially indicative of the strength of the year class in question (Hermann, 1951 and 1953; Hansen and Hermann in various research reports to ICNAF and contributions to the ICES series *Annales Biologiques* during the 1950s–1960s). Later, Hermann *et al.* (1965) found a significant correlation between the Fylla Bank June temperature and year-class strength for the period 1924 to 1950, as did Hansen and Buch (1986) for the period 1953 to 1979.

Table 1. Upper part: Biomass indices (tonnes) from German trawl surveys at West and East Greenland. Figures in parentheses are invalid because of incomplete sampling. Confidence intervals (CI) are given in percent of the stratified mean (8 strata at West Greenland, 6 at East Greenland) at 95% level of significance. Lower part: Relative biomass indices (upper part figures in per cent of total). Figures based on Table 5.1.5 of the ICES North-Western Working Group, May 1993 (ICES 1993), summed to conform with NAFO statistical divisions.

	B (south) + C	D	E	F	West Greenland	East Greenland	Total	CI
1982	2685	66316	29063	30426	128490	23617	152107	24.8
1983	559	28042	32400	21374	82375	34156	116531	25.2
1984	1058	7742	8273	8493	25565	19744	45309	33.7
1985	2779	15220	11720	5952	35672	33565	69236	39.2
1986	11125	26178	29933	19483	86717	41185	127902	26.1
1987	284136	200632	116610	37210	638589	51592	690181	63.1
1988	95542	411815	44686	55945	607988	52947	660935	46.0
1989	955	26270	231239	75386	333850	239546	573395	45.5
1990	338	3743	5778	24573	34432	65963	100395	33.7
1991	162	118	1798	3072	5150	32751	37901	35.5
1992	329	59	35	183	607	(1216)	(1823)	68.7
1982	1.8	43.6	19.1	20.0	84.5	15.5	100.0	
1983	0.5	24.1	27.8	18.3	70.7	29.3	100.0	
1984	2.3	17.1	18.3	18.7	56.4	43.6	100.0	
1985	4.0	22.0	16.9	8.6	51.5	48.5	100.0	
1986	8.7	20.5	23.4	15.2	67.8	32.2	100.0	
1987	41.2	29.1	16.9	5.4	92.5	7.5	100.0	
1988	14.5	62.3	6.8	8.5	92.0	8.0	100.0	
1989	0.2	4.6	40.3	13.1	58.2	41.8	100.0	
1990	0.3	3.7	5.8	24.5	34.3	65.7	100.0	
1991	0.4	0.3	4.7	8.1	13.6	86.4	100.0	
1992	(18.0)	(3.2)	(1.9)	(10.0)	(33.3)	(66.7)	100.0	

However, interpreting the effect of temperatures at West Greenland on cod recruitment is somewhat impeded by the complexity of the stock structure in Greenland. The variability in drift of 0-group cod from Iceland to Greenland must evidently be attributed to interannual differences in strength and direction of the Irminger Current, whereas direct or indirect temperature effects may well be more important for the stock spawning at Greenland. Unfortunately, we do not have a detailed knowledge of the mixture between cod of Greenlandic and Icelandic origin over the years. Schopka (1991, 1994), scrutinizing catch-at-age data from Iceland, lists the year classes 1919, 1922, 1924, 1932, 1936, 1937, 1938, 1942, 1945, 1950, 1953, 1956, 1958, 1961-63, 1973, and 1984 as being important in migration to Iceland and his list is generally confirmed by what has been interpreted from stock distribution given in annual national research reports to ICNAF and NAFO (see, for example, Meyer, 1969b; Jónsson, 1964). Year classes such as those of 1947 and 1957 have been classified as being of West Greenland origin because of a northern distribution of catches (Rasmussen 1959; Meyer, 1963). However, the conclusions drawn from catch information to describe the main origin of year classes are weak. For instance, to detect a year class as coming from Greenland on the basis of the Icelandic catch-at-age information requires at least 10 million immigrants at age 7, and to account for that number a larval drift in the other direction equivalent to 120 million age-3 cod is needed. In other words, only migration from larger year classes will be observed by this procedure, which is also evident when comparing the list of migrating year classes provided by Schopka (1994) with the estimated year-class sizes at West Greenland (Fig. 7). In contrast, tagging information shows that emigration is high for cod tagged in southern Greenland irrespective of year-class strength (Riget and Hovgård, 1989). For the less important year classes, little information regarding main origin is available.

Because of the problems associated with the mixing of stocks it will be very difficult to interpret stock-size measurements from the VPA, and hence, of course, to relate these to climatic factors. However, using the large body of information available, one may broadly relate the changes in the stocks to the climate changes in the twentieth century.

For the offshore Greenland stock the pre-1940 information does not allow very strict conclusions, but the high proportion of tags returned from Iceland suggests that the Icelandic contribution was quite significant. However, there is evidence of a Greenland offshore spawning in 1925 (Jensen, 1926) and also some year classes, viz. that of 1926, may be classified as Greenlandic because of the low proportion of tag returns from

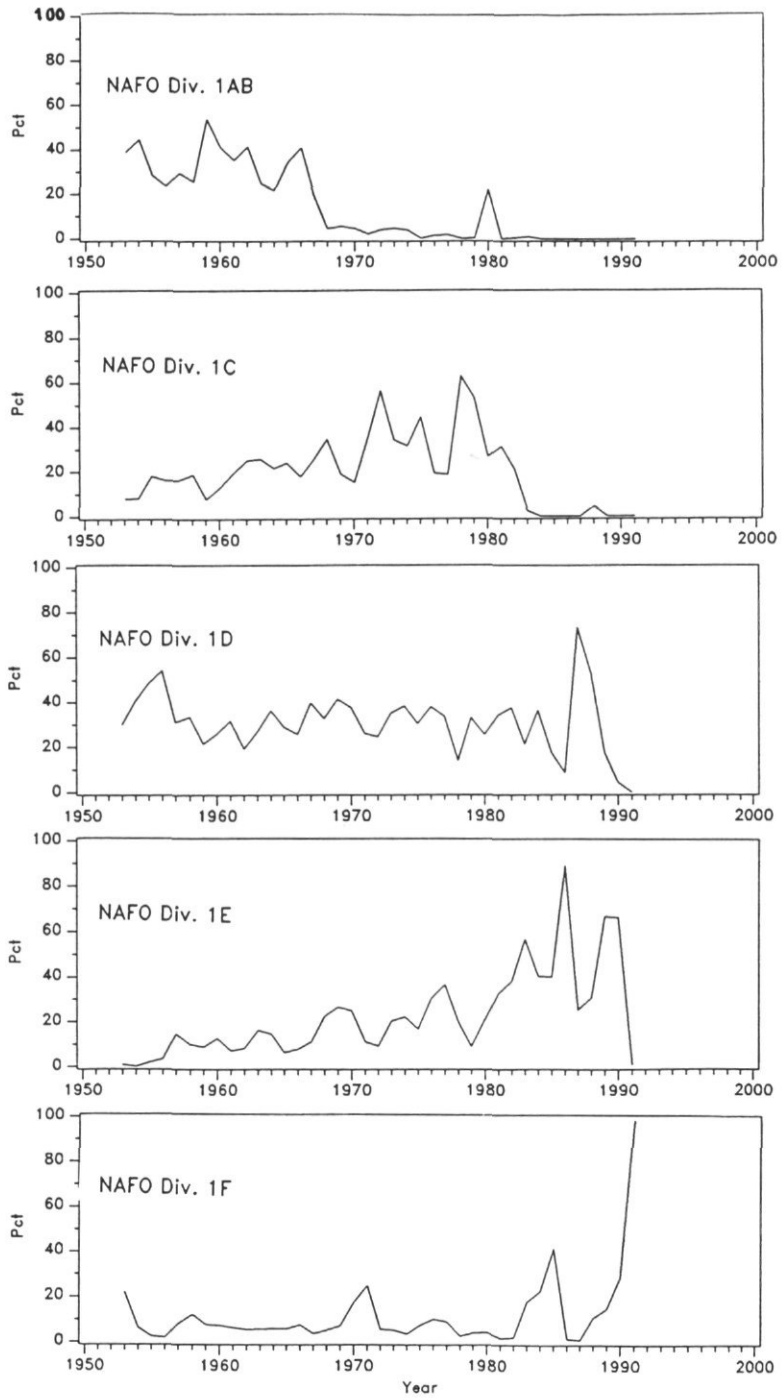


Figure 8. Distribution on NAFO divisions of offshore catches of cod at West Greenland (1953–1991) in per cent of total divisional catches. Offshore catches are taken as catches by all non-Greenlandic vessels plus catches of Greenland vessels above 50 GRT. Unallocated catches (Division 1 NK), not included, account for about 20–35% of total offshore catches before 1973; thereafter, virtually all catches are reported by divisions. *Source*: ICNAF/NAFO statistics and internal Greenland statistics.

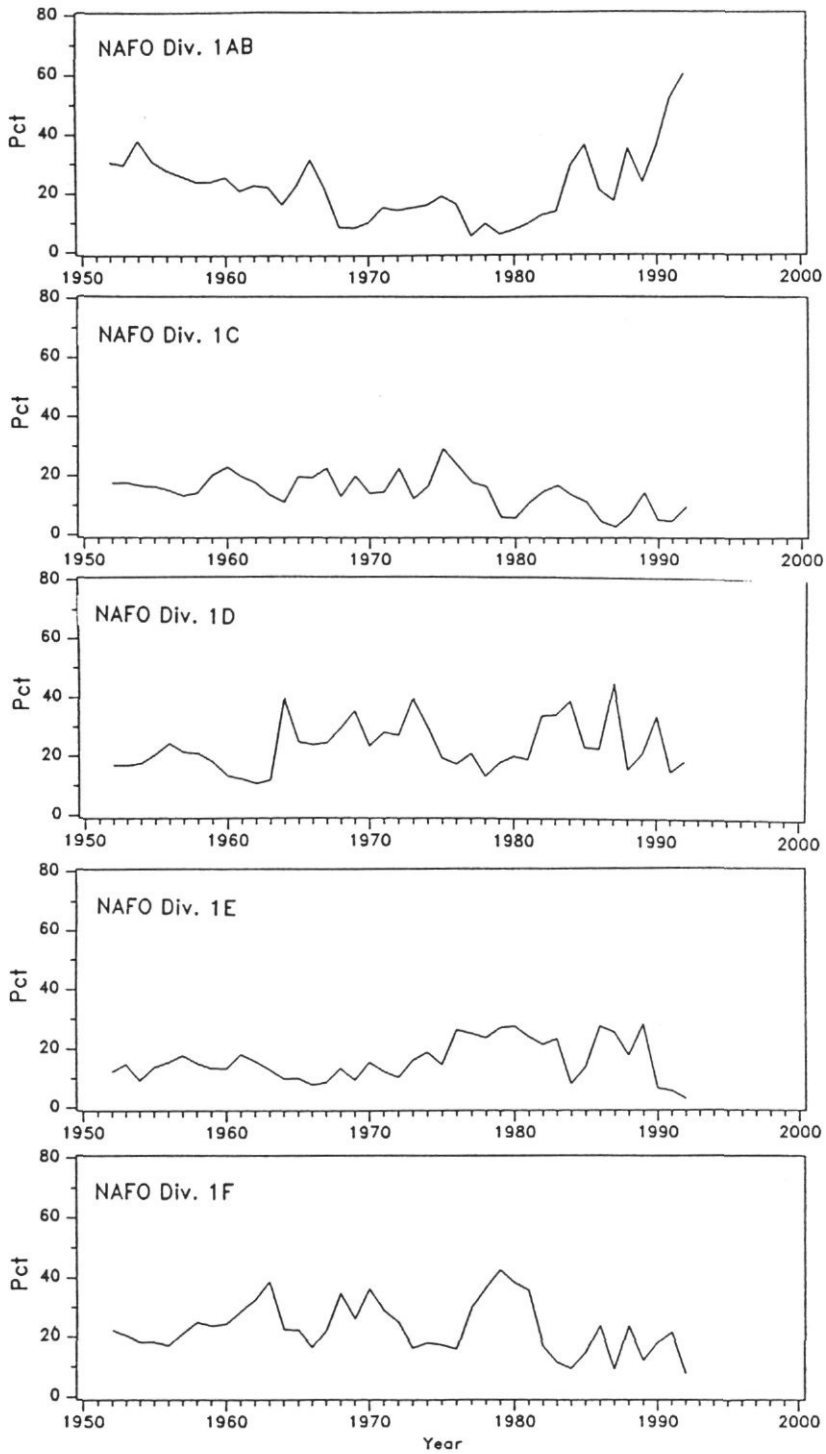


Figure 9. Distribution on NAFO divisions of coastal and inshore catches of cod at West Greenland (1953–1991) in per cent of total coastal and inshore catches, taken as all cod catches by Greenland vessels below 50 GRT. Only in the years 1981–1984 were considerable amounts (up to 30% of the total) reported as unallocated.

Iceland (Hansen, 1949). For the period 1953 to 1966 the high catches (up to 100 000 t per year) in the northern area from which tagging showed almost no migration to Iceland demonstrate the existence of a strong Greenland stock component. Catches declined dramatically in the northern areas during the late 1960s, and although some offshore spawning still occurred, as may be inferred from plankton surveys conducted annually until 1984, all year classes since the 1960s of any importance are classified to be of Icelandic origin. During the most recent years it seems clear that the West Greenland stock component has all but vanished. Overall, the development of this stock component parallels the changes in temperature with a gradual increase in stock size following the temperature rise in the 1920s, a decline taking place concurrent with the decline in temperatures in the 1960s, and a final disappearance taking place during the periods of intense coolings in the latest decade (Fig. 6).

Regarding the Icelandic component, Schopka (1991) notes that important migrating year classes have been less frequent in the last 20 years compared to previous years. Hovgård and Messtorff (1987) came to the same conclusion on the basis of declining haddock catches at West Greenland, where haddock is not known to spawn and its occurrence hence regarded as indicative of variation in drift from Iceland. Dickson and Brander (1994) note that although these observations are not very conclusive they generally agree with what would be expected, as low pressure distribution and associated windfields were generally favourable for a larval drift from Iceland to Greenland in the period before the mid-1960s.

It may, therefore, be that the period of very good cod fisheries at West Greenland as seen in the middle of this century was due to a simultaneous increase in the two offshore stock components. The increase of the Greenland cod stock spawning offshore at South Greenland may be attributed to the rise in temperature, whereas a frequent drift of young cod from Iceland, caused by a favourable current pattern in the Irminger Sea, boosted the more southern cod stock.

The foreseeable future for the Greenland cod fisheries does not seem bright, as the fishery now depends solely on local inshore stocks, which may sustain annual yields of 5000 to 10 000 t. This may be supplemented by an irregular occurrence of cod drifted from Iceland, as has been the case in the last two decades, resulting in a somewhat larger offshore fishery for a few years. Any improvement beyond that will depend on the re-establishment of a Greenland offshore stock. The historical information suggests that the large stock seen in the middle of this century is by no means typical. Palaeoclimatic investigations further indicate that periods as warm as the 1920–1970 period are rare (Dansgaard, 1985). In fact, the nearest such warm period was at the time when Erik the Red colonized Greenland about a thousand years ago.

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Fluctuations in the cod stock off Iceland during the twentieth century in relation to changes in the fisheries and environment

Sigfús A. Schopka

Schopka, S. A. 1994. Fluctuations in the cod stock off Iceland during the twentieth century in relation to changes in the fisheries and environment. – ICES mar. Sci. Symp., 198: 175–193.

Icelandic cod is one of the major cod stocks in the North Atlantic. Investigations on the biology and dynamics started early in this century. Sampling was more sporadic to begin with, but data on systematic sampling are available from the late 1920s. Variations in stock abundance and landings are compared with changes in recruitment and growth. This is discussed in the light of information on environmental changes and rate of exploitation. Further, the interrelationship between the Icelandic and Greenland cod stocks is investigated and the effect of the decline in the cod stock at Greenland on the stock abundance at Iceland is described. The fishable stock was at a maximum level of 3.3 million tonnes in 1928 and has been declining, with some fluctuations reflecting variations in recruitment and immigration from Greenland, to the lowest level on record of only 600 000 t in 1993. The spawning-stock biomass has also shown a similar trend; a decline from 1.5–1.8 million t in the 1930s to only 200 000–300 000 t in recent years. Fishing mortality increased throughout the whole period, from about 0.16 in 1928 to a maximum 1.0 in 1988, and is still above any acceptable level. In the prewar years, when fishing mortality was very low, fluctuations in stock abundance were caused by changes in environment in the Iceland-Greenland area, but with an ever-increasing fishing effort, the continuous reduction of the cod stock at Iceland appears to be a combination of both factors: the environment and the fisheries.

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Introduction

In order to understand the dynamics of a fish population in relation to climate and fisheries, it is desirable to have a time series spanning several decades and covering low and high exploitation periods under different environmental conditions. Investigations on cod in Icelandic waters started a century ago when Bjarni Sæmundsson, the first Icelandic marine biologist, began in 1894 to collect information on the fisheries and the biology of the most important commercial species in the waters around Iceland.

With the foundation of the International Council for the Exploration of the Sea (ICES) in 1902 more comprehensive investigations were started in Icelandic waters. At that time Denmark was responsible for the research in the waters around the Faroes, Iceland, and Greenland.

The first surveys (Schmidt, 1909) of the distribution of eggs and larvae of different fish species, plankton recordings, and hydrography were conducted in the early 1900s, when also the first tagging experiments were made. During these surveys, otoliths for age determination and growth studies were also collected.

In the period 1910–1923 Sæmundsson alone continued his research on marine fishes. His studies on cod were mainly devoted to age determination and hence the growth of cod; the first results were published in 1913.

Scientific sampling was sporadic to begin with, but from 1928 onwards samples for age determinations and length measurements were collected annually at various localities around the island at different times of the year. Sampling was more concentrated on the major fishing season, the so-called "spawning fishery", which takes place along the south and southwest coast of Iceland from January to May, when about 80% of the total Icelandic cod catch is taken. From the available age composition data, catch in numbers for the Icelandic cod fisheries can be calculated back to 1928.

Fishing at Iceland by foreign fleets (mainly German

and UK fleets) played an important role in the cod fisheries for most of the time under consideration (see below under "Development of the fisheries") and therefore cannot be ignored in the assessments. Age composition data and hence catch in numbers by age are also available for the two major foreign fisheries back to 1955 (ICES, 1976). For the German fisheries, the author had access to length composition data for the period 1929 to 1952 and some age composition data for the years 1953 and 1954. Unfortunately, there are no age or length composition data available for the most important foreign fishery, that of the United Kingdom, but detailed information on catches by rectangles and months is available back to 1930. The estimated catch in numbers for the period 1928–1952 is based entirely on the Icelandic age/length keys. In the present analysis the Icelandic age composition data for the same period and grounds have been used to convert the UK landings into catch in numbers. The present paper is a synopsis of an extended and revised analysis of a stock assessment made previously by Schopka (1993) and a more detailed study of the Iceland–Greenland cod stock complex is in preparation.

Some environmental data for the entire period examined are also available. Jens Smed's (1953–1977) data on sea-surface temperature cover the period 1876–1975 and hydrographical data off the north coast of Iceland have been collected irregularly during the period 1924–1939, but annually since the late 1940s (Stefánsson, 1962).

Physical environment and climate change

Iceland is situated on the Mid-Atlantic Ocean Ridge. The continental plateau of more than 100 000 km^2 within the 200 m depth contours is connected to the neighbouring countries by a submarine ridge which runs from Greenland (Greenland–Iceland Ridge) to the Faroes (Iceland–Faroe Ridge) onwards to Scotland.

Southwestwards of Iceland the continental shelf joins the Mid-Atlantic Ocean Ridge along the Reykjanes Ridge and, northeastwards of the island, continues as the Iceland–Jan Mayen Ridge. The Greenland–Iceland Ridge is broken by a narrow channel of 620 m depth which runs southwest to northeast and divides the continental shelf between Iceland and Greenland. The submarine ridges are separated by basins of 2000–3000 m depths. These topographic features divide the waters around Iceland into oceanographic regions such as the Iceland Basin, the Irminger Sea, and the Iceland Sea and influence the mixing and circulation of the water masses in the area (Malmberg, 1988).

The main surface currents in the Iceland–Greenland area are shown in Figure 1. Iceland is located at a boundary between warm Atlantic Water and cold water from the Arctic. The cold East Greenland Current carries low salinity polar water southwards through the Denmark Strait along the East Greenland coast to Cape Farewell. The warm Irminger Current flows northwards into two branches after crossing the Reykjanes Ridge. The main branch is deflected west and meets the East Greenland Current and flows parallel to (and partly beneath it) southwards into the Irminger Sea towards Cape Farewell. Here the water masses mix as they move northwards along the southwest coast of Greenland.

In some years the water masses from the spawning grounds off the southwest coast of Iceland flow to Greenland. From drift bottle experiments in the late 1920s one bottle released on the Icelandic spawning grounds in February 1929 was recovered at southwest Greenland 133 days later (Tåning, 1931a). These experiments were carried out in style: it was usual to use lemonade or ginger pop bottles, but Tåning used genuine champagne bottles!

The eastern branch of the warm Irminger Current flows clockwise north and eastwards off northwest Iceland into North Icelandic waters; the Iceland Sea, and dissipates off the east coast of Iceland (Stefánsson, 1962). The East Icelandic Current carries low salinity water masses from the Arctic southwards to the north and east of Iceland (Malmberg, 1984).

During this century, the climate in the Arctic and Subarctic regions of the Northern Hemisphere has undergone substantial change. This has been more pronounced in Greenland waters than at Iceland and has substantially affected the marine fauna there (Jensen, 1939). After a cold period in the latter half of the nineteenth century and the first two decades of this century a warm period followed which lasted into the late 1960s. This is well illustrated in Figure 8, which shows smoothed averages of Jens Smed's surface temperature anomalies for West Greenland and west of Iceland during the period 1910–1975. Also in the figure the air temperature at Stykkishólmur, west Iceland, is shown and the same pattern can be followed.

Information on the hydrographical conditions in the North Icelandic Waters is also available for some years during the period 1924–1939 and continuous data on temperature and salinity have been collected since 1947. Temperature and salinity at a depth of 50 m at one of the hydrographical stations off the north coast of Iceland are shown in Figure 2. During the warm period, i.e. 1924–1964, Atlantic water of high salinity (>34.9) with a mean temperature of 5.2°C dominated in the North Icelandic waters; this was also the case in 1972–1974, in 1980, and in 1984–1987. In the mid- and late 1960s and 1975–1979, 1982, and 1988, Polar Water of low salinity and low temperature predominated off North Iceland. In 1981–1983 the condition in the North Icelandic waters was characterized by unfavourable Arctic Water (t = 2–3°C,

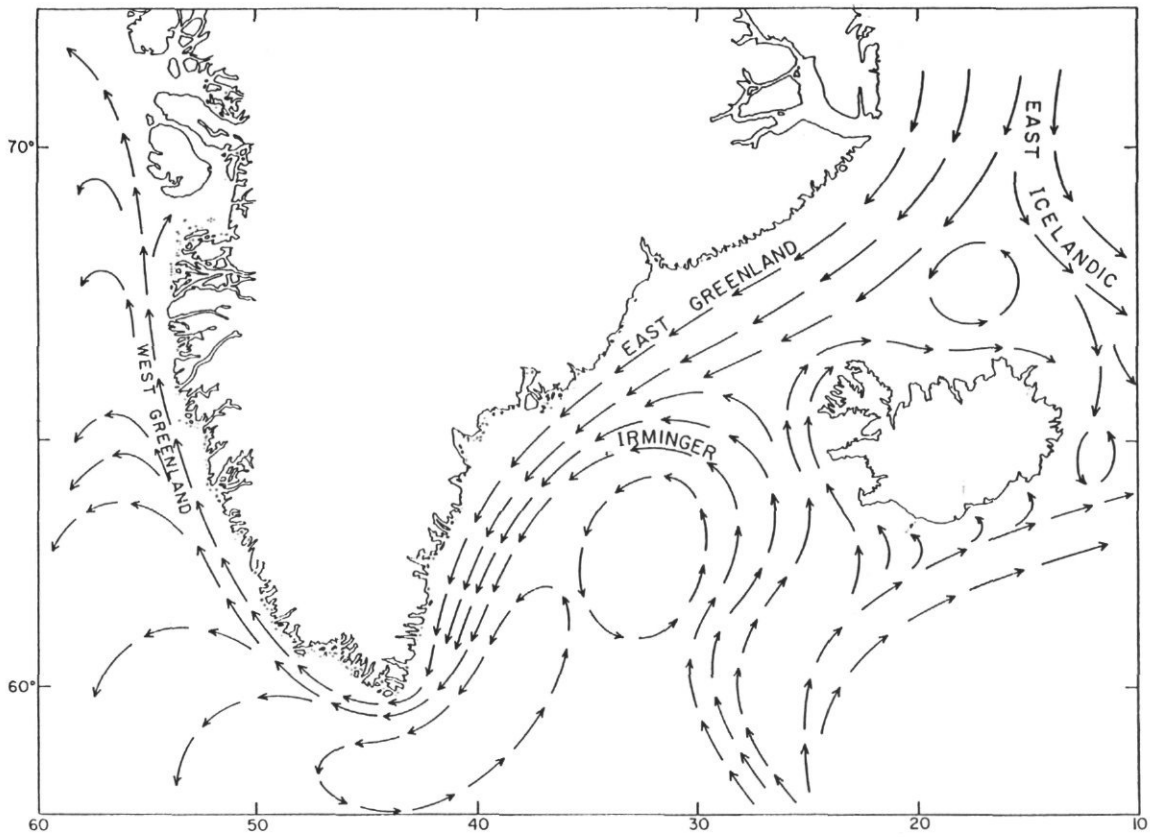


Figure 1. Surface currents in the Greenland–Iceland area (from Harden Jones, 1968).

$S < 34.9$; Malmberg and Kristmannsson, 1992). These Arctic conditions have been related to the so-called Great Salinity Anomaly (GSA) (Dickson *et al.*, 1988).

Connected with atmospheric variability and climate changes, the location of the oceanic Polar Front has been fluctuating, with great impact on the ecology in Icelandic (Jakobsson, 1980; Astthorsson *et al.*, 1983; Malmberg, 1988) and northern North Atlantic waters (Dickson *et al.*, 1988; Jakobsson, 1992).

The interrelationship between cod stocks in the Greenland–Iceland area

Very few cod tagged at Iceland have been recaptured outside Icelandic waters; there have been a few recaptures off the Norwegian coast, two from the Faroes, and one off Newfoundland (Tåning, 1937; Jónsson, 1953). Altogether 17 cod tagged on the spawning grounds at Iceland in the late 1920s and early 1930s were recaptured on the West Greenland banks (Tåning, 1937). In the postwar tagging experiments at Iceland, which started in 1948, only five recaptures have been reported from West Greenland (J. Jónsson, pers. comm.).

However, tagging experiments at Greenland, which were initiated in 1924, have shown that in some years cod migrate on a large scale to the spawning grounds at Iceland (Hansen *et al.*, 1935; Tåning, 1937; Hansen, 1949; and ICES, 1971). Tagging experiments at Iceland show that migrations of cod from Iceland to Greenland are virtually non-existent, so the migration from Greenland waters to Iceland can be regarded as a one-way migration.

After World War II, Jónsson (1953, 1965a, 1986) continued the cod-tagging experiments, confirming former results; the immature fish remain more or less in the nursery area along the north and east coasts and do not appear on the spawning grounds off the south and southwest coasts until they mature. The tagging of mature fish on the spawning grounds began in 1909. Schmidt (1931), Tåning (1937), and Jónsson (1986) have summarized the results, which show that spent fish disperse around Iceland but may be taken on the spawning grounds again in the following years. The latest

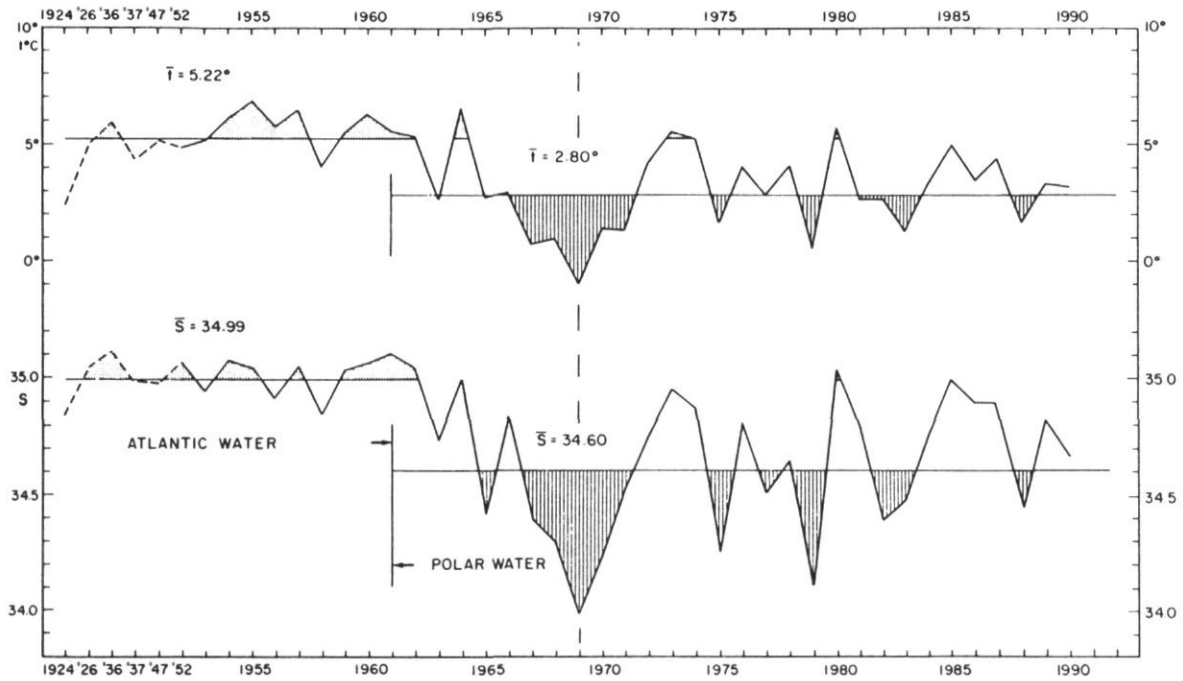


Figure 2. Temperature and salinity at 50 m depth at a hydrographic station off Siglunes, N Iceland in May/June 1924, 1926, 1936, 1937, 1947, and 1952–1990 (from Malmberg and Kristmannsson, 1992).

tagging experiments carried out on spawners in fjords on the east coast have confirmed Jónsson's (1986) previous findings (Thorsteinsson and Marteinsdóttir, 1993).

From the first egg and larval surveys, Schmidt (1909) concluded that eggs and pelagic larvae in this area move clockwise (anticyclonic) around the island. Results of the first tagging experiments showed that immature cod were stationary on the nursery grounds off the northwest, north, and east coasts. On reaching maturity these cod migrated to the warmer waters along the south and southwest coasts of the island for spawning (Schmidt, 1907; Sæmundsson, 1913).

It has long been known that in some years cod eggs and larvae from the spawning areas off the south and southwest coasts of Iceland drift towards Greenland with the branch of the Irminger Current that goes out across the Denmark Strait into East Greenland (Tåning, 1937). In the ICNAF NORWESTLANT (1963) survey, cod eggs were found in an almost continuous belt from Iceland to East Greenland, along the East Greenland coast, around Cape Farewell and over the banks at West Greenland (Hansen, 1968). During this survey larvae were concentrated in only two areas, one at West Greenland with larvae of West Greenland origin and the other in the Dohrn Bank area (65°N–30°W) (Fig. 3). As the 1963 year class was of great importance to the fishery at both West and East Greenland, and very few larvae could be detected off Southwest Greenland, it is thought that this year class found at Southwest Greenland and East Greenland originated from larval concentrations in the Dohrn Bank area in July and would have drifted there from the spawning areas at Iceland. When this year class reached maturity, large numbers of fish from West and East Greenland waters appeared in the spawning area around Iceland (Meyer, 1969).

Since 1970, international, and later Icelandic, pelagic 0-group surveys have been carried out in the Iceland–East Greenland area. In most years, no 0-group cod were found along the East Greenland coast, but in some years cod were found there but in very small numbers compared with the total of the whole East Greenland–Iceland area. In the Dohrn Bank area 0-group indices have also been very low, except in 1973 (Fig. 4) (Vilhjálmsson and Friðgeirsson, 1976) and in 1984 (Vilhjálmsson and Magnússon, 1984). These two year classes were very important to the fisheries at Greenland. Results of tagging experiments carried out at Greenland show that the 1973 year class immigrated to the spawning grounds off Iceland in 1980, and particularly in 1981, and that the 1984 year class did the same in 1990 (ICES, 1993). Astthorsson *et al.* (1994) reanalysed the 0-group survey results and found that in addition to the years 1973 and 1984, in 1981, 1985, and 1987 18–25% of the total indices were found in the Denmark Strait–Dohrn Bank area. However, the total 0-group indices were much lower in those years and these year classes contributed little to

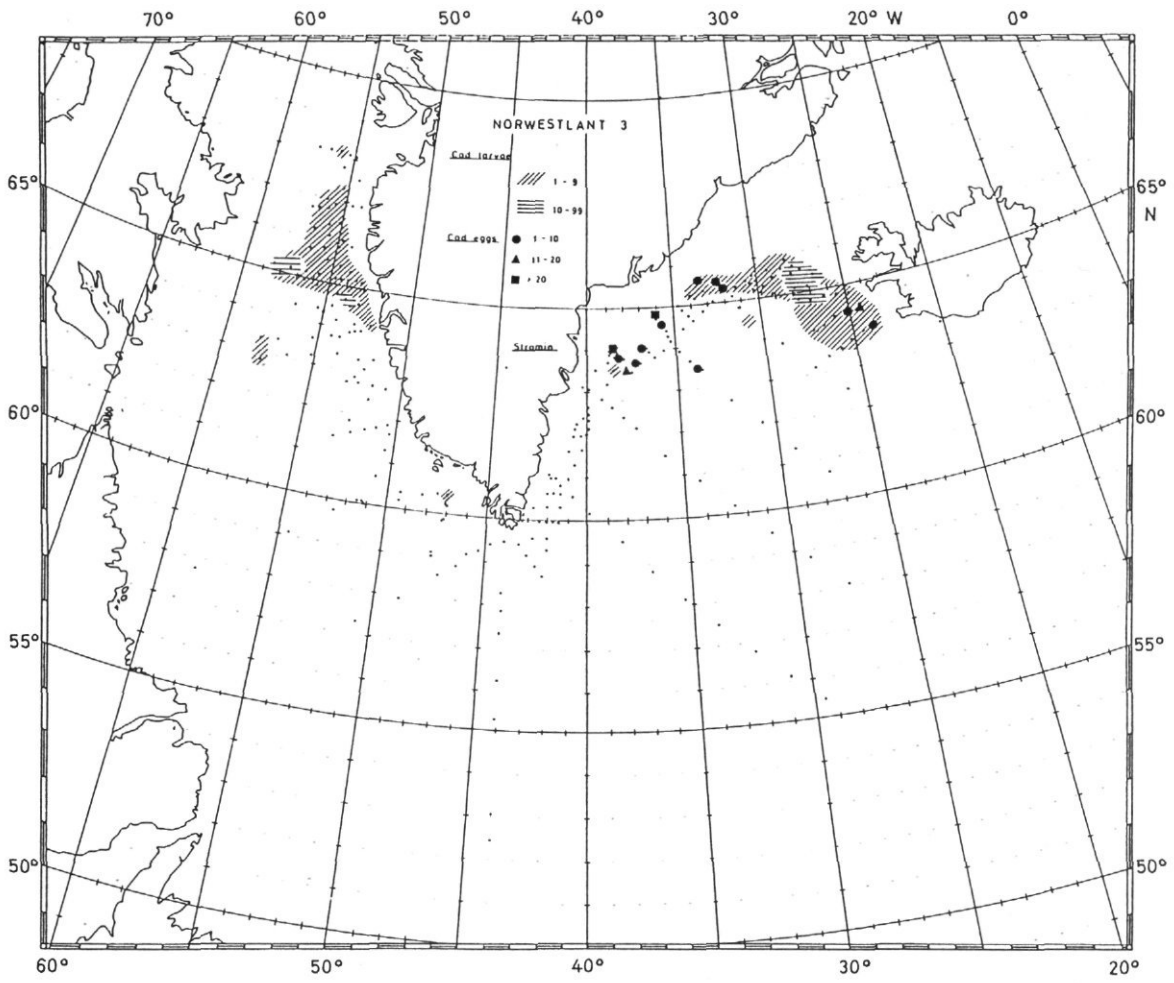


Figure 3. Distribution of cod eggs and larvae in 1963 (ICNAF NORWESTLANT 3) (from Hansen, 1968).

the fisheries at either Greenland or Iceland compared with the 1973 and 1984 year classes.

The drift of eggs, larvae, and 0-group fish seems to be dependent to greater or lesser extents on hydrographical and meteorological conditions in the Iceland–East Greenland area. Off the west coast of Iceland, in particular, the influx of Atlantic Water and the dominant wind direction during spring seem likely to be the two major factors which determine the direction of currents in the upper layers and hence the larval drift.

The immigration of mature cod from Greenland affects the stock abundance at Iceland, and in determining the fluctuations in the stock at Iceland it is important to take this interrelationship into account. It is therefore desirable to distinguish between the two cod stock components, i.e. the Icelandic and Greenland components.

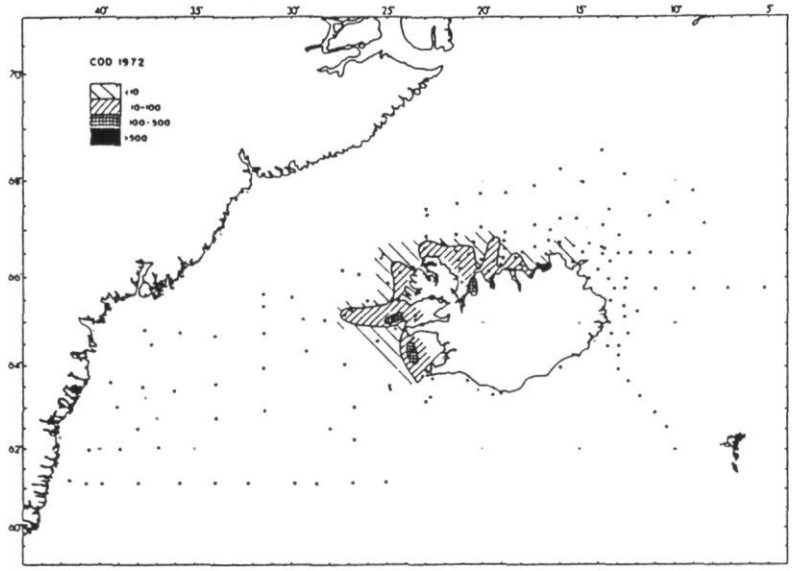
Schopka (1993) estimated the immigration rate by studying the changes in the fishing mortalities for those year classes at Iceland which were subject to such immigration during the period 1941–1990. By applying the same method in the present analysis the Greenland component at Iceland was estimated back to 1928.

Development of the cod fisheries

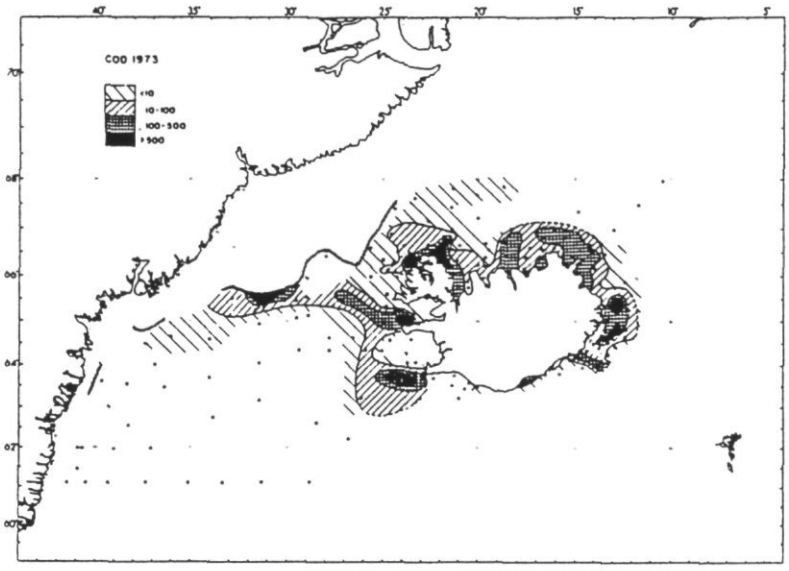
Fishery on cod has been carried out ever since Iceland was settled more than 1100 years ago. A description of the settlement of the country indicates that there was an abundance of fish in all fjords and rivers.

From available information the fishery throughout the centuries not only varied from year to year but also from one period to the next (Jónsson, 1994). This article does not describe development of the cod fisheries in former times, but rather the trends in the fisheries which have taken place in this century.

When the International Council for the Exploration of the Sea was established in 1902 it was decided that



Quantitative distribution of 0-group cod 1972



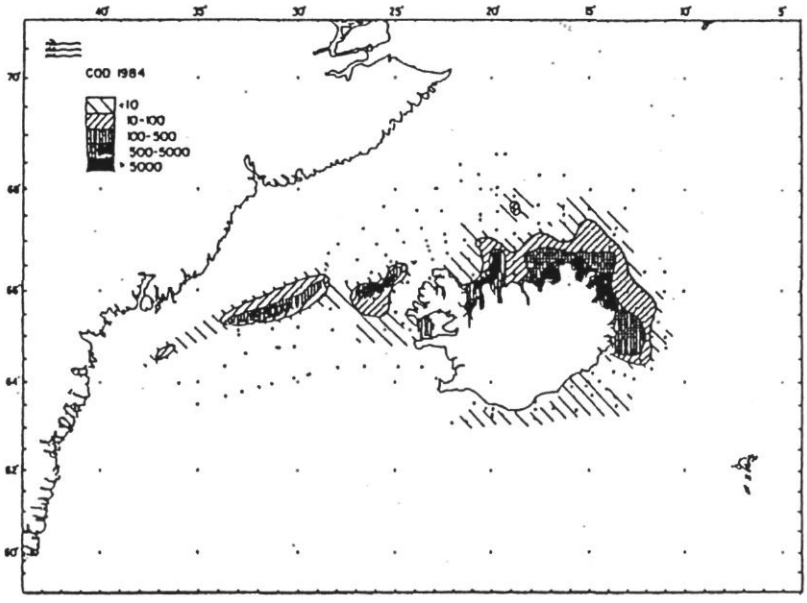
Quantitative distribution of 0-group cod 1973

Figure 4. Distribution pattern of 0-group cod, August 1972 and 1973 from Vilhjálmsson and Fridgeirsson (1976) and 1984 from Vilhjálmsson and Magnússon (1984). *Continued opposite.*

statistics on the fisheries should be collected by the member countries. The first summary of data on the cod fisheries for most of the countries fishing around Iceland was published for the year 1905. Prior to that, statistics are available for Icelandic, French, and Dutch fisheries (Jónsson, 1994).

The Icelandic fishery at that time was very primitive compared to later. Most of the fish were caught from open boats which had a limited operational range. Most vessels used hand lines or long lines and the use of other gears, i.e., active gears such as trawl or Danish seine, was exceptional. Iceland got its first trawler in 1904; foreign trawling on Icelandic grounds started just 12 years earlier. The use of gillnets was also very limited until after World War II. Developments in the cod fisheries have therefore taken place primarily in this century and are well documented by ICES statistics.

In 1905 Icelandic cod landings were less than 50 000 t



Distribution pattern of O-group cod, August 1984.

Figure 4. Continued.

(Fig. 5), but catches increased gradually as the number of Icelandic trawlers increased. From 1905 to 1916 the Icelandic cod catch almost doubled. In 1917 and 1918 the catches declined, as most of the Icelandic trawlers were sold out of the country in those years.

The catches of the international fleet also increased in these years because of increased effort. In 1914 the total cod landings reached a peak of almost 200 000 t. During World War I foreign landings declined rapidly, with the disappearance of most of the foreign vessels from these grounds, and in 1917 the foreign catch was less than one-tenth of the 1914 catch. The Icelandic catch remained unchanged in this period.

After World War I Icelandic and foreign cod landings increased steadily to a record peak of almost 600 000 t in 1933. These record catches were not only the result of increased fishing, there was also an outstanding recruitment in those years (see "Year-class strength").

In the years 1934 to 1938 landings of cod from Icelandic grounds declined steadily as poor year classes reflected the fishable stock. This was especially pronounced in the Icelandic fishery, which in those years was concentrated on the spawning population. From 1934 to 1936 the catches declined by more than 50%. In late 1939, most of the foreign vessels left Icelandic fishing grounds due to the outbreak of World War II; only Faroese and Scottish vessels continued fishing during the war years.

No statistical data are available for the Faroese fisheries in those years. The Faroes landings in 1939–1951 have been estimated by the author. As the Faroese vessels were fishing on the same grounds at the same time as the Icelandic vessels, available information on the number of Faroese vessels and the c.p.u.e. of the Icelandic fleet was used to estimate the Faroese catches taken at Iceland.

During World War II, Icelandic and Scottish landings increased but Faroese catches remained fairly stable, even though the c.p.u.e. of the Icelandic fleet was increasing during the same period. This was due to an overall reduction of the Faroese fleet, as many vessels disappeared during the war or were scrapped, and no renewal was possible until after the war (Patursson, 1979).

The Faroese fishing fleet was rebuilt in the postwar years, Iceland too renewing and increasing its trawler fleet in the late 1940s and early 1950s. This was connected with the overall increase in the fishing effort of other fleets fishing at Iceland and led to steadily increasing cod catches up to a new peak of about 550 000 t in 1954. Again this yield was combined with an outstanding recruitment.

Since 1955, landings have gradually declined, but with some fluctuations as a result of changes in effort and/or abundance of cod. Even though the c.p.u.e. declined in the late 1950s, the relative abundance was still attractive

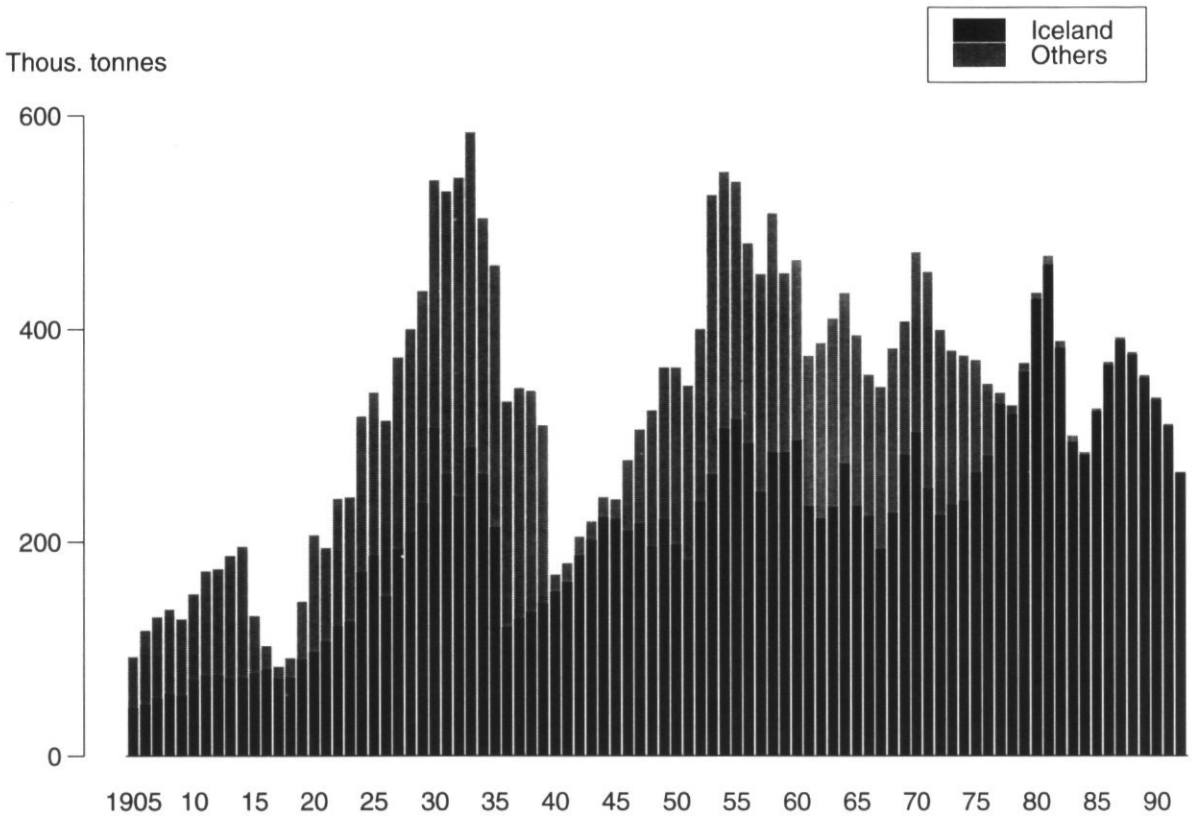


Figure 5. Total landings of cod from Iceland grounds (Va) in the period 1905–1992.

for foreign vessels and the Icelandic fleet was still growing. This development also continued in the 1960s and, despite an increase in overall effort, catches were diminishing. In the late 1960s when the herring fisheries collapsed, Icelandic vessels engaged in that fishery turned to cod. At the same time the cod fishery in the Barents Sea flourished and part of the foreign fleet left for that area.

In the early 1970s, when catch rates declined in the Barents Sea, foreign vessels returned to Icelandic waters. In those years Iceland started to replace the side-trawler fleet with highly modern stern trawlers. Fishing effort increased up to 1976, when the fishery changed with the extension of the fisheries jurisdiction to 200 nautical miles. Even though the major part of the foreign fleet ceased fishing in 1977, this did not bring about the reduction in fishing effort that fishery scientists had hoped for, as the still increasing Icelandic fishing fleet quickly filled the gap, and by 1977 was attaining record catches.

With the extension of the national fishery zone in 1975, foreign fishing has almost disappeared. The catches of the few foreign nations fishing at Iceland have been steadily cut, especially the Faroese, and now foreign cod landings are less than 1% of the total.

In the same period fluctuations in Icelandic cod landings were largely caused by the availability of cod. In the first years after the extension of the fishing limits, restrictions were more directed towards the protection of small fish with area closures and mesh regulations than to strict effort or TAC regulations. At the same time some new fishing vessels were being built.

It was not until 1984 that a quota system was first enforced, even though the Marine Research Institute (MRI) had been giving advice on TACs since 1975. The quota set by the Ministry of Fisheries was somewhat higher than that recommended by the MRI. The system itself is an open one because not all of the fleet is bound by the established quota. Catches of the smallest vessels (boats less than 20 GRT) and half of the catch of the long-liners, taken in the period November–February, are not counted against the quota.

Also, in order to reduce discards, limited quantities of undersized cod in the catches were accepted as being outside the quota. This resulted in catches far above the recommended TACs. Fishing effort has therefore con-

tinued to be high even though the 1992 catch was the lowest since 1946.

Fluctuation in population parameters

Previous analysis

Jónsson (1954) made the first attempt to calculate the relative size and total mortality of the spawning stock. In the years 1930–1953 the stock declined significantly and mortality increased steadily (see also Jónsson, 1960). The estimate of stock abundance at that time was relative (Gulland, 1961; Jónsson, 1966), but first stock estimate using the VPA technique was made by the North-Western Working Group in 1970 (ICES, 1971). This assessment covered the years 1960–1969 and in the joint ICES/ICNAF Working Group on Cod Stocks in the North Atlantic (ICES, 1973) a similar period was reviewed. The conclusion from these two assessments indicated that the stock was fully exploited.

In re-assessing the cod stock at Iceland, Schopka and Jónsson (1973) stated that it was heavily overexploited. This was also the conclusion of the 1976 assessment by the North-Western Working Group (ICES, 1976), which covered the period back to 1955 and showed that there had been a considerable decline in both the total stock and the spawning stock component (7+) during these years.

In another assessment some years later, Schopka (1980) showed that measures taken to protect juvenile cod, i.e. closure of nursery areas and an increase in mesh size to 155 mm in trawl codend, had reduced the fishing mortality of the youngest age groups (3–4) considerably.

Cushing (1982) extended the stock analysis further back by using Jónsson's (1949–1972) published age composition data of the mature population, but as he had no data on the immature part of the stock he had to assume a certain exploitation rate for that part to generate the stock size. He therefore chose to call his analysis a "simulacrum".

Based on available, but unpublished, age composition data of the Icelandic non-spawning fishery collected by Friðriksson and Jónsson plus Jónsson's data on the mature population, length compositions of the German fisheries at Iceland and the monthly catches by statistical retangles of the UK fleet at Iceland, Schopka (1993) extended the VPA for Icelandic cod back to 1941. He found that fishing mortality had increased steadily between World War II and the extension of the fishery limits to 200 miles in 1975.

Data sources and VPA tuning

Even though cod was not systematically sampled during the first decades of the century, samples taken on board the research vessels and the commercial fleet provide some information on the age composition and year-class strength of the stock during a period when fishing intensity was low. Systematic investigations on the age distribution of cod in the landings from Icelandic vessels started in 1928. Tåning (1931b) described large fluctuations in the age composition of the landings of cod from year to year and between different fishing grounds.

In 1931, Friðriksson took over Tåning's work on cod and sampled the cod fisheries until 1946. The age compositions of cod were published annually for the years 1931–1937 (Friðriksson 1932–1937), but only in certain years for the period 1938–1945 (Friðriksson 1939, 1941, 1942, 1943a, b).

During the period 1946–1970, Jónsson continued the research on the cod stock in Icelandic waters. He published the age composition of the spawning cod fishery at Iceland annually in the ICES periodical *Annales Biologiques* (Jónsson, 1949–1972). Jónsson (1951) discovered that during the period 1928–1950 there was a strong relationsship between year-class strength and fluctuations in the catches of cod.

Young cod surveys were carried out during the years 1977–1984 (Pálsson, 1984). Groundfish surveys directed for cod started in 1982 (Schopka *et al.*, 1983). These surveys were combined and extended in 1985 and carried out by five trawlers (Pálsson *et al.*, 1989). The indices from the groundfish surveys, together with effort data of the trawler fleet, have been used to tune the VPA in the most recent assessments (ICES, 1993).

Fishable stock

Based on the available catch in numbers data derived back to 1928, and using the VPA technique, stock abundance has been estimated for the same period. Some estimate on the size of the stock prior to 1928 can be obtained by extending the analysis further and assuming similar fishing pattern and mean weights at age as 1930. This exercise was mainly done to get some idea of the size of the very large 1922 and 1924 year classes. The estimation of the size of the fishable stock cannot be generated many years back as little information is available on year classes which went through the fisheries prior to 1927 (i.e. year classes 1909 and earlier). However, for the years 1924–1927 the approximate size of the fishable stock can be derived from such a back calculation, as the stock was largely composed of year classes of known size.

The fishable stock (4 years and older) in those years (i.e. 1924–1927) was in the order of 2.5–2.8 million tonnes (Fig. 6). The highest level of around 3.3 million tonnes was reached in 1928; it was 2.8 million tonnes in 1929 and increased in 1930 to about 3 million tonnes. In 1930 the strong 1922 year class immigrated from Green-

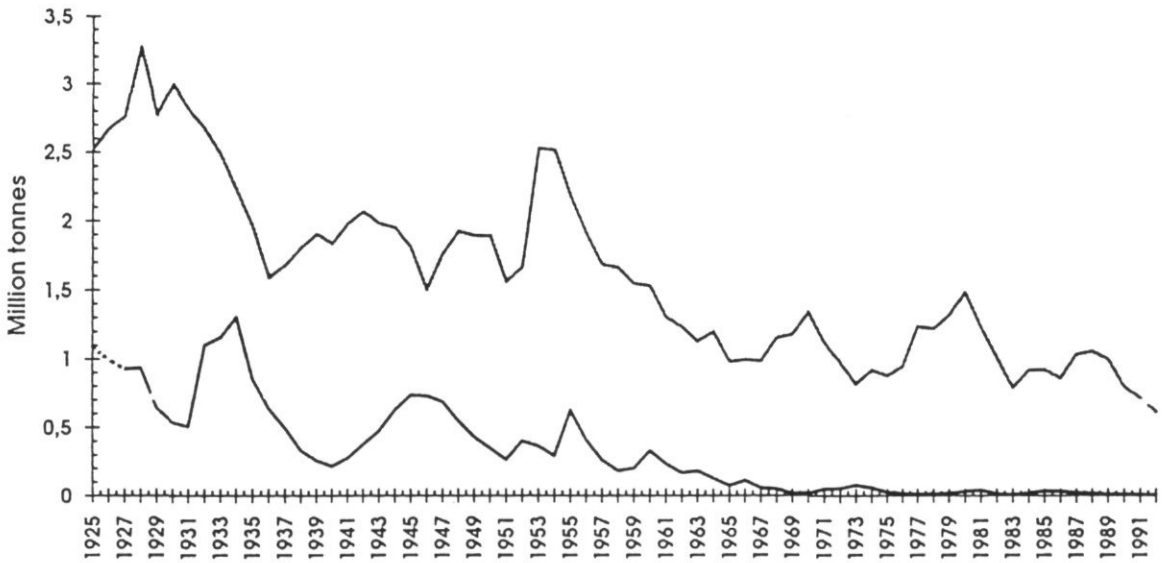


Figure 6. Cod at Iceland. Estimated size of total fishable stock biomass (upper line) and the biomass of 10 years and older cod (lower line) during the period 1925–1992.

land and the stock remained at a level of around 3 million tonnes up to 1932, even though catches taken were high compared to the whole period. Because of poorer recruitment in the late 1920s the stock declined and reached a minimum of 1.7 million tonnes in 1936. It increased due to better recruitment to about 2 million tonnes in 1938, around which level it remained during the next 6 years. Although most of the year classes were well below average, fishing effort had declined during World War II and thus the stock was maintained at this level. The stock declined to a minimum of 1.5 million in 1946 tonnes, but soon recovered to almost 2 million tonnes in 1948, when immigrants from Greenland recruited to the stock at Iceland. The stock decreased slightly to 1.6 million tonnes in 1951 and 1952. Then the strong 1945 year class immigrated from Greenland, with the result that the fishable stock in 1953 and 1954 reached the early 1930 level of 2.5 million tonnes.

During the next years the stock declined, reaching the low level of only 1 million tonnes in 1965. After that it began to rise gradually to about 1.3 million tonnes in 1970, but fell again due to heavy fishing to a level of 800 000–900 000 t in the period 1973–1976. This happened in spite of the fact that the 1970 year class was abundant.

The stock began to increase again, largely owing to the large 1973 year class, which was the highest observed since 1945, but also because of the increased protection afforded by the extension of the fishing limits to 200 nautical miles in 1975. The stock biomass amounted to about 1.5 million tonnes in 1980, but fell rapidly to less than 800 000 t in 1983, and then increased slightly to almost 1.1 million tonnes in 1988 when the 1983 and 1984 year classes recruited to the fishable stock. Since then, the stock has declined and the estimated stock size at the beginning of 1994 is only about 600 000 t, the lowest observed level.

The changes in the biomass of the older component of the population, i.e., cod 10 years and older, are striking (Fig. 6, lower line). In the mid-1920s and mid-1930s this component of the population was about 1 million tonnes. There was a continuous drop until 1940 and subsequently an increase during World War II to some 700 000 t. This component of the stock has been declining ever since. There was an increase when the 1945 year class reached this age in 1955, but with increased fishing this part of the population continued to decrease; since 1968 the old cod have contributed very little to the spawning and the catches. Nowadays very few are captured.

Spawning-stock biomass

Data on maturity are available for the Icelandic material only since 1945. In order to calculate the spawning-stock biomass (SSB), maturity ogives were required for the entire period examined. The relationship between mean weight-at-age in the catches and the maturity-at-age was derived and this was then used to calculate maturity-at-age back in time. The estimated spawning stock is shown in Figure 7. The extension of the analysis earlier than 1928 is more questionable for estimating the spawning

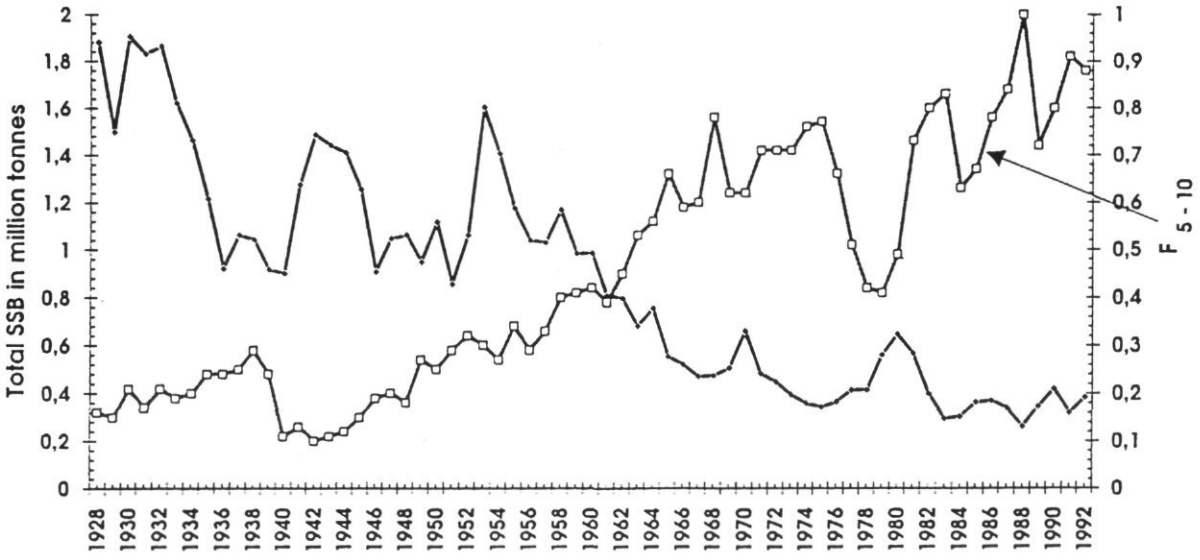


Figure 7. Cod at Iceland estimated total spawning-stock biomass (closed circles) and fishing mortality of the age groups 5–10 (open boxes) during the period 1928–1992.

stock than the fishable or the total stock, as the oldest (not known) age groups contribute fully to the spawning stock. Generally it can be said that the SSB during the years 1925–1927 was about at the level of 1.5 million tonnes. The spawning stock was at a level well above 1 million tonnes in the years when the two outstanding year classes 1922 and 1924 were produced.

Fluctuations in the spawning stock of cod have been even more pronounced than those seen in the fishable stock. During the years 1928–1933 the spawning stock was almost 2 million tonnes. It declined to less than 1 million tonnes in 1936, increased slightly in 1937 and 1938, decreased slightly in 1939 and 1940, but increased rapidly during World War II owing to the lower fishing effort. As poorer year classes entered the spawning stock during the period 1945–1952 the spawning stock was almost at the level of around 1 million tonnes. When the 1945 year class entered Icelandic waters the spawning stock almost doubled from 850 000 t in 1951 to 1.6 million tonnes in 1953. It remained at about 1.0–1.2 million tonnes in the period 1955–1960, before gradually declining, though with some fluctuations, to about 300 000 t in 1974. Because of reduction in fishing effort in 1976 to 1978, combined with maturation of the 1973 year class, the spawning stock almost doubled by the year 1980. It fell below 300 000 t in 1983, remaining at that low level until 1989, when it rose slightly to about 450 000 t, with some immigrants of the 1984 year class entering the spawning grounds at Iceland. In recent years the SSB (on the 1st of January) has been fluctuating at around 300 000 t, which is only 16% of the early 1930s maximum level.

Fishing mortality

Despite the fact that cod catches in Icelandic waters in the years around 1930 were more than 300 000 t annually, the size of the total fishable stock was so enormous that fishing mortality generated on the age groups 5–10 was less or around the same as the assumed natural mortality of 0.2 (Fig. 7). When the second portion of the 1922 year class immigrated to the spawning grounds at Iceland in 1931, fishing mortality fell almost to 0.1. The good fishing at Iceland resulted in increased effort in the coming years and fishing mortality increased to 0.3 in 1938.

In 1939 there was a slight decrease in fishing effort because of the outbreak of World War II. Foreign fleets fishing at Iceland left and fishing mortality in 1940 dropped to 0.1. It remained at a very low level during the war years but when foreign fishing was resumed after the war fishing mortality again began to increase gradually.

With the extension of fishery jurisdiction in 1975 most of the foreign vessels fishing around Iceland left the grounds and fishing mortality dropped by about 50%.

However, in those years the Icelandic trawler fleet was renewed and increased and, simultaneously, fishing mortality rose to a new record level in 1983. It was obvious that measures undertaken to protect the cod, such as the increase in mesh size in 1977, temporary closures of nursery grounds, and the implementation of the "scratch-days system", a way to reduce the fishing effort on cod by diverting effort to other demersal species, failed to limit fishing effort on cod sufficiently and therefore a quota system was adopted in 1984. To

begin with, the quota system led to some decline in effort (and hence fishing mortality), but almost every year the quota recommended by the Marine Research Institute was never fully adhered to. As the stock declined the fishing mortality continued to increase, reaching a historic record level of 1.0 in 1988. Since then there has been a slight decrease in fishing mortality, but it is still far above any acceptable level.

Year-class strength

The present VPA allows us to calculate the year-class strength back to 1925. As the fishing mortality on the youngest age groups was low it is also possible to estimate the 1924 year class accurately. We can similarly estimate the approximate strength of the 1922 and 1923 year classes. Assuming the same fishing pattern in the 1920s as around the 1930s, the projection could be extended further back to get an idea of the size of some other year classes prior to 1922 (Fig. 8). The 1922 year class was large in Greenland waters and may have originated from spawning at Iceland. This year class immigrated to Icelandic spawning grounds in the years 1930–1933. Back-calculation estimates, assuming low fishing mortality during the years when this year class was still at Greenland, indicate that this year class may have been the most abundant of this century. It is estimated at about 1.3 billion at 3 years of age. The 1924 and 1945 year classes are also large. These three year classes are two to three times stronger than any other strong year class and are classified as superabundant year classes (Fig. 8). Other strong year classes are those from 1936, 1942, 1950, and 1973. It should be noted that all the year classes mentioned above include immigrants, sometimes on a large scale. The three super year classes were to a large extent of Greenlandic origin. Outstanding but pure Icelandic year classes never seem to be stronger than 300–350 millions, i.e., year classes 1923, 1935, 1949, 1964, 1970, and 1983. For the combined Iceland–Greenland year classes the Iceland component seems to have exceeded 350 million at age 3 only once; the 1922 year class at Iceland is estimated to have been 540 million at age 3.

There are several year classes in the order of 250–300 million individuals, or above the long-term average of 225 million fish. Most of them are in the order 150–220 million fish. Very poor year classes below 100 million individuals have been infrequent. Only the 1928, 1940, and 1986 year classes are less than one hundred million individuals, and first estimates of the 1991 year class of only 70 million indicates that it may be the poorest of this century. For Icelandic cod, no extreme poor year classes have ever been observed, not at least in the period considered here, as has been the case at Greenland where the difference between the poorest (the 1982 year class of only 4 million (ICES, 1991)) and the strongest (1953 year class of 451 million (Hansen and Buch, 1986)) year classes is greater than 1:100 or almost 10 times greater than at Iceland.

It is noticeable that there is a kind of periodicity in the recruitment at Iceland. After a period of some good year classes, there follows an interval of poor recruitment succeeded by stronger year classes and so on. These periods seem to be of 3–5 years, but it is remarkable that after 1970 the periods of poor recruitment, compared to those of better recruitment, are longer than during years when the spawning stock was of considerable size. It is also interesting to note that outstanding year classes show up regularly in a period of 10–12 years. There is evidence prior to the period in view, from both the present analysis and earlier information (Tåning, 1931a), that the 1912 year class was also an outstanding one. Bodvarsson and Jónsson (1961) stated that strong cod year classes were definitely linked to periods of low solar activity! The relationship between recruitment and sunspots still holds, i.e., it is significant but only if the 1922 and 1924 super year classes are included in the series.

Spawning stock and recruitment

Recruitment plotted against total spawning-stock biomass for the period 1928–1991 is shown in Figure 9. Of the three super year classes, only that of 1945 could be included, as exact information on the spawning stock size in the early 1920s is not available. However, it is clear that the spawning stock at that time was greater that 1 million tonnes and more likely in the order of 1.5 million tonnes.

Both the Ricker and Beverton and Holt models were fitted to the data by the method described in Jakobsson *et al.* (1993). The correlation is poor (Ricker $r^2 = 0.080$; Beverton and Holt $r^2 = 0.0691$) and the stock–recruitment relationships described by the two models are hardly distinguishable in the plot, as the sum of squared deviations (SSE) is similar (Ricker SSE = 11.74; Beverton and Holt SSE = 11.89). By assuming the spawning stock size during the 1920s at the level of 1–1.5 million tonnes another calculation of stock–recruitment relationship, including the two super year classes of 1922 and 1924, was carried out but the correlation between these parameters did not improve.

More questionable is the minimum size of a spawning stock able to generate average and good year classes. Trends in the most recent years indicate that poor recruitment is more frequent after the spawning stock reached the present low level. All year classes since 1985 have been below average except the 1993 year class. Initial indications from the 1994 groundfish survey indicate that this year class is an average one. This is the

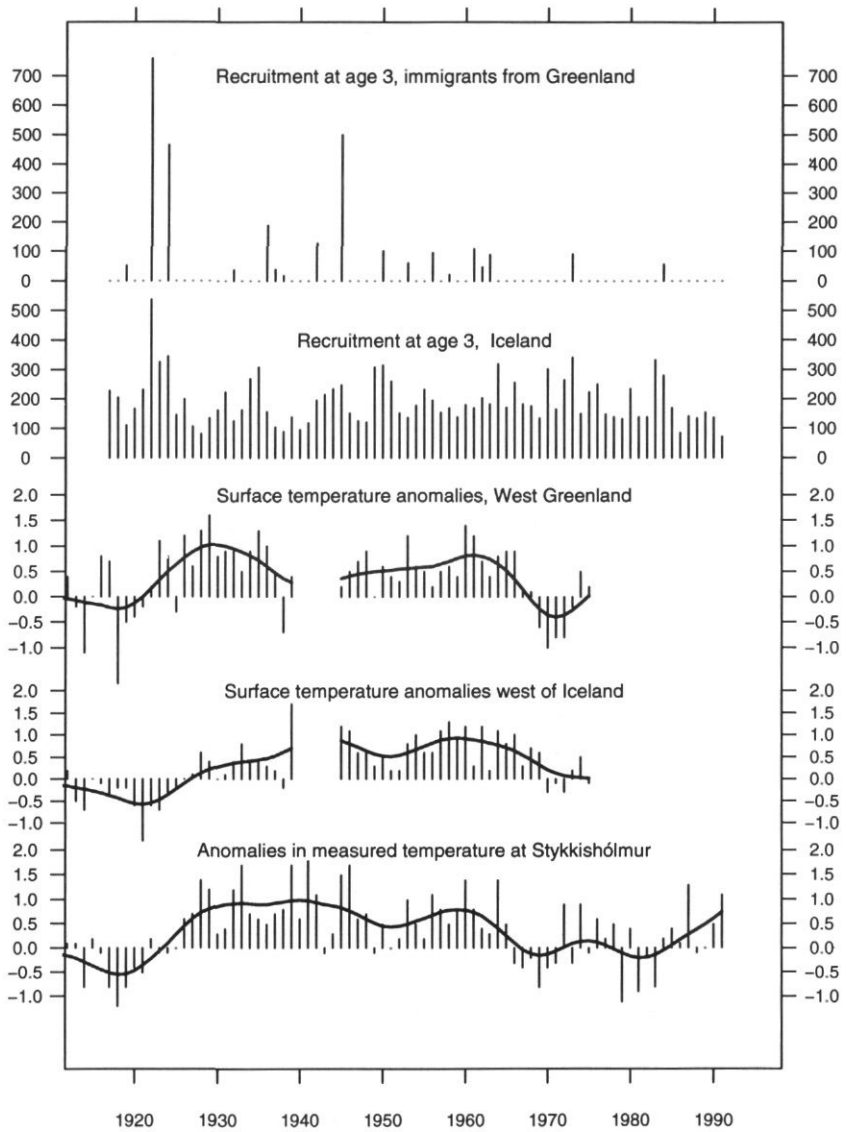


Figure 8. Cod at Iceland. Year-class strength at age 3 needed to account for Greenland immigrants at Iceland, recruitment at age 3 at Iceland, surface anomalies at West Greenland and west of Iceland (from Smed 1953–1976) and air temperature anomalies at Stykkishólmur, West-Iceland (data from Icelandic Weather Bureau).

longest period of continuous poor recruitment ever observed. It has been pointed out by Stefánsson (1992) and ICES (1993) that a possible stock–recruitment relationship may exist. Fishing mortality in the stock has been increasing over a long long period, with a resulting decline in both total stock and spawning-stock biomass (Fig. 7). Recruitment overfishing cannot therefore be excluded, but is hard to detect because of the variability in the recruitment, which may mask a possible stock collapse.

It has been argued that old cod (10 years and older) may contribute more to the spawning potential than the younger first-time spawners (Marteinsdóttir, 1995). This old cod (multispawners) hypothesis is also supported by that fact that when strong year classes reach approximately the age 10 or 11 another large year class is born (Fig. 8). As mentioned above under "Fishable stock", the proportion of 10 years and older cod in the stock had shown a more pronounced decline with time than the total stock. Therefore recruitment was plotted against

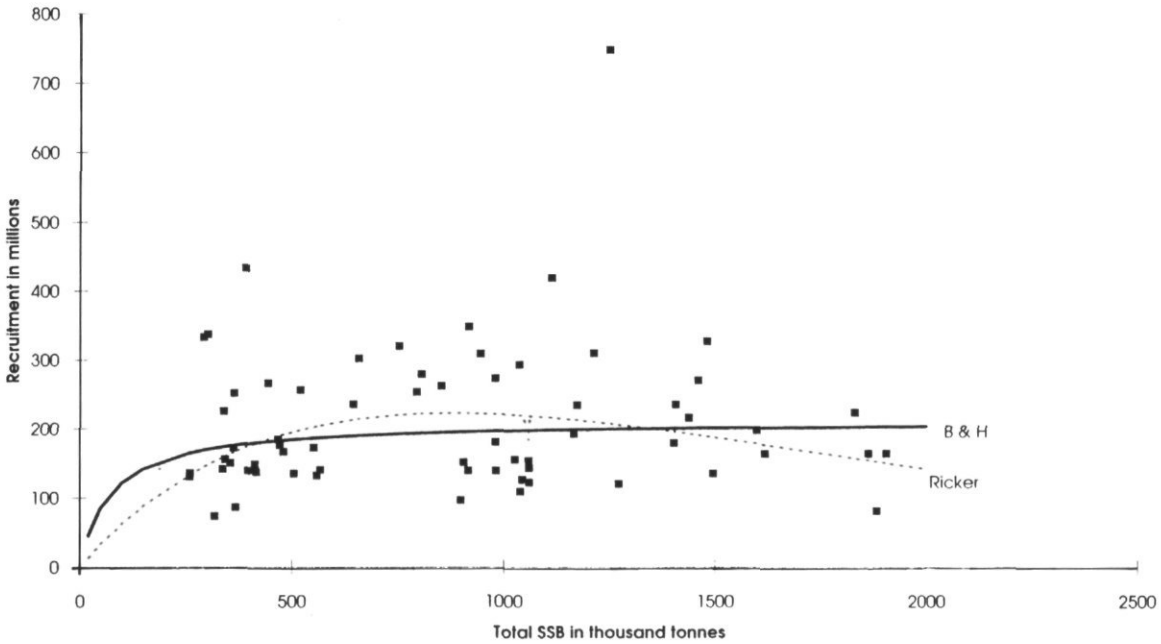


Figure 9. Cod at Iceland. Recruitment at age 3 versus total spawning-stock biomass for the years 1928–1991.

SSB of 10 years and older cod (Fig. 10). Owing to the large variability in the data, no clear relationship could be found between these parameters.

Trends in growth

It is well known that growth is interrelated with stock size in the way that growth rate declines with increase in stock, i.e., growth is density-dependent. Jónsson (1954) showed that average length of 8–12-year-old Icelandic cod increased by declining stock abundance in the years 1930–1950. Changes in the environment (temperature) also affect the growth rate (Taylor 1958; Jónsson 1965b, 1969). In the case of Icelandic cod, studies on the changes in growth rate are more complicated than for many other cod stocks because of the mixture of the

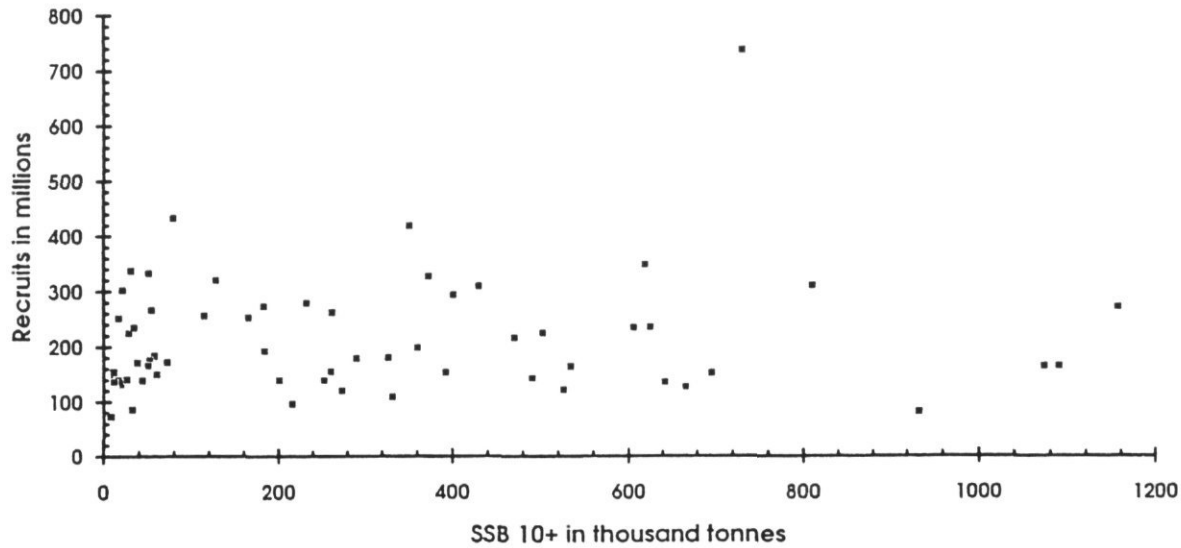


Figure 10. Cod at Iceland. Recruitment at age 3 versus spawning biomass of 10 years and older cod for the years 1928–1991.

slow-growing Greenland component with the faster growing Icelandic cod.

Cod in the warm water area off the south- and south-west coasts of Iceland grow much faster than cod in the cold waters off the north and east coasts of the island (Sæmundsson, 1923). Another factor which makes growth studies of Icelandic cod complicated is the diversity of the available data. Data for growth studies are based on samples from the commercial fisheries. They show only the mean length-at-age or the mean weight-at-age in the catches; they do not necessarily reflect these parameters in the stock, especially as the proportion of the gears used in the fisheries have been changing with time and the selectivity of the gears used is different. However, some simple calculations have been carried out.

Figure 11 shows the mean weight-at-age in the catches of 5–8-year-old cod. Catches of younger ages were not considered because they are biased through gear selection and older ages are biased through inadequate sampling during part of the period. In earlier periods fishing was concentrated more on the mature (older) population, and in the most recent period an increase in mesh size and a temporary closure of certain areas on the nursery grounds has reduced catches of the youngest age groups. In the same way, the reduction of the older cod in the population with time does not allow comparison throughout the whole period, as the biomass of the age 10 and older cod has been reduced to only 1% in 1992 compared to the 1930 level (Fig. 6).

There are also yearly fluctuations in the mean weight-at-age for the older age groups on the impact of the Greenland immigrants. Therefore the trends in mean weight-at-age with time can be better demonstrated by a 5-year running mean (Fig. 12). For all age groups, including those not shown, the mean weight-at-age increased from a minimum level in the early 1930s to a maximum in the early 1960s. Since then there has been a slight decline in weight-at-age but with some fluctuations which are more pronounced for the older ages.

In the same figure the fishable biomass is plotted with time as 5-year running average. At the beginning of the period examined the fishable stock was at a maximum of about 3 million tonnes. With a decline in stock size during the 1930s the mean weight-at-age increased and reached a maximum at the beginning of World War II. This coincided with a minimum in the stock size. As the stock increased as a result of better recruitment to the stock and hence the stock biomass, there was a decline in the mean weight-at-age in the mid-1940s, but then it started to increase in spite of an increased stock size. This is likely to be connected with favourable environmental conditions during the early 1950s. In the early 1960s, when the mean weight-at-age had reached a maximum, the stock biomass was about 40% of the early 1930s level.

Statistical analysis for weight-at-age on fishable biomass (4^+), based on the annual values, show that these parameters are negatively but significantly correlated pointing to a density dependence (Table 1).

Therefore the increase in mean weight since the early 1930s can largely be explained by the decline in stock abundance. Of course the growth of cod has also gained from the overall warming, but statistical analysis of the

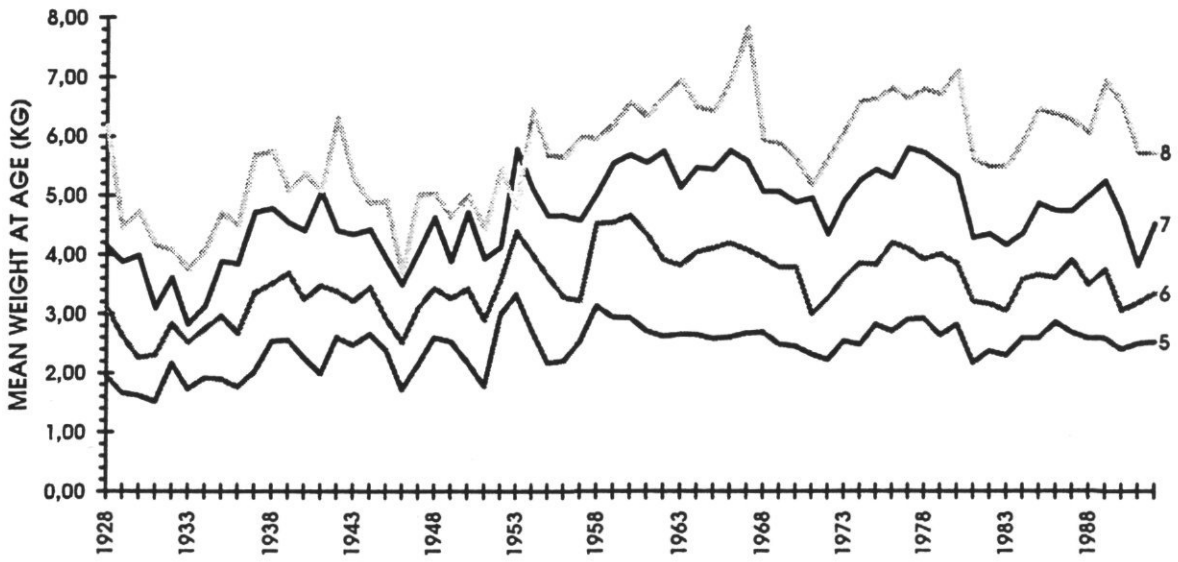


Figure 11. Cod at Iceland. Mean weight-at-age of the ages 5–8 during the period 1928–1992.

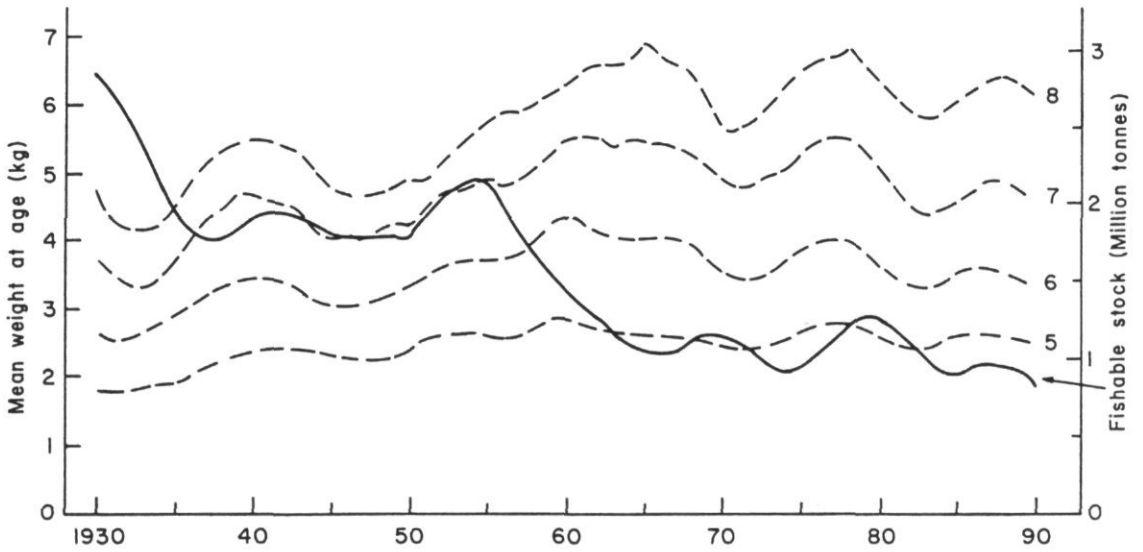


Figure 12. Cod at Iceland. Mean weight-at-age of the ages 5–8 during the period 1928–1992. Five years' running averages. Fishable stock biomass during the same period is also shown.

relationship between surface temperature off West Iceland and mean weight-at-age for the periods 1928–1939 and 1945–1975 (where data are available) is positive but not significant except for age 6. Since 1965, cod growth rate has been fairly stable, even though the stock size has continued to decline, but it must be kept in mind that temperature since the late 1960s is somewhat lower than in the earlier years.

The decline in growth during the late 1960s was caused by a combination of an increase in stock abundance and the deteriorating environmental conditions in Icelandic waters in those years. For the older age groups the growth is also affected by slower growing Greenland immigrants of the 1961–1963 year classes. The decline in mean weight-at-age in the early 1980s is a combination of the adverse hydrographic conditions known as the Great Salinity Anomaly (Dickson *et al.*, 1988), especially the collapse of the capelin stock in those years (Steinarsson and Stefánsson, 1991).

Table 1. Cod at Iceland. Regression analysis for weight-at-age on fishable biomass (B_{4+}) W_i is the mean weight at age i, i = 5 . . . 8.

Dependent variable	Biomass	F value	F significance
W_5	B_{4+}	15.0	0.0003
W_6	B_{4+}	12.2	0.001
W_7	B_{4+}	15.6	0.0002
W_8	B_{4+}	29.6	<0.0001

Discussion

Drift of cod larvae from the spawning grounds at Iceland to Greenland waters greatly extends the nursery area for cod of Icelandic origin. Therefore both climate and fisheries around Greenland directly affect the state of the cod stock at Iceland and the outcome of the fisheries there. It was not possible in this study to take into account the reduction of Icelandic cod at Greenland caused by the fisheries there, but such an analysis could be carried out if data for a combined assessment of the Iceland–Greenland cod stock complex were available. Because of the very low fishing effort in Greenland waters prior to World War II the effect of the fisheries at Greenland on year classes originating from the spawning at Iceland is thought to be negligible. In the early 1950s when the large fisheries at West Greenland started, fishing mortality reduced the year classes from Iceland inhabiting West Greenland waters, especially the 1945 year class. It is therefore likely that the size of the 1945 year class is somewhat underestimated in the present analysis.

The sudden warming in the early 1920s, especially in Greenland waters, after a relatively cold period extended the distribution area of cod along the west coast of Greenland north to Disko. Combined with favourable larval drift from Iceland in 1922 and 1924 this warming is the main reason for the outburst of the 1922 and 1924 superabundant year classes. As there was almost no cod at West Greenland for many decades prior to 1920 (Hansen, 1949) there might have been a

supply of different food resources available for cod larvae, and favourable conditions for young cod survival and competition and predation might have been at a minimum at that time. However, the enormous size of these year classes seems to have limited growth rate through the density-dependence mechanism, as the growth rate of cod has been increasing in recent decades at the same time as the stock biomass has been declining.

It might be more difficult to explain the outburst of the third known super year class in this century, the 1945 year class, which was of similar size as the 1924 year class. A preliminary assessment of the West Greenland cod (Buch *et al.*, 1994) shows that during World War II the stock was at a level of 2–3 million tonnes or two–three times larger than in the mid-1920s. The conditions which could explain the richness of this year class seem therefore not to have been the same as in the early 1920s. The SSB at that time of almost one million tonnes was able to generate a super year class. SSB in the years 1922 and 1924 was also at least similar in size as in the year 1945, possibly larger (see above under "Spawning-stock biomass").

Year classes other than those presented in the analysis and defined as immigrating year classes might also have included some migrants, given results from tagging experiments carried out at Greenland (ICES, 1971). However, compared with the stock size at Iceland, 5–10 million immigrants are barely detectable and are hardly likely to influence the analysis. It should be noted that immigration took place more often prior to 1970 than during the last two decades. This might be connected with a much poorer state of the stock at Greenland. If the immigrants from Greenland have originated from the spawning at Iceland there must have been a decline in the frequency of larvae drifted towards Greenland, possibly caused by changes in the environment and/or connected with the reduction of the stock at Iceland. So there might be a kind of feedback mechanism in the Iceland–Greenland cod stock complex: a reduction in the stock at Greenland gives fewer immigrants to Iceland, which will reduce the spawning potential at Iceland. This will then reduce the larval drift to Greenland, and so on.

The changes in the fishing mortality indicate that during the period of low fishing mortality at the $F_{0.1}$ level or about the assumed natural mortality of $M = 0.2$, the fluctuations in the stock abundance reflect variations in the recruitment more than the effect of fishing. Spawning stock size in this period is more or less on a level which ensures recruitment and therefore the annual changes in the recruitment basically reflect variations in the environmental factors.

With further increases in fishing mortality above F_{max} (0.4; ICES, 1993), there are signs that increased fishing reduces the stock biomass, especially the older component of the stock. The reduction in stock abundance increases the growth rate but only to a certain extent, so any further increase in the fishing mortality will result in an overall decline in stock biomass. At that point one can conclude that fluctuations in the stock are a combination of fisheries and environment.

The unfavourable changes in environment after 1965 combined with high fishing mortality has driven the spawning potential of the Icelandic cod stock to a historical low level. The risk of continuous recruitment failure and hence a stock collapse is greater than ever.

Acknowledgments

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Fluctuations in the Faroe Plateau cod stock

Stein Hjalti í Jákupsstovu and Jákup Reinert

Jákupsstovu, S. H. í, and Reinert, J. 1994. Fluctuations in the Faroe Plateau cod stock. – ICES mar. Sci. Symp., 198: 194–211.

This article overviews the biology, stock fluctuations, and fishery of the Faroe Plateau cod stock. Despite very high fishery intensity during most of this century, landings have been fairly stable throughout the period, fluctuating between 20 000 and 40 000 t. Several investigations have shown the Faroe Plateau cod stock to be a self-sustaining stock unit, so the relatively stable catches must reflect a stable environment and/or a robust stock together with adaptable behaviour of the fishing fleets. In the most recent years the catches and stock sizes have decreased dramatically to the lowest level on record. It is shown that this is due to the combined effect of high fishing mortalities, poor recruitment, and declining mean weights-at-age. Possible causes of biological and environmental changes are listed and discussed together with the anthropogenic influences on the stock.

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Introduction

The existence of two self-sustainable cod stocks in the Faroe area, one on the Faroe Plateau and one on the Faroe Bank, is generally accepted; evidence for this is given below. One main reason for the two stocks remaining distinct is the anticyclonic circulation systems which dominate the shallower region in each of these two areas (Fig. 1) and result in large retention times for the water and planktonic organisms. These anticyclonic current systems are created by the combined effect of the North Atlantic Drift, the topography in the area, and the coriolis and tidal forces. The persistency of the flows and the relatively high temperature of the Atlantic water ensuring high productivity in the area and very stable ecosystems are reflected by the fact that throughout this century the waters on the Plateau and on the Faroe Bank have varied little in temperature and salinity. However, in recent years the front north of the Faroes separating the North Atlantic Current from the cold East Icelandic Current (Fig. 1), has moved closer to the islands, and the intensity of the North Atlantic Current, which passes the Faroes, has decreased (Gaard *et al.*, 1994). Such changes might affect the stability and productivity of the systems. A comprehensive description and analysis of the physical environment in the Faroe area is given by Gaard *et al.* (1994).

With the exception of the 1939–1945 war period, the total landings of cod from the Faroe area (Faroe Plateau and Faroe Bank combined) have fluctuated between 20 000 and 40 000 t, with remarkable stability (Fig. 2). In 1990 the fishery collapsed, yielding only 14 000 t, and has since declined further to only 7000 t in 1992.

Analytical assessments are only available for the cod stock on the Faroe Plateau, and, although the yields from both stocks at present are equally depressed in this

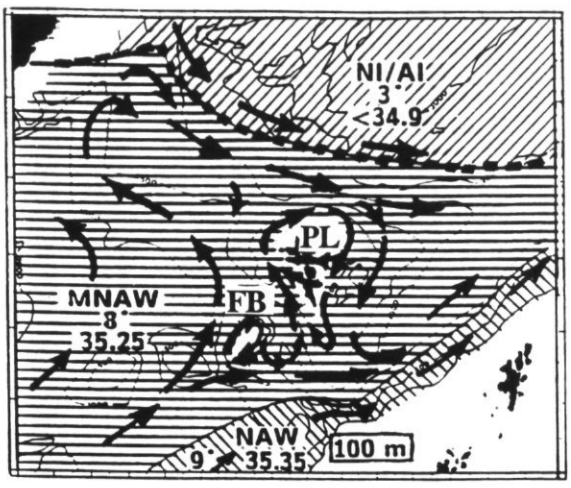


Figure 1. Distribution of main water masses and circulation patterns in the upper layers of the waters surrounding the Faroes. MNAW derives from the North Atlantic Current, NI/AI from the East Icelandic Current. FB = Faroe Bank. PL = Faroe Plateau (adapted from Hansen *et al.*, 1990).

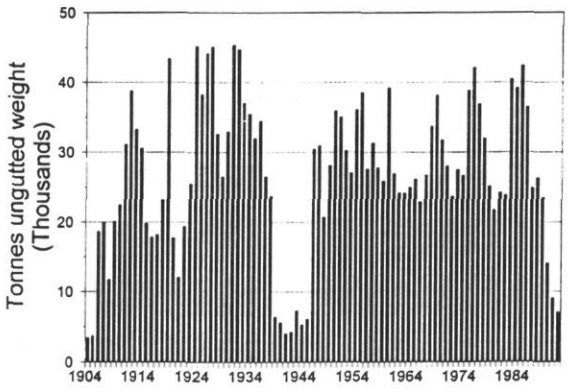


Figure 2. Landings of cod from the Faroe area (Vb) in 1904–1992. Tonnes ungutted weight.

paper we deal only with the Plateau stock. In May 1993 the Faroe Plateau stock was assessed to be below the minimum biologically acceptable level (MBAL), and as a consequence the advisory committee on fisheries management (ACFM) of ICES advised it not to be fished at present (ICES, 1993a).

The biology, stock fluctuations, and fishery of the Faroe Plateau Cod stock are examined. Although not a complete review of all the work done on the Faroe Plateau cod, this study is based on a comprehensive selection of published material and on some new information. In addition, the recruitment to this stock in relation to recruitment overfishing, natural variations in the stock, and changes in the environment is discussed, and some management implications are included.

Biology

Stock identity

Tagging

Experiments on the tagging of cod at the Faroes have been reported by Strubberg (1916, 1933), Tåning (1940), Joensen (1956), and Jones (1966). The main figures from the experiments are given in Table 1.

All the tagging experiments confirm that there are two self-sustainable stocks in the Faroe area, one on the Faroe Bank and the other on the Faroe Plateau, with very little interchange. Only three tag recoveries have been reported outside the Faroe area. Only a few recoveries reported from the Plateau have been tagged on the Bank (0.8%), and vice versa (0.7%). A certain amount of area misreporting will have taken place (Jones, 1966), due to vessels fishing on both the Bank and the Plateau on the same trip and due to tags being recovered at the market or fish plant rather than by the fishermen. The above figures on migration between the two areas can therefore only be tentative, but they do show that the migration between the two areas is negligible. Similarly, only very few cod tagged in other areas have been reported caught at the Faroes (Tåning, 1934, 1943a; Jones, 1966).

Morphometry and meristics

Schmidt (1930) found that cod on the Faroe Plateau had a mean number of vertebrae including the urostyle of 52.28, with a range of 52.0–52.5. This is lower than cod from the west coast of Norway, Iceland, and Greenland, but higher than cod from the North Sea and the area north and west of Scotland, including the Faroe Bank. Mean number of vertebrae of the Faroe Bank cod was 51.77, which Jones (1966) found significantly different from the number of vertebrae of the Plateau cod ($p < 0.001$). The mean number of rays in D_2 was also lower in the Faroe Bank cod (18.74) than in cod on the Plateau (19.65) and the areas north and west of Scotland (Schmidt, 1930). The Icelandic cod has a longer snout and a more slender body than the Faroe Plateau cod, which, in turn is more slender than the Faroe Bank cod; the base of the tail is broader in the latter (Joensen and Tåning, 1970). Differences can also be seen in the structural pattern of the otoliths, reflecting different growth patterns in the Faroe Plateau cod compared to surrounding areas (Holden, 1960; Jones, 1966).

Table 1. Tagging experiments of cod in Faroese waters. The columns "No tagged", "No recovered", and "% recovered" refer to the total liberation period, whereas the column "Range % recovered" gives the range of recoveries from the single experiments in the period.

Author	Year of liberation	No. tagged	No. recovered	% recovered	Range % recovered
Strubberg (1916)	1909–1913	4086	1658	40.6	15–62.3
Strubberg (1933)	1923–1927	1871	489	26.2	9.3–40.9
Tåning (1940)	1932–1937	895	163	18.2	16.8–21.4
Joensen (1956)	1952	523	94	18	18
Jones (1966)	1959–1963	3026	836	27.6	16–40

Biochemical analysis

Based on analysis of transferrins in the blood sera of cod, Jamieson and Jones (1967) found significant genetic isolation between the cod in the Faroe area and the cod on the Faroe Bank ($p < 0.01$). Jamieson and Birley (1989) came to the same conclusion when studying the haemoglobin types using electrophoresis.

In addition to tag returns, morphometric, meristic, and biochemical differences, there are also differences in length-at-age and age-at-maturity (see later) between the Plateau cod and the cod in the neighbouring areas. In addition, the existence of discrete spawning grounds on the Plateau and the Bank and the retention of eggs and larvae by the persistent anticyclonic current system in each of these areas (see Gaard *et al.*, 1994), explain why two self-sustainable cod stocks can exist in the Faroe area.

Spawning

Spawning grounds

Spawning cod is found almost everywhere on the Plateau, but the most important spawning grounds are located to the north and west of the islands at depths of about 80–150 m (Tåning, 1943a). Joensen (1954a) and Joensen and Tåning (1970) state that the spawning grounds north of the islands are by far the most important, and that those to the west are of secondary importance (Fig. 3). The catch in numbers of mature cod in the Faroese groundfish surveys for 1983–1993 has been plotted for each year in Figure 4. These surveys are carried out prior to and during the spawning period; details on survey design, results, etc., are given in Kristiansen (1988) and Grástein (1992). The location of two main spawning grounds on the Plateau, one to the north and the other to the west, is confirmed by these results, although there are considerable interannual variations in this period. In the first years the northern spawning grounds were by far the more important ones, but the western grounds are gradually increasing in importance and seem to be of most importance in the late 1980s. From 1990 the situation is reversed again. In 1993 the survey indicated both regions to be of equal importance.

Joensen (1954a) noted a shift in spawning locations to the north of the Faroes from about 6–8 nautical miles north of the islands at depths of about 100 m in the 1920s to about 10–15 nautical miles north of the islands at depths of 140–170 m in the late 1940s and early 1950s. The same tendency was seen to the west of the islands; the spawning depth changed from about 100 m in the 1920s to 150–180 m in the late 1940s and beginning of the 1950s (Fig. 3).

In the Faroese groundfish surveys some variations with respect to depths have been observed, but in most years spawning depth is about 100 m, shallower to the north than to the west.

Joensen (1954a) analysed the age distributions on the two main spawning grounds in 1933–1938 and 1951–1952 and found that the older cod concentrated on the northern spawning grounds, whereas the younger fish preferred the western spawning grounds; this was especially clear during the 1930s.

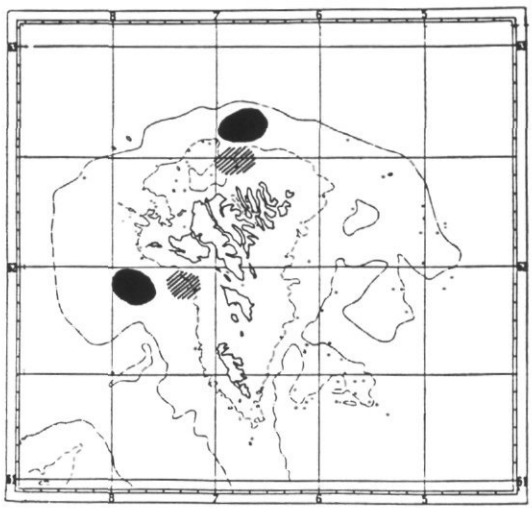


Figure 3. The two main spawning grounds of the Faroe Plateau cod. Hatched areas indicate the location in the 1920s, black areas the location in the late 1940s and the beginning of the 1950s (Joensen, 1954a).

Timing and duration of spawning

Tåning (1943a) and Joensen and Tåning (1970) state that the spawning takes place from February to May, April being the important month. Analyses of roe landings (Hoydal and Reinert, 1978) and length distributions of pelagic larvae and juveniles (Reinert, 1979) verify this spawning period but indicate the main spawning to be in the second half of March. Kristiansen (1990) estimated the timing of maturation and spawning from data collected during the groundfish surveys (Fig. 5). The maturation stages, determined on a scale from 1 to 7 with 6 as spawning, showed the spawning of cod on the Plateau to start on a low level in the middle of February, and in the second half of March most of the sampled cod were ripe to spawn or running.

Information on the timing and duration of the spawning can also be obtained from landings of cod roe by Faroese vessels fishing on the Faroe Plateau. Compared to the scale mentioned above, roes will be of interest to the market from late stage 3 to the end of stage 5. Landed roes are therefore mainly in stages 4 and 5, and

the peak and subsequent decline in roe landings therefore indicate the onset and duration of the spawning.

The landings of cod roe in the period 1977–1993 are given in Figure 6. In the presentation, each month is divided into periods of 10 days, and the landings in each period are normalized to landings per day. The figure indicates a main spawning period in the second half of March with a duration of 2–3 weeks. Analysing each year separately (Fig. 6), the onset and duration of spawning varies by about one week from one year to another. However, using the available data it has not been possible to relate differences in the timing and duration of spawning to differences in year-class strength.

The early life history

Systematic investigations on the early life stages of cod in Faroese waters based on samples taken with a Hensen net and a 2-m stramin net were carried out in the late 1940s and first half of the 1950s by Danish and Scottish research vessels and the results published in *Annales Biologiques* (Bertelsen, 1949–1952; Saville, 1949–1952; Joensen, 1954b, 1955). Annual 0-group surveys have been carried out in Faroese waters since 1972. The participants were: England in 1972–1976 (ICES, 1972, 1973; Blacker, 1974, 1975), France in 1976–1979 (Fontaine et Lamolet, 1976; Hoydal, 1977–1979) and the Faroe Islands in 1974–1993 (ICES, 1975c, 1976, 1980; Hoydal, 1974, 1977–1979; Kristiansen, 1984; Reinert, 1988, 1993). The gear used has been a capelin trawl with 5 mm mesh size in the codend; in some years additional samples with Bongo and GULF III have been taken.

Distribution of eggs, larvae, and juveniles

After fertilization, the eggs ascend towards the upper layers, where the development up to hatching occurs. In March–April the mean temperature in the surface layers is about 6–6.5°C. According to Russell (1976), the incubation period at this temperature will be about 100 days-degrees, and the larvae will therefore hatch approximately 15–17 days after spawning. This compares well with the 16–20 days given by Joensen and Tåning (1970). The youngest larvae sampled are about 4 mm.

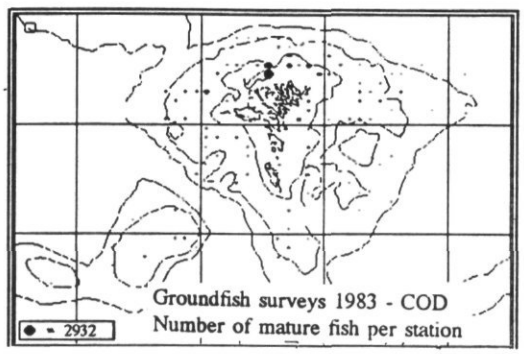
Data from sampling with the GULF III High Speed Sampler in early April 1978 indicate a dispersal of embryos and larvae by the anticyclonic current systems around the islands. Later on the larvae are distributed horizontally throughout the Plateau (Reinert, 1979). This concurs with the older observations mentioned above. As shown by Gaard *et al.* (1994), the location of the two main spawning grounds is strategically placed in relation to advection of the cod spawning products onto the shelf and to the influx and consequent spawning of copepods, notably *Calanus finmarchicus*, which is believed to be the principal food source for the larvae.

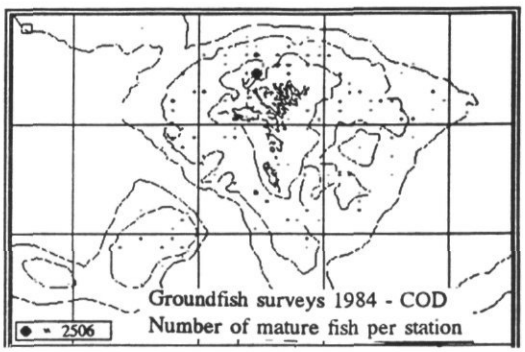
The 0-group surveys since 1972 are used to illustrate the distribution of postlarvae and pelagic juveniles, as the standard gears used in the years before that time have been hampered by avoidance problems for fry of these sizes. In the Faroese 0-group surveys, specially designed to determine the year-class strength of cod, the Faroe area is divided into three strata. Stratum IN is mostly shallower than 100 m north of 62°N, stratum IS mostly shallower than 100 m south of 62°N, and stratum II is between 100 m and 200 m. In the first years of the surveys a fourth stratum with depths of 200–500 m was included in the investigations, but was later disregarded because of the absence of 0-group cod. In June and early July the pelagic juveniles in most years in the 1970s and beginning of the 1980s showed a very characteristic distribution on the Plateau (Fig. 7), with heavy concentrations near the islands to the north, almost like a cap, with different southern limits in different years on the west and east sides of the islands; in other areas the distribution is more scattered (Hansen *et al.*, 1990). On the other hand, the horizontal distribution from 1983 onwards is variable from year to year (Fig. 8). No clear relationship between the horizontal distribution of the 0-group and the corresponding year-class strength estimated from the VPA could be traced. Figure 9 summarizes the relative densities of postlarvae and pelagic juveniles in each stratum per year for the period 1974–1993. It is worth noting that in spite of large variations in total abundance and in spite of shifts between the northern and southern strata inside the 100 m depth contour line, the density in stratum II has remained well below the density in strata IN and IS. Thus the shallow part of the Faroe Shelf enclosed by the anticyclonic current system must be the main habitat of these early stages of cod.

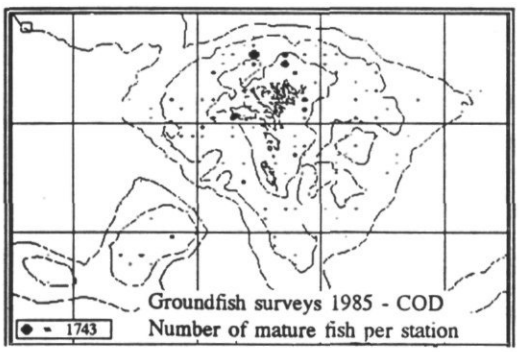
Growth

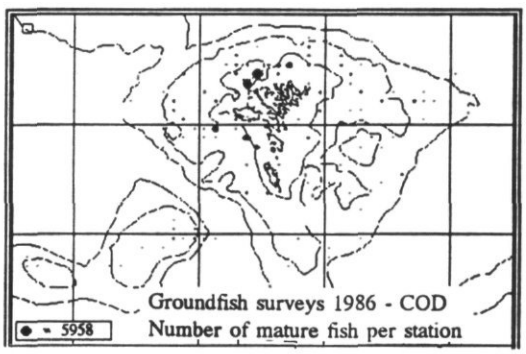
The information on growth in the pelagic phase is scarce, but has been studied by Saville (1950, 1951, 1956) and Reinert (1979). Based on samples from Bongo, Gulf III, and capelin trawl in the late 1970s, Reinert (1979) estimated the growth as: $L = L_0 \cdot 10^{0.012t}$ = number of days. This means a weekly growth increment of 1–1.5 mm in the first month after hatching, 2–3 mm in the next month, and 4–5 mm in the third month (Fig. 10).

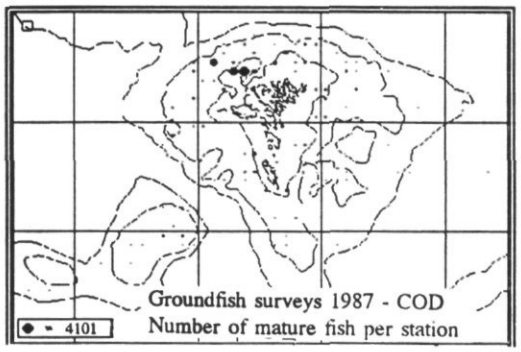
As shown by the 0-group surveys in 1974 and 1975 (Hoydal, 1974; ICES, 1975), most juveniles at lengths about 3.5–4.0 cm leave the pelagic phase from the second week of July (Reinert, 1979). In late July, demersal stages about 4.5 cm long are found in the seaweed in the littoral zone. In mid-August the mean length is about

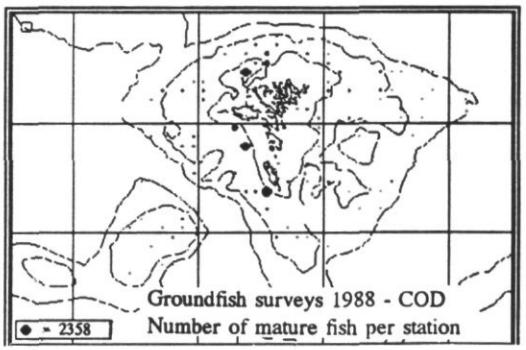












5 cm, in mid-September about 7 cm (Joensen and Tåning, 1970). The growth of cod from one year and onwards is dealt with in the section on adults.

After 1–2 years in the littoral zone of the fjords the young cod migrate towards deeper waters. It has been shown from tagging experiments that the cod is fairly stationary in nearshore areas up to about three years, i.e. while sexually immature (Joensen and Tåning, 1970).

Feeding

Very little study has been made of the feeding of pelagic larvae and juveniles. Unpublished qualitative stomach analysis of the juveniles by the Fisheries Laboratory of the Faroes reveal, as in most other regions, copepods (nauplii, copepodits, adults) as being the most important diet. The food in the littoral zone is mainly crustaceans and the young of other fish species, e.g. saithe and sandeel (Joensen and Tåning, 1970).

Year-class strength

The abundance indices per year estimated from the Faroese 0-group surveys 1974–1980 and 1982–1992 are shown in Figure 11. The year 1981 was omitted from the series because of difficulties that year in connection with the introduction of a new research vessel (Reinert, 1988). Figure 11 also shows the abundance indices for two-year-olds from the Faroese groundfish surveys and

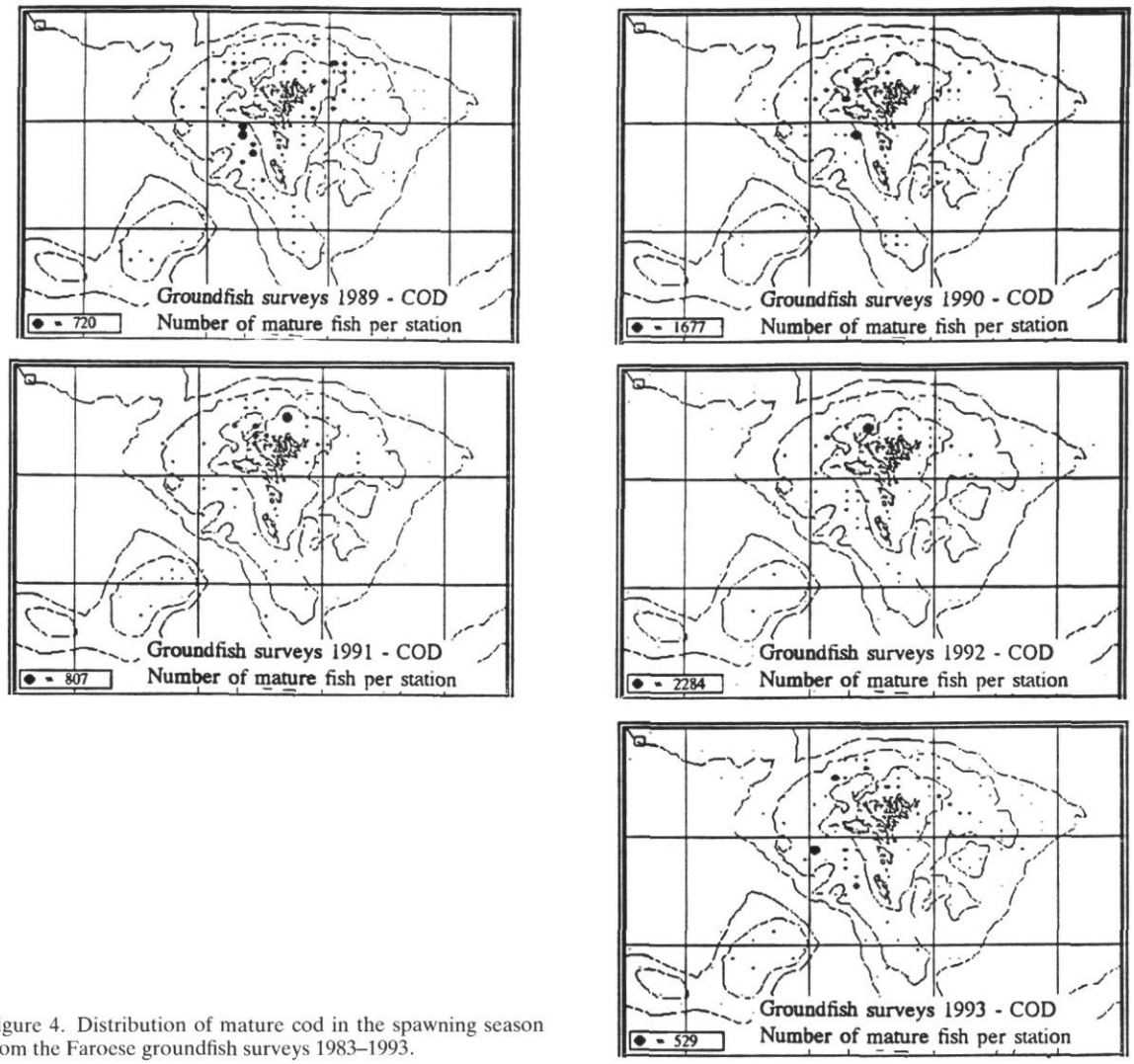


Figure 4. Distribution of mature cod in the spawning season from the Faroese groundfish surveys 1983–1993.

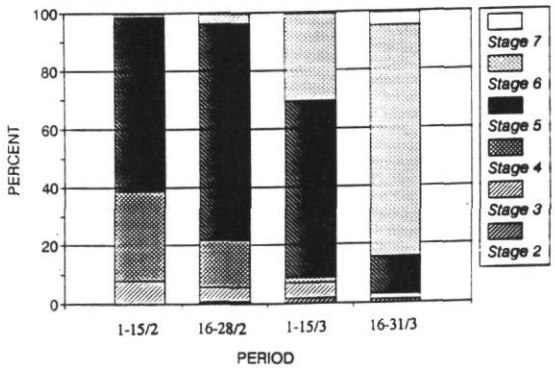


Figure 5. Gonadal development of the Faroe Plateau cod from the Faroese groundfish surveys 1982–1989 (Kristiansen, 1990).

the numbers of two-year-olds estimated in the VPA. Generally, there is good agreement between these three series. This shows that year-class strength of cod in most years is determined during the period from spawning to the time prior to settling about three months later. However, compared to the VPA estimates, the 0-group surveys overestimate the year-class strength severely in some years, i.e. 1976, 1987, and 1988. These discrepancies, especially large in 1976 and 1988, might indicate large mortalities during or after settling in these years, possibly due to high predation on the young fish before they recruit to the fishery. It is notable in this context that there were good year classes of cod 3–5 years before the years with these high 0-group indices, i.e. in 1972–1973 and 1981–1983. Correspondingly, an increase in

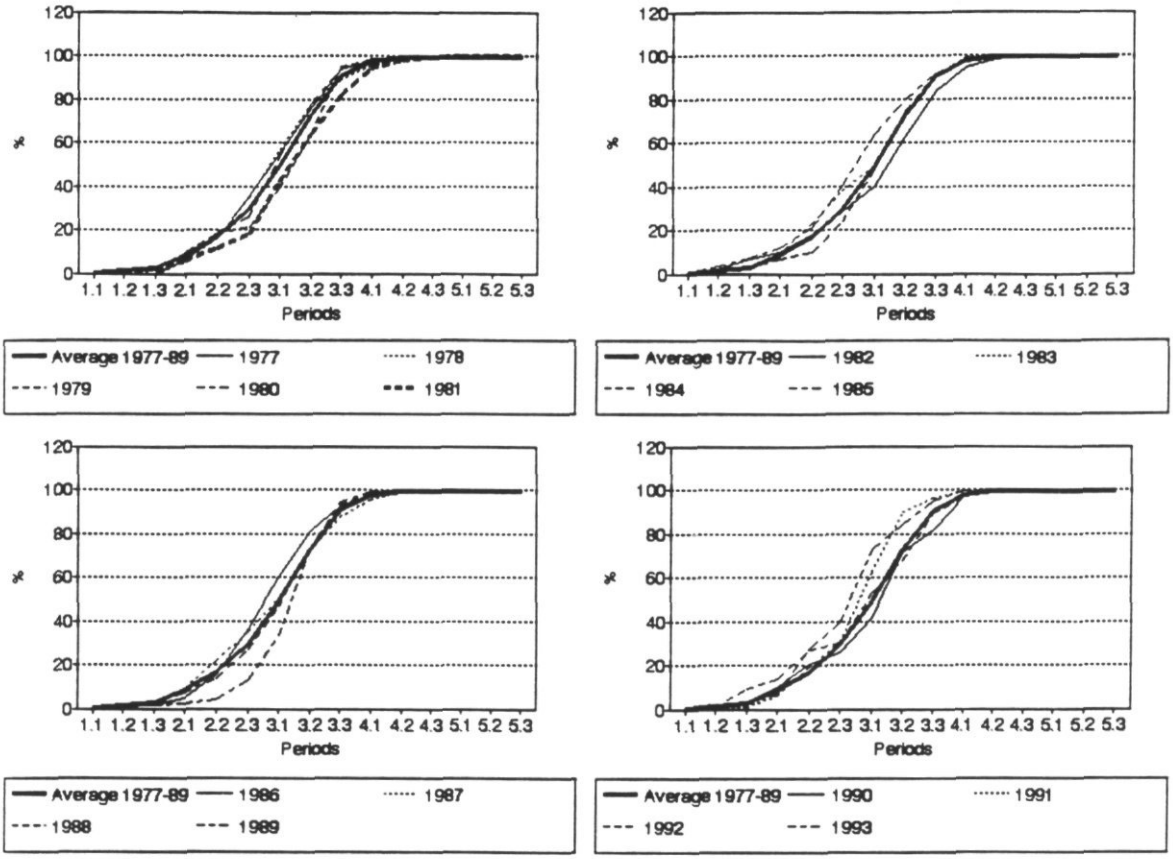


Figure 6. Cumulative landings (%) of cod roe by Faroese vessels, fishing in ICES Division Vb1, to Faroese factories 1977–1993. Each month is divided into three periods, and landings for each period are normalized to landings per day, e.g. 1.1 = 1–10 January; 1.2 = 11–20 January; 1.3 = 21–31 January.

mean weight-at-age for ages 4–6 have been observed in these years (see the section on mean weight-at-age).

Adults

Migrations

As discussed in the section on stock identity, immigrations to and emigration from the Faroe Plateau can be regarded as negligible. Strubberg (1916, 1933), Tåning (1940), and Joensen (1956) have shown from extensive taggings that the immature cod are stationary on the Plateau, but when sexually mature most of the fish migrate to the spawning grounds north and west of the islands at the spawning time. After spawning, the mature fish disperse throughout the Plateau. This is illustrated in Figure 12.

Growth

Tåning (1943a) gives length ranges for fish of various ages but no mean lengths. The mean lengths-at-age given by Joensen and Tåning (1970) and depicted in Figure 13 are somewhat lower than those given by Jones (1966) and Jones (1978) for 1959–1962; the parameters of the von Bertalanffy growth equation were determined by Jones (1966) as $L\infty = 115.3$ cm, $K = 0.19$, $t_0 = -0.42$ years. Figure 13 also shows the mean lengths-at-age for the Faroe Plateau cod based on ages determined from otoliths collected over the period 1973–1982 (Kristiansen, 1990). It can be seen that the growth has changed considerably during this period.

Mean weight-at-age

Mean weights-at-age for the Faroe Plateau cod for the period 1959–1992 are presented in Figure 14 for the year classes 4–6. There is a striking decline in weight-at-age of more than 40%. The data were drawn from the following sources: for the period 1959–1977, mean lengths-at-age from English landings, kindly provided by B. W. Jones of the Fisheries Laboratory in Lowestoft, UK, were converted to mean weight-at-age using the re-

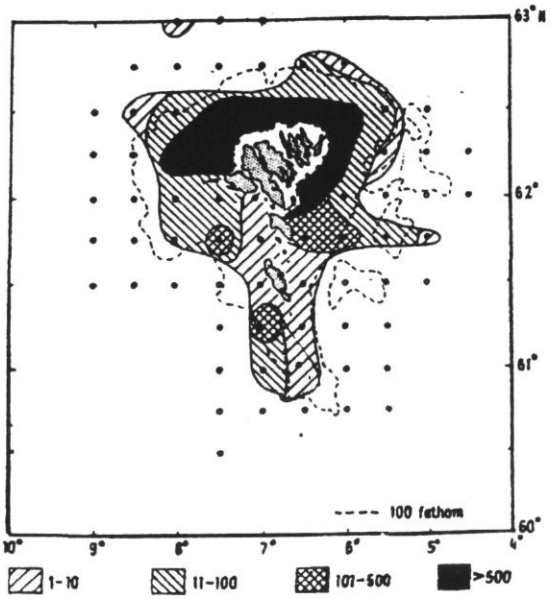


Figure 7. Example of a typical distribution of 0-group cod (numbers per 30 min haul) in late June in the 1970s and beginning of the 1980s (adapted from ICES, 1976).

lationship $w(g) = 0.0075206 \cdot 1\ (cm)^{3.062555}$, calculated from the length/weight relationship for English landings of Faroe Plateau cod presented in ICES (1966). For the period 1978–1992, mean weights-at-age are reported in Working Group reports (ICES, 1987, 1993b).

The large fluctuations in mean weight-at-age over relatively short periods are also striking. For instance, there is a sharp increase from 1972 to 1974 and a sudden return to low values in 1977. With the decline in mean weights-at-age over the period, it is difficult to analyse the annual variations in relation to for example year-class strength, and in order to do so the data have been analysed as deviations from average for the two sets separately, i.e. for the period 1959–1977 the average mean weight-at-age was calculated for the Lowestoft data set, and then the deviations from this estimated for each year. The same procedure was applied for the Working Group data set for the period 1978–1992. The results are presented in Figure 15. This exercise to a large extent filters out the overall decline in mean weights-at-age, but the variability is still very obvious, and one could argue for two relatively long periods with declining weights. As an example, for the five-year-old the mean weight-at-age declined by 1.2 kg from 1960 to 1966, increased by 1.8 kg from 1972 to 1974, and declined again by about the same amount from 1974 to 1977, remained steady from 1977 to 1984, when there was a further decline until 1992.

These variations are not caused by density-dependent growth (resource limitations), as shown in Figure 16, where the deviations in mean weight-at-age plotted against year-class strength reveal no correlation whatsoever. This suggests that there are large variations in the food resources available to cod on the Faroe Plateau over time, which are not correlated to the size of the year classes.

When the deviations in mean weight for older ages are plotted against the year-class strength at age two, however, there seems to be a weak positive relationship (Figs. 17, 18). This could indicate an enhanced environmental condition associated with good year classes (e.g. cannibalism).

Theoretically, the general decline in mean weight-at-age observed since 1959 could be explained by density-dependent factors, long-term changes in the environment or genetic changes due to selective fishing. As shown above, it is not possible to relate the changes in growth to density-dependent factors, and based on Gaard *et al.* (1994) there are no published data on the environment which could explain them either.

Genetic changes in natural populations due to selective cropping have been demonstrated both in theory and in practice by a number of authors (e.g. Jørgensen (1990), Law and Gray (1989), and Sutherland (1990)). The main result of the genetic changes would be maturation at an earlier age as compared to the unfished stock, and reduced growth.

As mentioned in the section on maturity, the Faroe Plateau cod stock has matured one year earlier in the 1980s than in the postwar period, and from this and the decline in mean weight-at-age it can be concluded that the changes in growth are due to selective forces induced by the fishery.

It this is the case, it is reasonable to assume that concurrent with the selection for earlier maturity and reduced growth, the selection forces could also act negatively on other components in the gene pool, e.g. time and area of spawning, of vital importance for the well-being of the stock.

Before any final conclusions can be drawn on genetic changes of the Faroe Plateau cod stock due to selective fishing, however, it is necessary to analyse the data in much more detail then we have been able to do in this paper.

Maturation

Very few data have been published on the maturation of cod at the Faroes. Tåning (1943a) and Joensen and Tåning (1970) state that on the average the cod on the Faroe Plateau becomes mature at an age of four years. Maturity ogives have been estimated from samples collected during the groundfish surveys in February and March (Fig. 19). Fifty percent of the cod matured at age

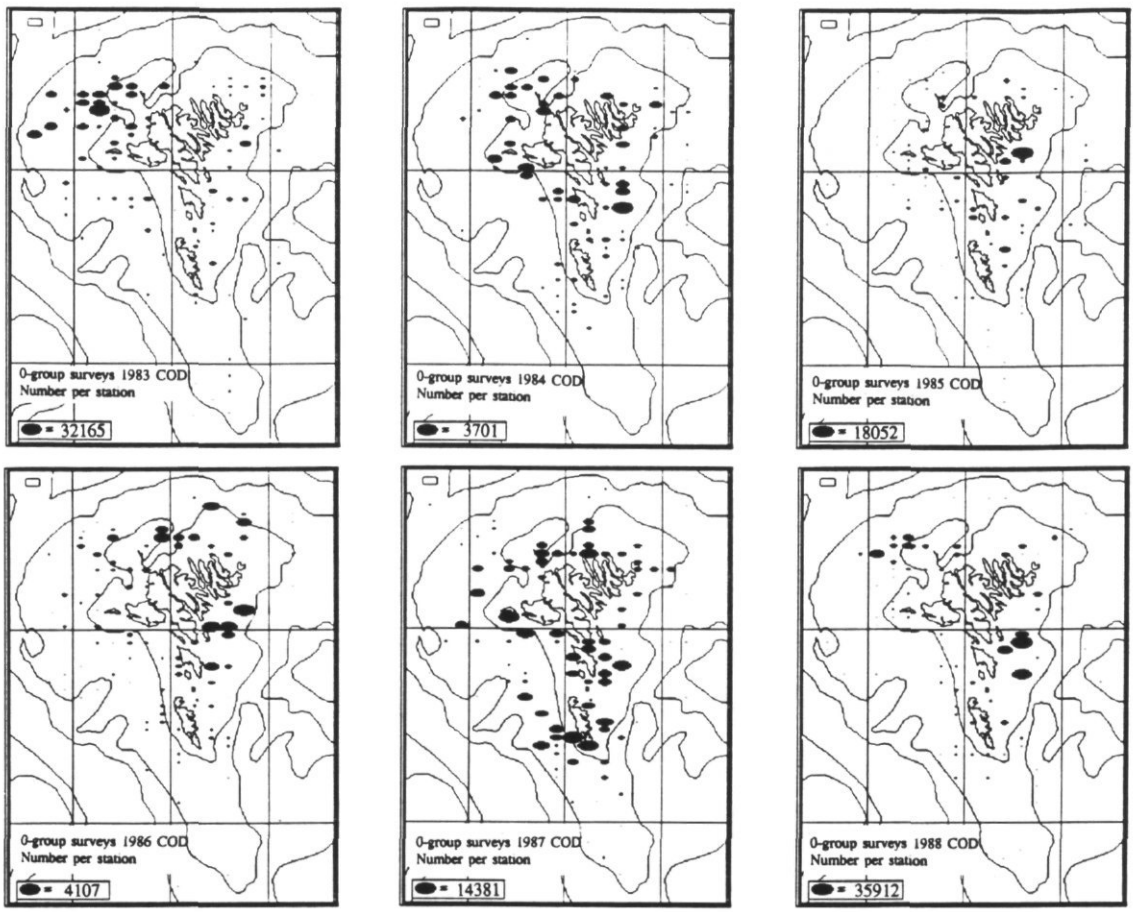


Figure 8.

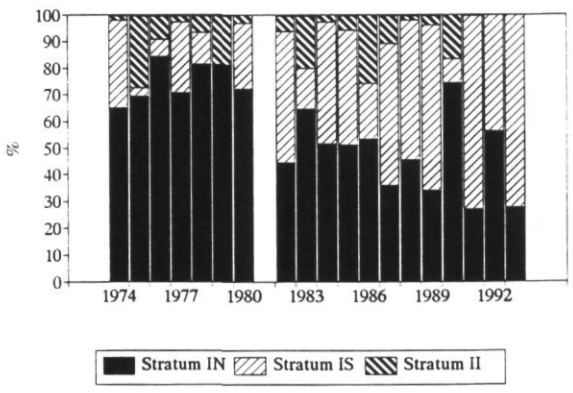


Figure 9. Relative densities of 0-group cod in each stratum per year in the period 1974–1980 and 1982–1993.

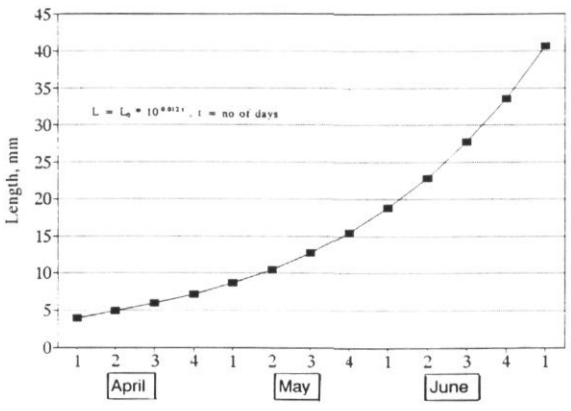


Figure 10. Average growth in the pelagic phase based on data from 1974–1978 (adapted from Reinert, 1979).

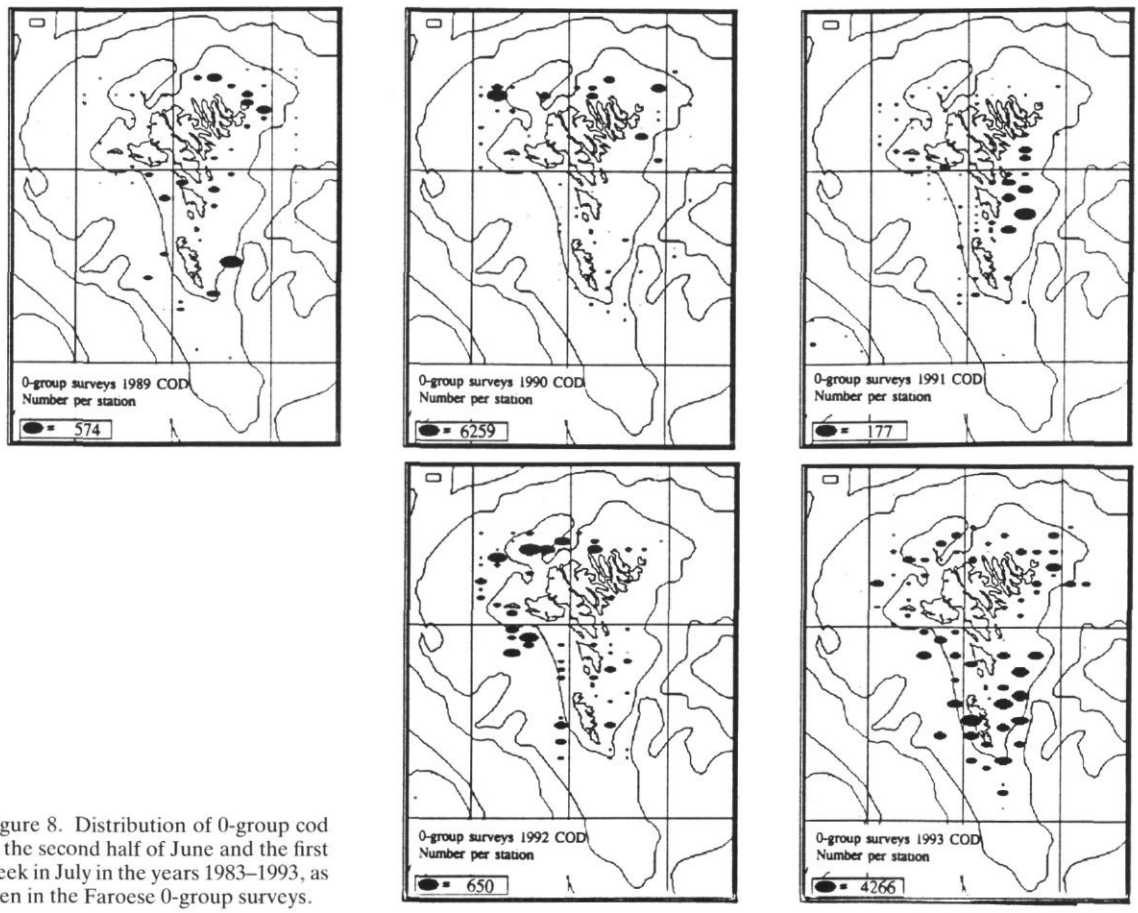


Figure 8. Distribution of 0-group cod in the second half of June and the first week in July in the years 1983–1993, as seen in the Faroese 0-group surveys.

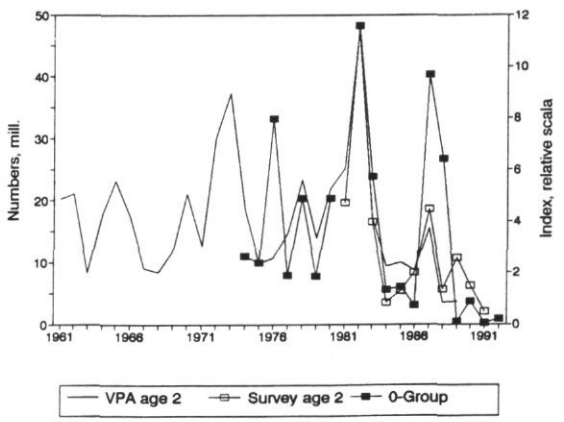


Figure 11. Estimates of year-class strength of the Faroe Plateau cod in the period 1961–1992, based on estimates of two-year-olds from the VPA (1961–1989), indices of two-year-olds from groundfish surveys 1983–1993, and indices of age 0 from 0-group surveys 1974–1992 (adapted from ICES, 1993b).

three years, i.e. one year younger than stated by Tåning (1943a) and Joensen and Tåning (1970). This corresponds to lengths of about 40–45 cm.

Feeding

In the years 1949–1962, Scottish research vessels sampled cod stomachs in Faroese waters. The results are summarized by Rae (1967). Based on the proportion of empty stomachs, the feeding intensity was determined as follows: feeding is fairly heavy in January and April, but declines sharply in May, which tentatively is related to the spawning. A rapid recovery occurs in June, reaching a maximum feeding intensity in July. By September, feeding is again declining and reaches a minimum intensity in October, after which there is again a slight recovery. The cycle in feeding intensity was found to be similar to that of cod in Scottish waters, but about one month later. Qualitative information on the diet of cod in Faroese waters was given as percentages of cod

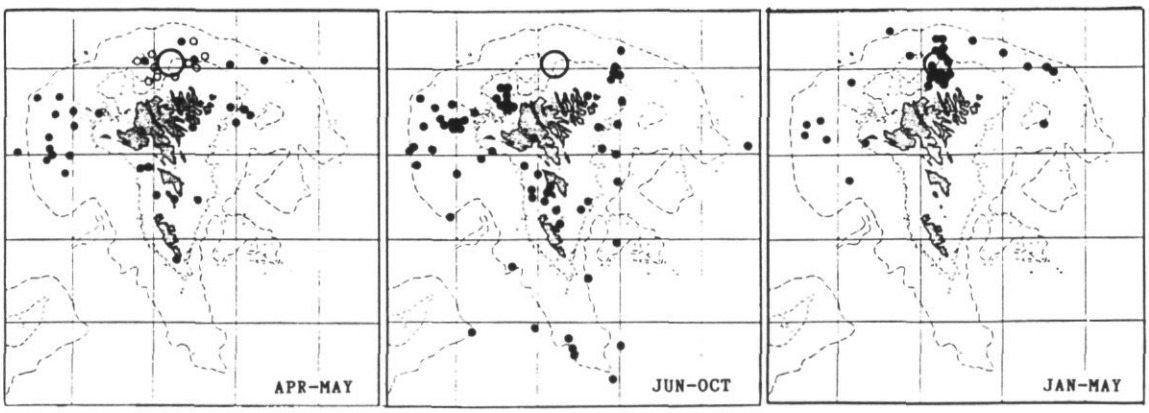


Figure 12. Migrations of mature cod on the Faroe Plateau based on taggings of cod larger than 70 cm on the spawning grounds to the north of the Faroes (encircled area) in the spawning period in 1927, 1932, 1935, and 1937. The figure shows periods and places of recaptures up to one year from tagging (Tåning, 1943).

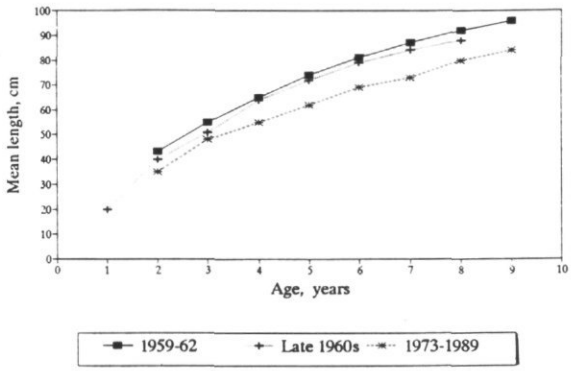


Figure 13. Mean length-at-age for Faroe Plateau cod in three different periods (adapted from Jones (1966), Jones (1978), Joensen and Tåning (1970), and Kristiansen (1990).

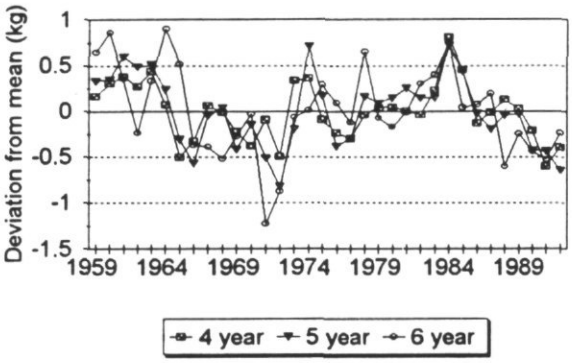


Figure 15. Deviations (kg) from averages in mean weight-at-age, see text.

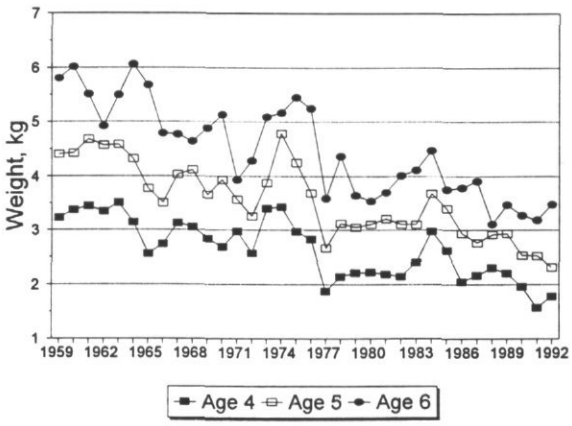


Figure 14. Mean weight-at-age 1959–1992 of Faroe Plateau cod. For the years 1959–1977 the weights have been estimated from mean length-at-age from English landings. Mean weights for 1978–1992 have been taken from ICES Working Group reports, see text.

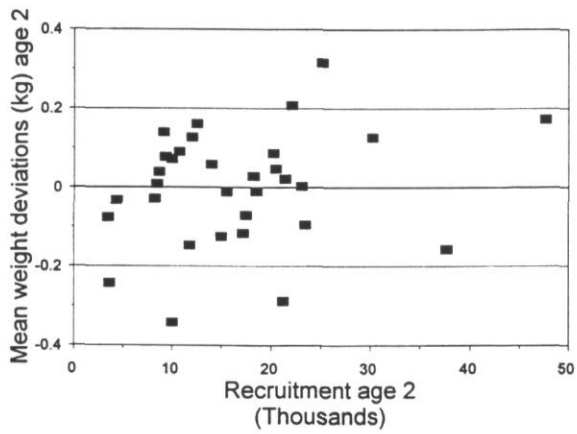


Figure 16. Mean weight deviations (kg) at age 2 plotted against number of two-year-olds from the VPA.

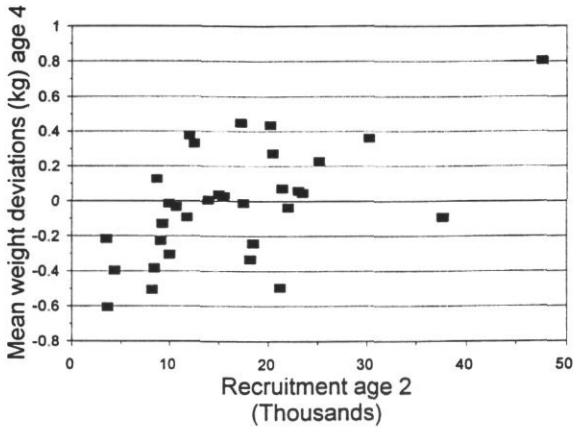


Figure 17. Mean weight deviations (kg) at age 4 plotted against number of two-year-olds from the VPA.

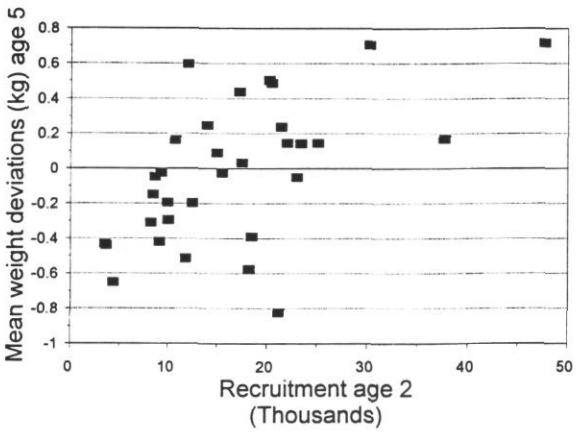


Figure 18. Mean weight deviations (kg) at age 5 plotted against number of two-year-olds from the VPA.

Table 2. Stomach analysis of Faroe Plateau cod. Frequencies of occurrence (%) in cod stomachs of main prey groups (from Rae, 1967, and Du Buit, 1983).

Sampling year	1949–1962	1949–1962	1974–1975
Size group	21–50 cm	50 cm and over	
Crustacea	62.5%	34.0%	81.5%
Pisces	47.2%	76.8%	81%
Mollusca	13.8%	14.8%	6.7%
Polychaeta	3.1%	2.2%	0.6%
Ophiuroidea	3.4%	4.4%	1.7%

feeding on chief food types. Du Buit (1983) analysed in similar ways Faroe cod stomachs sampled in April 1974 and May 1975 in depths of 140–360 m. A summary of the results is given in Table 2.

A predominance of decapod crustaceans and fish was observed in both investigations, and the Scottish samples showed a shift from crustaceans to fish with length. In the 1949–1962 stomachs, *Pandalus* was outstanding of the crustaceans in most localities, while *Eupagurus, Hyas, Galathea,* and *Munida* were also well represented in some localities. Of the fish, sandeels clearly formed the principal food on most localities, followed by haddock, Norway pout, blue whiting, and other gadoids, as well as some species. The species composition in the 1974–1975 stomachs was quite different, which could be explained by the restricted sampling time. Of the crustaceans, *Euphausiacea* and *Munida+Galathea* were equally common (22%), with *Natantia* in second place (15%). Of the fish, Norway pout was most common in the diet (44%), followed by sandeels in second place (19%).

Lack of *Pandalus* and the greater importance of *Euphausiacea, Munida+Galathea* and Norway pout could be related to the greater depth of sampling, but a

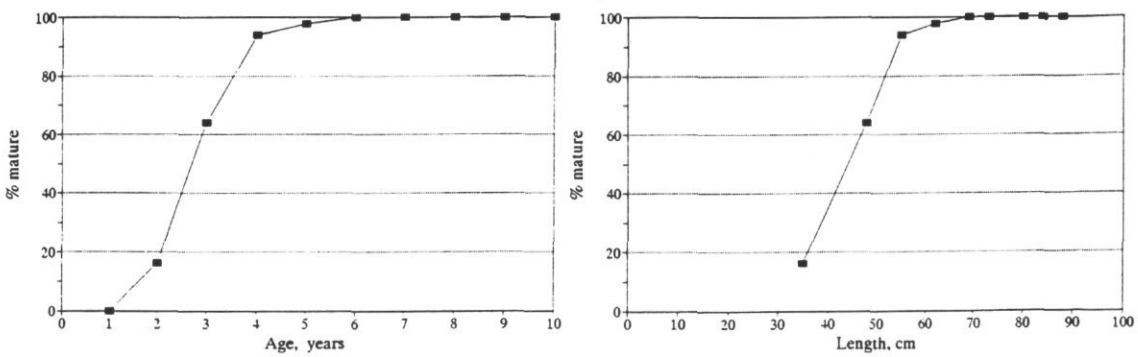


Figure 19. Average maturity ogives for Faroe Plateau cod 1973–1989 by age (left) and by length (right) (adapted from ICES, 1993b).

change in the abundance or distribution of prey cannot be ruled out. The relatively minor importance of sandeels in the diet as compared to the 1949–1962 samples concurs with the very poor recruitment indices in the middle of the 1970s, as estimated from the 0-group surveys.

A comprehensive stomach sampling was carried out by the Fisheries Laboratory of the Faroes in 1990 and 1991. The analysis is not yet finished, but preliminary results show sandeels to be of even less importance than found in the French samples, and Norway pout seems to be the principal fish in the diet of cod. Of crustaceans, *Munida* is very common. This must be related to the relative abundance of prey species.

Quantitative estimates of the food consumption of Faroe Plateau cod are given by Jones (1978), based on the Scottish material as described above. Two methods were used, one based on estimates of the energy required for maintenance, growth, and reproduction, the other on mean stomach content weights, which both gave results in the same order of magnitude. Bearing in mind that growth and diet composition have changed during the last decades, the results are not necessarily valid for the recent period. But the conclusions were that energy intake can be treated as proportional to (body weight)^b, b being in the range 0.8–1.3, and the Faroe Plateau cod requires more food (energy) than Faroe haddock with a similar body weight.

Du Buit (1983) also gives total consumption for the sampling period based on the consumption rates estimated by Jones (1978).

Fluctuations in stock abundance

Landings

The total annual landings of cod from Vb are shown in Figure 2. The figures for the years 1904–1923 were derived from files at ICES Headquarters with some unpublished corrections. The figures for 1924–1938 and 1946–1960 are taken from ICES 1966, for 1939–1945 from *Bulletin Statistique* together with some corrections, and for 1960–1992 from ICES Working Group Reports (see reference list). As the landings of cod from the Faroe Plateau are on average approximately 90% of the landings from the Faroe area, Figure 2 reflects the landings from the Plateau to a large extent.

The most striking features of Figure 2 are the apparent stability of the landings, which in the entire period 1911–1989 apart from the World War II years, has only fluctuated between 20 000 t and slightly in excess of 40 000 t, and the dramatic collapse of the landings since 1990. In the postwar period it may also be noted that the gap between the high and low landings became increasingly wider up to the collapse.

Catch and effort statistics

Data on catch and effort for the English and Scottish trawlers fishing for cod and haddock at the Faroes for the period 1924–1938 and 1946–1972 are reported by Jones (1966), ICES (1966, 1975a,b). The data are given as tonnes per million ton hours for Scottish and English steam trawlers, British stream trawlers (combining the Scottish and English data), and finally British trawlers combined (combining steam and motor trawler data).

The Danish Institute of Fisheries and Marine Research started to collect catch and effort data from smaller long-liners fishing for cod at the spawning grounds north of the Faroe Islands during spawning time in 1936 and continued to the outbreak of World War II in 1939. After the war, the time series was continued from 1949 until 1972 (Tåning, 1943b; Joensen, unpublished data; ICES, 1984, 1993b). In the years just after the war this was done by the Danish Institute, and since 1951 by the Fisheries Laboratory of the Faroes. The Faroese Fiskhag system was established in 1973 and since then catch and effort statistics for the Faroese fishing fleet have been collected; the data are reported in several Working Group reports. From 1982 onwards, fishery independent data have been collected during the annual groundfish surveys.

In order to get a time series of c.p.u.e. data as long as possible, the c.p.u.e. by British trawlers and the c.p.u.e. from Faroese long-liners based on a whole year's fishery have been combined, and the result presented in Figure 20. As the two c.p.u.e. series in the period of overlap (1960–1972) show the same trend, it could be argued that the c.p.u.e. series probably reflect the fluctuations in the Faroe Plateau cod stock since 1924. The effect of the reduced fishing mortalities during World War II on the stock abundance is obvious. However, with the increased exploitation in the postwar periods, the stock decreased gradually, and in 1960, based on the c.p.u.e. data, Jones (1966) estimated the cod stock to be only 20% of the unexploited stock.

Analytical assessments

The first analytical assessment of the Faroe Plateau cod stock was presented in the report of the Working Group on Fish Stocks at the Faroes (ICES, 1975a), when data from 1961 onwards were analysed by the Working Group, and since then the stock has been assessed annually or biannually.

The main results of the latest assessment (ICES, 1993b) are presented in Figure 21A–D for the period 1961–1992. The spawning stock biomass (Fig. 21A) increased considerably during the latter half of the 1960s and 1970s from a very low level in the early 1960s to almost 100 000 t in 1978. The main reason for the

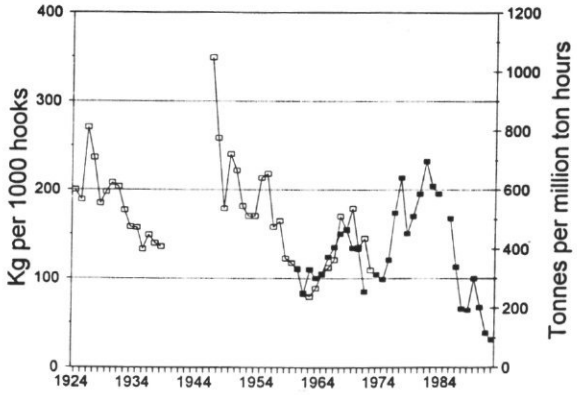


Figure 20. Two c.p.u.e. series for the Faroe Plateau cod derived from catch and effort data by British trawlers (open squares) and Faroese long-liners (filled squares). See text for further explanation.

increase in the first part of this period was due to the reduced fishing effort, as can been seen from the mean fishing mortality (Fig. 21D), which in the same period was halved from 0.6 in 1961 to 0.3 in 1974. The two very good year classes from 1972 and 1973 (Fig. 21B) were the main contributors to the peak in 1976. From 1975 the average fishing mortality increased again to 0.7 in 1978. In the years following the introduction of the 200 n.m. EEZ at the Faroes in 1977, the fishery for cod by non-Faroese vessels was very much reduced, and so also was the fishing mortality. The above average year classes from 1980 to 1981 increased the spawning stock to the record high level of almost 115 000 t in 1984. In the years after 1977 the Faroese fleet fishing in Faroese waters increased considerably. Whereas before 1977 the local fleet fishing for cod and haddock in the Faroe area used mainly long-line and hand-line, in the years after 1977 a large fleet of demersal trawlers was introduced. This again resulted in a great increase in fishing mortality, and as the availability of cod was very good because of the large stock size, the fleet was also increased by a

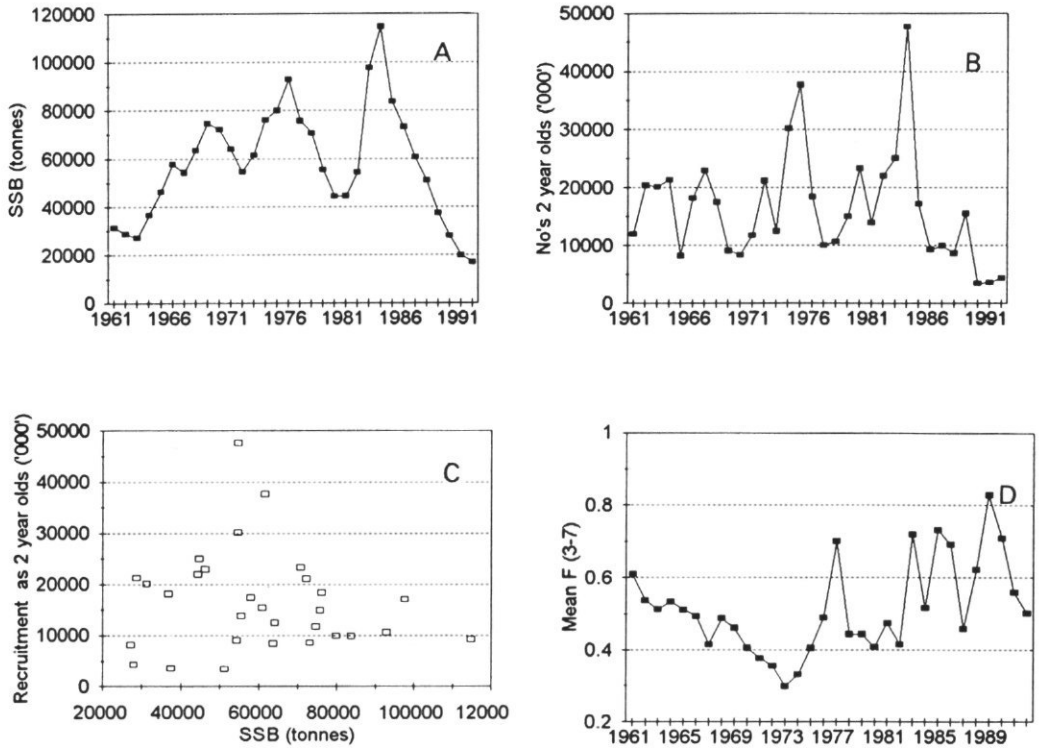


Figure 21. A. The spawning-stock biomass of Faroe Plateau cod 1961–1992 as assessed in the most recent VPA (ICES, 1993b). B. Recruitment at age 2 of the Faroe Plateau cod 1961–1992 from the most recent assessment (ICES, 1993b). C. Stock–recruitment relationship for Faroe Plateau cod from the most recent assessment. Numbers of recruits at age 2 plotted against the spawning-stock biomass (ICES, 1993b). D. The average fishing mortalities for ages 3–7 of the Faroe Plateau cod stock as estimated in the most recent assessment (ICES, 1993b).

large number of smaller fishing vessels using hook and line. This increase in effort seriously reduced the spawning stock size, and even the record high year class of 1982 could not reverse this decline.

Since 1982 only one of the year classes produced has been of average strength, one slightly below average, three poor, and the year classes produced since 1988 have all been extremely poor. The combined effect of poor recruitment and consistently high fishing mortality has dramatically reduced the spawning stock to below 20 000 t, only 1/6 of the level in 1985. And, based on the historic c.p.u.e. and landings data, probably the lowest level ever throughout this century.

Recruitment

The period with low recruitment at age 2 since 1986 is the longest in the period of analytical assessment of this stock, and, based on the landing and c.p.u.e. figures presented above, presumably also the longest period in this century. Some factors which could be responsible for this recruitment failure are discussed below.

Spawning stock size

No clear conclusions can be drawn from the stock–recruitment relationship (Fig. 21C). Two above average year classes have been produced from an almost record low spawning stock, and the two largest year classes were produced from average spawning stock sizes, but several below average year classes have been produced from equally large spawning stocks or even larger. All the evidence from VPA, groundfish surveys, and 0-group surveys (Fig. 11) indicates that the year classes since 1988 have been very poor, and that they are all produced from very small spawning stocks. Bertelsen (1949a) considers the 1947 year class to have been one of the largest year classes ever, and infers this to have been caused by the large increase in the cod stock during the war.

Quality of the spawning stock

It is often observed that fish of different age groups spawn at different times. A spawning stock composed of several year classes should therefore have a prolonged spawning period compared with a spawning stock composed of only a few year classes. A prolonged spawning period would be of great importance in a match/mismatch scenario. Figure 22 shows the weight of the year classes (four years and older) comprising the bulk of the spawning stock for some years producing very good year classes (1972, 1973, and 1982) and some producing very poor ones (1963, 1984, and 1988). It should be noted that in the years with good year classes, the biomass of fish seven years and older is larger compared with the years with poor year classes. It has not been possible from the cod roe landings, however, to link the duration of the spawning period to the size of the spawning stock or to year-class strength. But the larger proportion of older fish could ensure a better quality of spawning products.

The importance of the different age compositions on the two main spawning grounds and the recent shift in the relative importance of these spawning grounds coinciding with poor recruitment is unknown at present, as are the continuous decline in mean weight at age and the earlier age at maturity compared to the earlier years. In theory, this could imply a worse quality of the spawning products.

Environment

Effects of environmental changes on cod recruitment have been discussed in detail by Gaard *et al.* (1994). Although the data available are not sufficient for firm conclusions to be drawn, Gaard *et al.* suggest that the most likely environmental cause of the recruitment collapse in the late 1980s was increased winds from the southwest in spring combined with a reduction in the flow of Atlantic water past the Faroes with the implied reduction in stability of the shelf water, which is the main habitat for the pelagic larvae and juveniles of cod. In addition to the increased likelihood of the eggs and larvae being carried out of the area, this could reduce both the advection of cod spawning products onto the shelf and the influx of copepods, especially *Calanus finmarchicus*, which is probably one of the principal food sources of the cod larvae.

Coinciding with the poor recruitment of cod in recent years, a number of other indices have been low in the 0-group surveys, e.g. those of haddock, Norway pout, and sandeel. In addition, a high number of young puffins and other seabirds were reported to have died of starvation (B. Olsen, pers. comm.). Together with observations on reduced growth rates in several fish species this could point to a very low productivity on the shelf in recent years. This apparent low productivity may be explained by the reduced influx of Atlantic water to the shelf, as observed by Gaard *et al.* (1994), which could imply a reduced transport of nutrients to the shelf.

Management implications

It is generally assumed that it is not possible to reduce a demersal stock to a level of recruitment overfishing, as the fishery would be uneconomical before that happened. However, with ever-improving gear and fish-finding technology, and the widespread policy of subsidizing the fishery, this assumption is open to question.

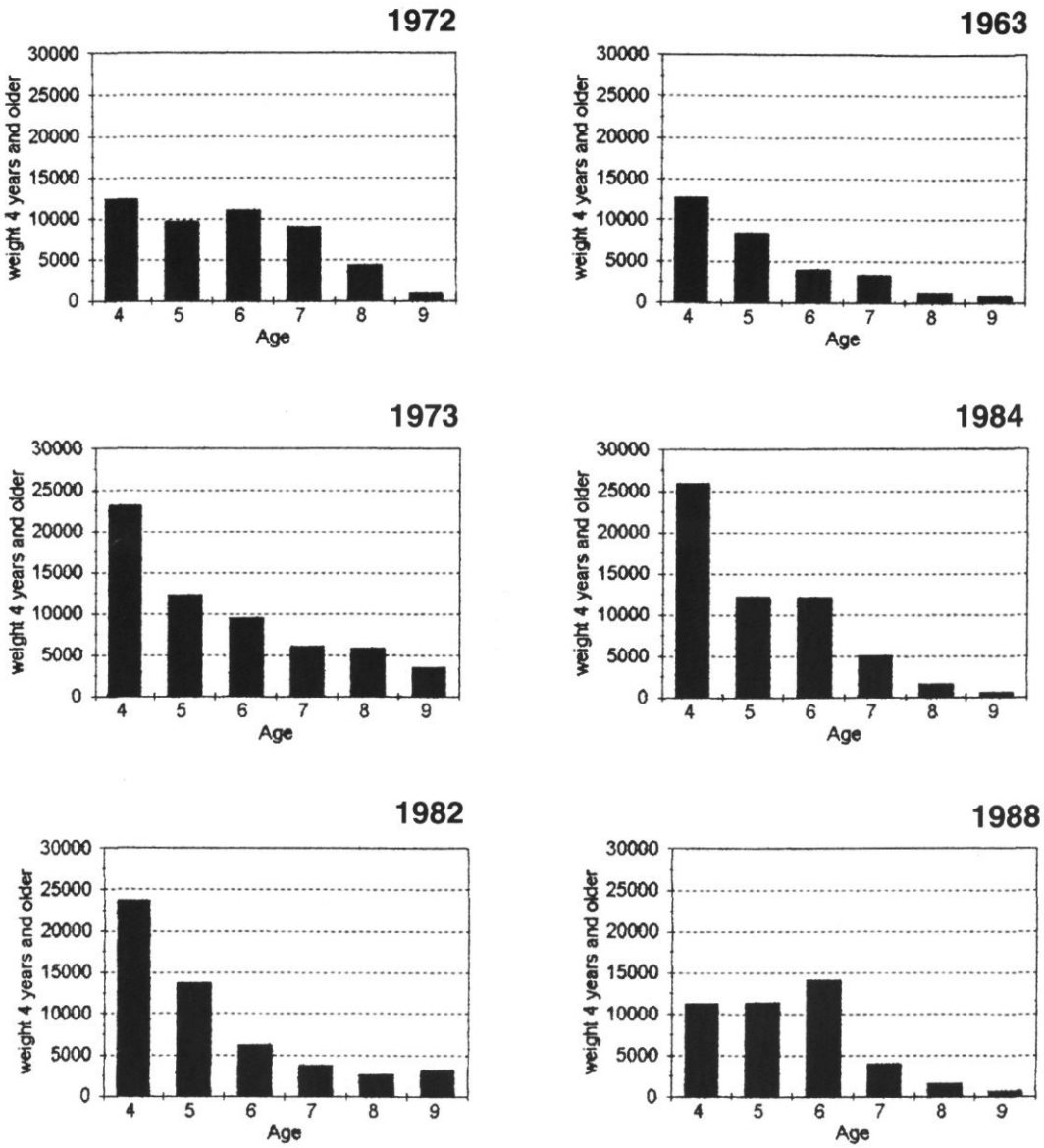


Figure 22. Weight distribution of cod in the spawning stock (here 4 years and older) in three years with very good year classes, i.e. 1972, 1973, and 1982, and in three years with poor year classes, i.e. 1963, 1984, and 1988 (adapted from ICES, 1993b).

The high growth rate of the cod stock on the Faroe Plateau allows recruitment to the fishery at an age of 2–3 years. With a fishing mortality of 0.6, a recruiting year class is reduced by 80% after only 2 years. A combination of high fishing mortalities and reduced recruitment in any period longer than 2–3 years will therefore significantly reduce the stock below acceptable levels.

The depressed stock in the early 1960s made the fishery uneconomical, as can be deduced from the reduction in the fishing mortality in the following years.

With the introduction of the EEZ, the Faroese fishing fleet increased, and with few alternatives for fishing in other areas, the high effort on the cod stock has continued up to the present. Following the EEZ no proper management system for the area was established, and with the combined effect of the high fishing effort and reduced recruitment for many years, the effect on the stock had to be dramatic.

The surplus production (Lockwood, 1987) of recruits in the period 1961–1992 shown in Figure 23 illustrates

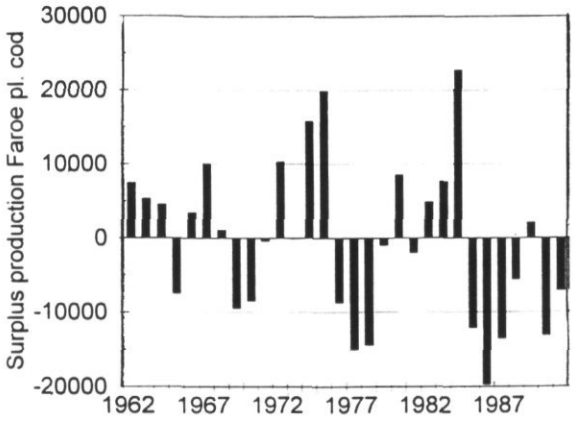


Figure 23. The surplus production of two-year-old recruits in the Faroe Plateau cod stock in 1961–1992 calculated by Lockwood's (1987) formula and based on data from the most recent assessment (ICES, 1993b). The zero line is the case where the annual numbers removed from the stock by fishing and natural mortality combined is equated by the recruitment in the following year.

the inevitable fate of the Faroe Plateau stock in the late 1980s. Since 1984, in all years except 1987, the numbers removed from the stock by fishing and natural mortality combined have by far exceeded the recruitment, and the positive contribution from the 1987 year class was of minor importance only.

Management of the stock must take into account its vulnerability during periods of greatly reduced recruitment. As shown by the latest assessment of this stock (ICES, 1993a,b), the spawning stock size with fishery continuing at the 1992 level will not increase above the lowest level on record in the next few years. Although no clear stock–recruitment relationship can be detected (see above), there is some evidence of good year classes being produced from spawning stocks with relatively many old fish in the stock. And, even if it is difficult to link the size and quality of the spawning stock to recruitment success directly, a reasonable stock size composed of many year classes would be the best strategy in cases of recruitment failure brought on by environmental changes like those which have been discussed above and in Gaard *et al.* (1994). In order to allow the spawning stock to increase, the fishing mortalities have to be reduced as much as possible and, bearing in mind the possible genetic changes in the stock due to a combined effect of high fishing mortalities and selective fishing, as seen in the decline in the mean weight-at-age and the earlier maturation of the fish, management of this stock should in future be at more moderate fishing mortalities than in the past, and perhaps with another composition and strategy of the fishing fleet. Further studies on the effects of different gears and fleets on the fish are necessary.

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Causes of trends and fluctuations in the Arcto-Norwegian cod stock

Odd Nakken

Nakken, O. 1994. Causes of trends and fluctuations in the Arcto-Norwegian cod stock. – ICES mar. Sci. Symp., 198: 212–228.

Published information is used to review trends and fluctuations in landings and stock characteristics/variables (abundance, growth, maturation, distribution, and migrations) in relation to changes in environmental and anthropogenic factors as well as interactions with other species. The stock declined from about 4–5 million tonnes in the 1950s to less than 1 million tonnes in the 1980s owing to exploitation. For more than 30 years the annual fishing mortality rate was well above any calculated safe level, so that the spawning stock was at times reduced to levels at which recruitment was impaired. Age of maturity fell as the stock declined. Recruitment is positively related to temperature. A temperature-regulated mechanism of interaction between cod larvae and their prey, and driven by variations in inflows of Atlantic waters to the area, determines larvae survival and probably also the abundance and size of the 0-group at age 5–6 months. Predation from birds and marine mammals as well as cannibalism are shown to cause considerable interannual variations in the mortality of juveniles and young cod, and thus variations in the number of fish recruiting to the fisheries at ages 3–5 years. Large short-term variations in the growth of cod caused by varying availability of prey (capelin) have been observed; growth is also positively related to the temperature within the distribution area of the stock.

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Introduction

The stock of Arcto-Norwegian cod, or Northeast Arctic cod, as it is called in most ICES publications, is potentially the largest stock of true cod (*Gadus morhua* L.) in the world. Spawning areas, migration routes, and feeding areas are shown in Figure 1. Bergstad *et al.* (1987) and recently Sundby and Godø (1993) have reviewed the available information on life history. Jakobsson (1992) has provided an overview of the development of the stock during the past 20 years including a discussion of factors which may explain the large fluctuations in abundance and growth which occurred in the 1980s. Recently, Jakobsen (1993) described and evaluated the history of management and discussed possible strategies for the future.

The cod reach maturity at an age of 6–9 years (Table 1), and the mature fish undertake spawning migrations southwards along the Norwegian coast (Fig. 1). Eggs and larvae are transported northwards in the upper water layers during April–August, and in August–September the 0-group is distributed in the upper 100 m over large areas in the Barents Sea and off Svalbard. During autumn the 0-group descends towards the deeper layers.

The immatures feed at both the bottom and in the midwater layers and make seasonal east–west and north–south migrations (Maslov, 1944, 1960). The amplitude or range of these migrations increases with age, and at an age of 3–4 years, when capelin become a major food item, the cod follow the spawning migration of capelin to the coasts of northern Norway and Murman. Some older immatures will join the mature stock on its migration towards the spawning fields farther south, the so-called "dummy runs" (Trout, 1957; Woodhead, 1959).

In addition to seasonal displacements of cod concentrations, temperature-related displacements have been reported on both small and large time and space scales (see Nakken and Raknes (1987) for references). In periods of warm climate in the Barents Sea the cod distribution area is extended towards east and north, as

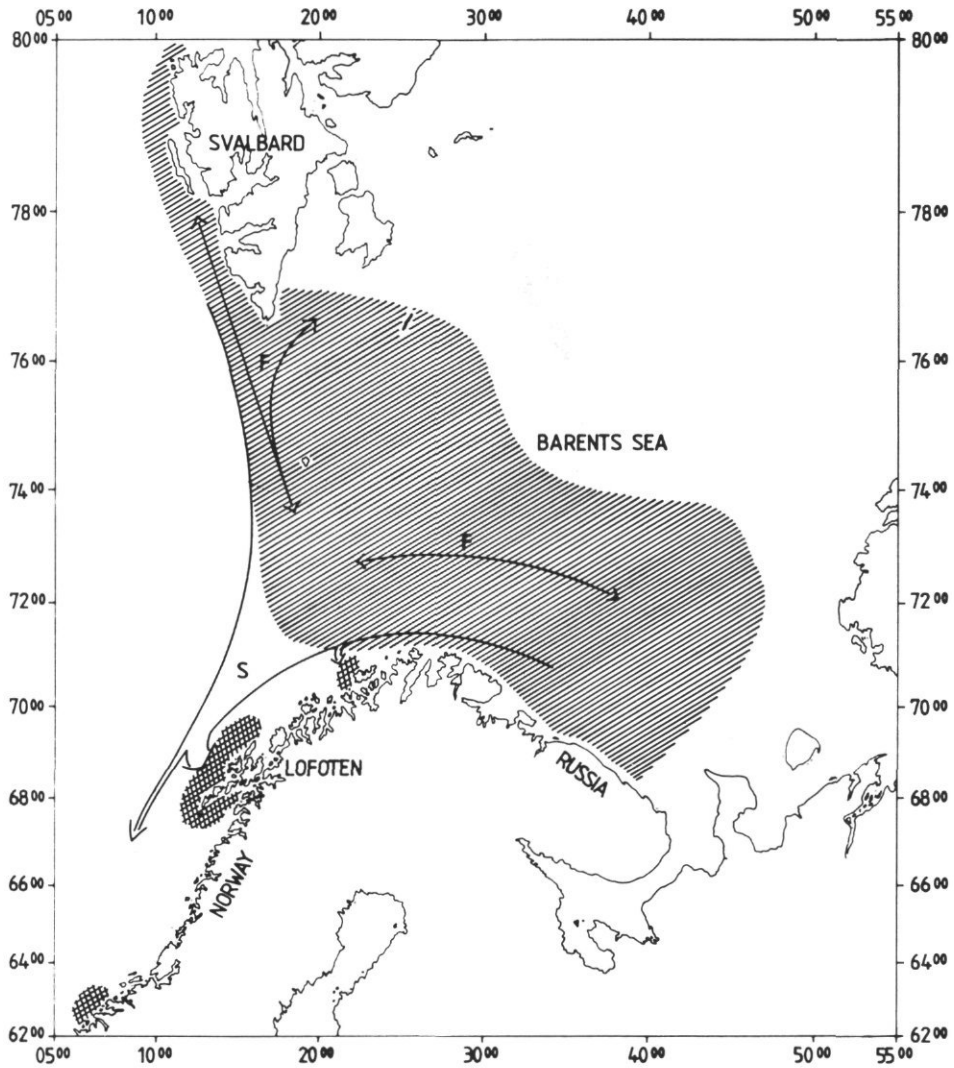


Figure 1. Main feeding area (hatched) and spawning areas (cross hatched) of Northeast Arctic cod with spawning (S) and feeding (F) migration routes (after Mehl, 1991).

compared to periods of cold climate when the fish tend to concentrate in the southwestern parts of the sea (Midttun *et al.*, 1981).

Landings have fluctuated considerably (Figs. 2 and 3). Official landing statistics date back to 1866 for spawning cod (skrei) and to about 1900 for total catches. Information on distribution, abundance, and biological characteristics for the various stages and age groups increased rapidly from 1950 owing to intensified scientific survey work. Systematic international scientific cooperation on stock monitoring started in 1958 when the ICES Arctic Fisheries Working Group was established; since the early 1960s as a stock assessment group at ICES.

Prior to 1920 the bulk of the landings came from two traditional coastal fisheries which have taken place for centuries: the fisheries for spawning cod (the skrei fisheries) during winter/spring on the spawning grounds (Fig. 1) and the fishery for immature cod (the spring cod fishery) that followed the capelin to its spawning fields along the northern coasts (Finnmark and Murmansk) in March to June.

During the 1920s and particularly in the 1930s an offshore fishery, predominantly with trawl, developed in the Barents Sea. The expansion continued after a period of low fishing activity during World War II (1940–1945). Simultaneously the efficiency of the coastal fleet increased. Average annual landings amounted to about

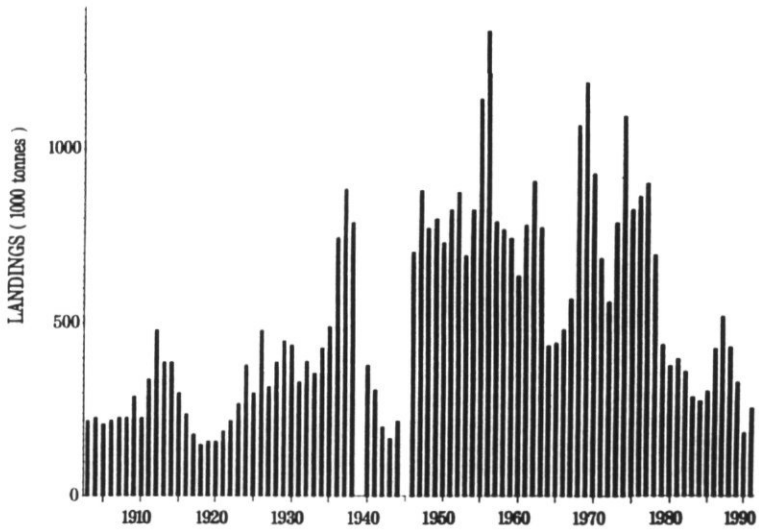


Figure 2. Landings (tonnes, thousands) of Northeast Arctic cod. (*Sources:* 1903–1929, Bergstad *et al.*, 1987; 1930–1960, Coop. Res. Rep. Cons. int. Explor. Mer, Ser. B. 1964; 1961–1991, ICES Coop. Res. Rep., 1962, 1993.

Table 1. Data on reproductive biology and life history of Northeast Arctic cod.

		Sources
Age at first maturity (years)	6–12	1
Length at first maturity	65–100	1
Approximate absolute fecundity (millions of eggs per female)	1–19	2
Spawning season	March–April	2
Egg diameter (mm)	1.2–1.7	2
Length at hatching (SL, mm)	4.2–4.3	2
Length at end of yolk sac (days)	4.8–5.0	2
Age at end of yolk sac (days)	9	2
Length at metamorphosis (SL, mm)	10–12	2
Length by August–September (TL, mm)	25–140	2
Age at recruitment to fishery (years)	3–4	3
Minimum allowable catching size (TL, mm)		
Norwegian EZ	47	4
Russian EZ	43	4

Sources: 1 Jørgensen (1990), 2. Bergstad *et al.* (1987), 3. Reports of the Arctic Fisheries Working Group, 4. Reports of the Mixed Norwegian–Russian Fishery Commission.

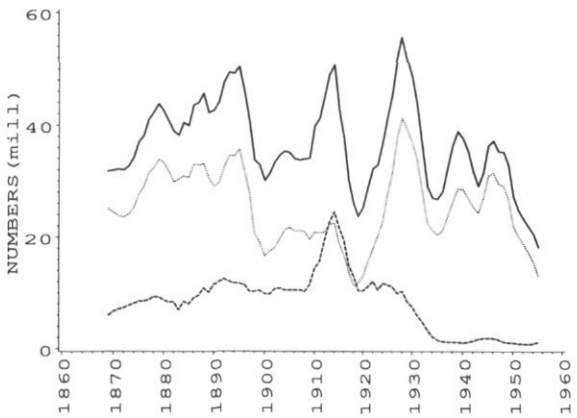


Figure 3. Landings (no. of fish, millions) of spawning cod from the Norwegian skrei fisheries. Running five-year mean values. —— Total; ···· Nordland (Lofoten); ---- Southern district (Møre) (after Godø and Sundby (1993), redrawn from Sætersdal and Hylen (1964)).

800 000 t for the period 1946–1978, with peak landings exceeding 1 million tonnes in five of those years. During the 1980s, landings declined. The 1990 landings were among the lowest on record and about 25% of the average for the period 1946–1978. In the most recent years, landings have been increasing rapidly.

The present paper is an attempt to summarize and evaluate the published information on trends and fluctuations in the stock and to discuss their causes.

Fisheries and their influence on stock size

Directed fisheries, landings

In the 1950s, Sætersdal and Hylen (1964) were concerned with the declining trend of the landings of spawning cod (Fig. 3). They compared time series of catch per unit of effort (c.p.u.e.) in the skrei- and springcod fisheries and concluded that, "*the skrei population has apparently been less abundant as compared with the*

population of young cod than it was before the war. This is the type of effect we must expect to find if the reduction of the stock of skrei is not largely a result of natural fluctuations, but has been caused by an increase in the total exploitation of the arctic cod. The number of old and large fish is reduced relatively to that of the younger and smaller fish". They also found that the mean age of the spawning cod decreased over the same period, as the reduction in abundance occurred, and interpreted this as an effect of increased exploitation.

The influence of fisheries on stock development and yield was the main subject of study of the Arctic Fisheries Working Group from the very beginning. Important results of the Group's work are summarized as follows:

1. In 1961, on the basis of c.p.u.e. studies, the Group recommended an increase in mesh size in order to protect small fish from being caught, and thus increase future stock biomass and yield.
2. In the mid-1960s, partly on the basis of cohort analysis in addition to catch-and-effort studies (the first VPA was carried out in 1965 (Gulland), it became evident that the overall fishing mortality rate was far above the rate giving maximum yield per recruit. The 1965 report from the Group (ICES, 1965) included a presentation of measures which could limit the catches (closed areas, increased mesh size, catch quotas, reduced effort).
3. From 1969 and onwards the Group consistently expressed concern at the future size of the spawning stock, considering that at low levels of spawning stock the risk of poor recruitment was increased.
4. In the mid-1980s the Group predicted, on the basis of high abundance indices of 0 to 2-year-old fish, a substantial increase in stock size and catches by the end of the 1980s. The predictions failed completely because of interrelations with other stocks, which the group did not foresee.

The increase in the spawning stock biomass in the early 1970s caused by the abundant 1963 and 1964 year classes probably convinced managers that the concern of scientists at that time was not justified. Fishing mortality rates remained high for many years, and in due course the stock decreased and the spawning stock fluctuated at low levels (Figs. 4 and 5). At the end of the 1980s, when it was evident that the stock was in a very poor condition, catches and fishing mortalities were drastically reduced through regulations implemented by Norway and the USSR.

In the early 1970s, Garrod and Jones (1974) calculated a spawning stock and recruitment relationship for the stock and used it to conclude:

1. If annual fishing mortality rates are sustained at a level of F = 0.43 or above, the stock will tend to extinction. The maximum catch, 800 000 t, is obtained with a spawning stock equal to that observed in the early 1950s and a fishing mortality of F = 0.26.
2. Because of instability in recruitment at low spawning stock levels, only very large year classes contain enough recruits to offset the level of exploitation which has been characteristic of recent years (1965–1972).

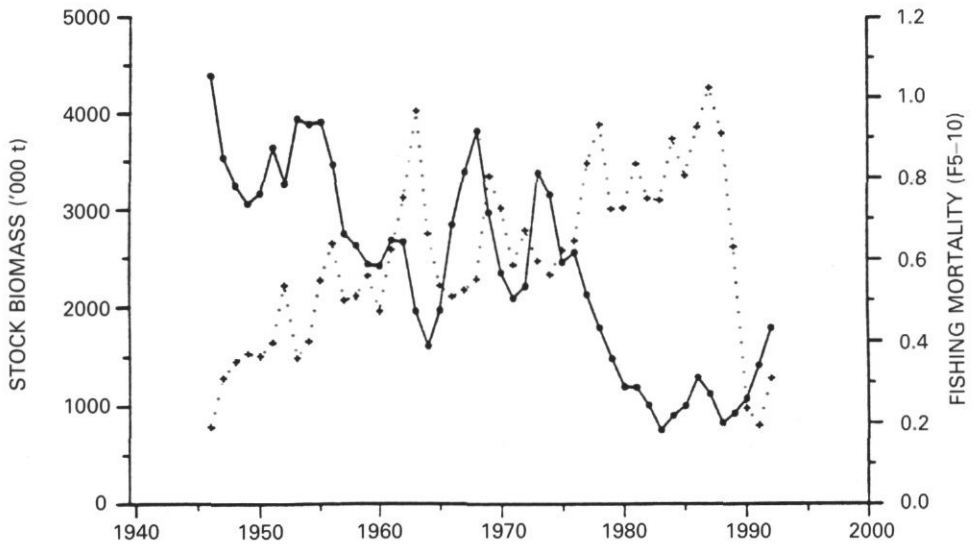


Figure 4. Northeast Arctic cod. Stock biomass (ages 3+) and fishing mortality (after Jakobsen (1993)).

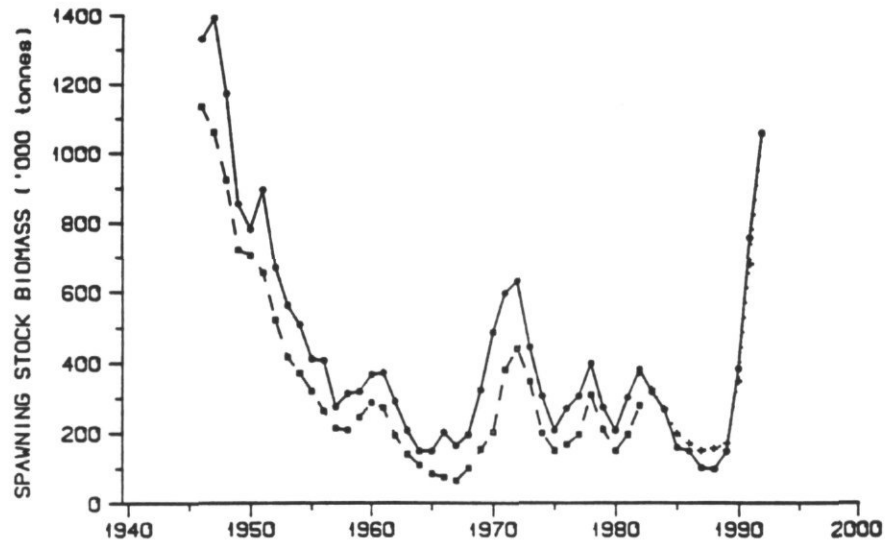


Figure 5. Northeast Arctic cod. Spawning-stock biomass for various maturity ogives (after Jakobsen (1993)).

The fact that the largest year class ever recorded, the 1970 year class, recruited to the fisheries and increased the annual catches for some years (Figs. 2 and 6) seems to have weakened the effect these findings ought to have had on the management of the fishery. In hindsight, it can be seen that the appearance and fate of that year class and the development of the stock in the following years supported Garrod and Jones (1974) conclusions. It is also interesting to note that recent works on stock and recruitment relationships and the incorporation of such relationships in stock assessment work largely support the figures arrived at by Garrod and Jones (1974). Jakobsen (1992) estimated the level of fishing mortality where the recruitment to the stock in half of the observed years has been more than sufficient to balance the losses due to mortality (F med) at F = 0.46. Serebryakov

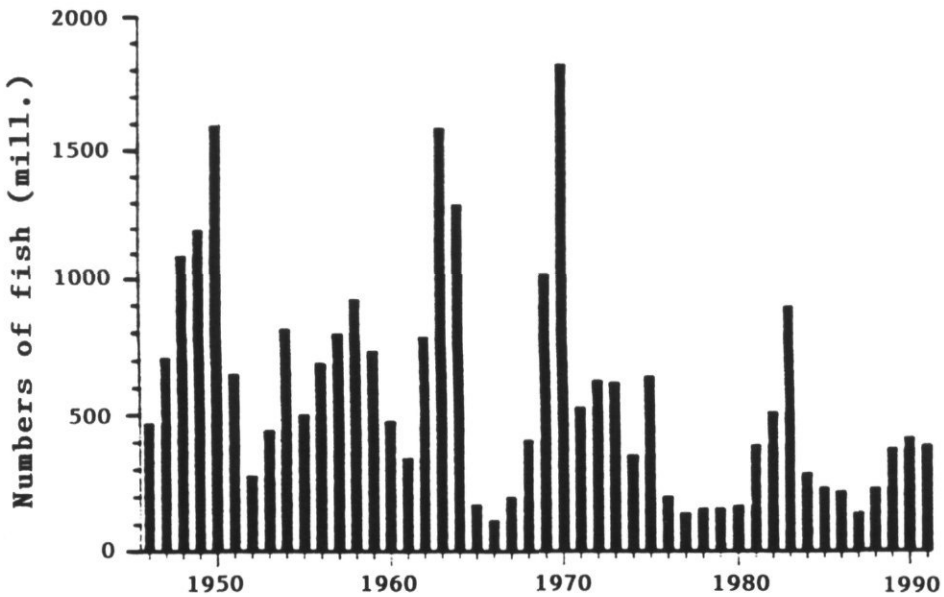


Figure 6. Northeast Arctic cod. Year-class abundance (no. of fish, millions) at age 3 (after Jakobsen (1993)).

(1991) and Jakobsen (1993) indicated that in order to maintain sufficient levels of recruitment a spawning stock of 500 000 t or more is needed, and Jakobsen (1993) concluded that a lower level of exploitation than $F = 0.46$ should be aimed at in management.

The time series of stock size and fishing mortality are shown in Figure 4. For a period of more than 30 years the annual fishing mortality was well above any calculated safe level ($F < 0.46$). Consequently, the number of fish removed (the total mortality) from the stock was on average higher than the number recruited to the stock, and stock numbers and biomass decreased. Hence, the main trend in Figure 4, the decline from a stock biomass of about four million tonnes in 1955 to less than one million tonnes in the 1980s was caused by the fisheries. The fluctuations around this main trend were caused by variation in recruitment (Fig. 6). Ulltang (1987) demonstrated that accumulated yields for the period 1970–1982 as well as the stock size in the mid-1980s would have been considerably higher than experienced if the fishing mortality rate, particularly on small fish, had been reduced during the 1970s.

Discards in directed fisheries

Estimates of discards are relatively few. In its early assessments the Arctic Fisheries Working Group (1961) used discarding rates of 30% by numbers for English trawlers (ICES, 1965). Observations in the mid-1960s indicated cod discards up to 24 and 40% by numbers for Norwegian and British trawlers (Hylen, 1966; Garrod, 1967). In 1973, Hylen and Smedstad (1974) observed discarding rates of 24 and 39% by numbers for bottom trawl and midwater trawl respectively. According to ICES (1990), discarding was known to have taken place in the 1980s, particularly in 1986–1987, owing to the poor condition of young fish in these years.

The proportion of young fish discarded at sea has probably fluctuated with the size composition of the stock, with the market demand for small fish, and with the effective mesh size used. Actual mesh sizes increased from about 80 mm and/or less in the 1950s to 110–120 mm in the 1960s, and since the early 1980s have been 125 and 135 mm in the Russian and Norwegian zones, respectively. In addition to mesh size regulations, an area closure system was established in the 1980s; areas where the amount of undersized fish (Table 1) in the catches exceed 15% by numbers are closed in fishing. It is thus not surprising that discarding rates on average were considerably reduced during the period 1946–1990 for which estimates of stock size exists. A consequence of a reduction in discarding rates over this period is that the abundances at age 3 (Fig. 6), which are calculated from landings, might be underestimated for the early part of the period.

Mortality of fish escaping through meshes

Mortality of fish that are injured when escaping through the meshes in trawls will reduce the recruitment of fish to the fisheries and the expected gains of increased mesh sizes. According to Soldal *et al.* (1993) Scottish and Russian investigations in the 1980s indicated that mortality rates of escaped cod were high. On the other hand, in their review of Norwegian experiments on demersal gadoid species Soldal *et al.* (1993) concluded that the mortality of cod was negligible and that of haddock less than 10%. On that basis they expected high survival rates of gadoids that escape through the meshes in demersal trawls.

Bycatches in shrimp and capelin fisheries

The fisheries for shrimps with small-meshed bottom trawls in the Barents Sea region developed rapidly, from landings amounting to some few thousand tonnes in the mid-1970s to 126 000 t in 1984. Since the early 1980s these fisheries have been managed using a closed area system in order to limit the catch of young gadoids; areas where the number of specimens of cod + haddock exceed 3 per 10 kg shrimp catch are closed to shrimp fishing. Hylen and Jacobsen (1987) estimated the number of cod caught in the shrimp fisheries in 1983–1986 as ranging from 7 million in 1983 to 49 million in 1985, mainly 1–4 year olds. Assuming a natural mortality rate ($M = 0.2$) for the cod aged 1 and 2 years equal to that of older fish they found that the number of cod aged 1–3 years removed by the shrimp fisheries of the 1982 and 1983 year classes would generate losses in yield from these year classes of 20 000 and 30 000 t, respectively. Since 1 and 2 group fish were predominant in the shrimp catches and these age groups are probably subject to somewhat higher natural mortalities than $M = 0.2$, it is likely that actual losses were less.

Catches of various age groups of cod in capelin fisheries (purse seine and trawl) are regularly monitored by the coastguards. Areas are closed for fishing when bycatches of cod exceed specified limits agreed upon by Norway and Russia. The total amount of cod bycatch in the capelin fisheries is unknown. In recent years it is assumed to be low because of strict enforcement of the closed area system.

Seismic exploration, pollution, and changes in freshwater run-off

During the past 10–15 years seismic exploration has been undertaken at an increasing rate at locations within the cod distribution area. Engås *et al.* (1993), studying distribution and catch rates at and around an area of seismic shooting (airguns) before, during, and after the

shooting, found that catch rates were reduced (up to 70%) in the vicinity of the shooting area when shooting started, and significant reductions were observed at distances of 15–20 nautical miles from that area during the shooting period. The cod evidently avoided the seismic area and the bigger fish that showed the most pronounced avoidance did not reappear in the area within 5 days of shooting at the end of the observation period.

Studies of the effect on fish eggs and larvae from airgun shooting have indicated that lethal injuries are caused very close to the explosion (1–3 m). Unless future investigations reveal damage at greater distances, and taking into consideration the great extent of horizontal and vertical distribution of cod eggs and larvae, it must be concluded that seismic shooting, as performed nowadays, hardly affects the mortality of cod eggs and larvae.

Monitoring of various pollutants in the environment as well as in fish meat and liver has not revealed concentrations that with the present state of knowledge can have influenced the stock.

In several papers, Skreslet (1981) has focused on freshwater runoff as an important factor for the formation of survival conditions for cod larvae. During the past decades the runoff from many Norwegian rivers has been adjusted through storage of water for hydroelectric power; in particular, the peak in runoff to the sea in spring due to snow melting in the mountains has been levelled off compared with earlier periods. However, Sundby (1979) found no relation between freshwater outflow and survival indices of Northeast Arctic cod for the period 1946–1978.

Interactions with other species

The cod is prey throughout its entire life from the egg stage and predator from the time the yolk sac is finished. Studies on interactions between cod larvae and other species during the northward drift have been directed mainly towards the diet, abundance, distribution, and behaviour of cod eggs and larvae in relation to food availability, and effects on larval growth and survival. These studies and findings are discussed in the section on Environmental Influences. In the present section, interactions between other species and cod older than 8–10 months, at the end of the 0-group drift, are considered.

The bulk of quantitative information available originates from the joint project between the Institute of Marine Research (IMR), Bergen, and the Polar Research Institute (PINRO), Murmansk, on multispecies assessment studies, and is present in Bogstad and Tjelmeland (1992a).

Food, feeding and consumption

Figure 7 shows the main food web in the Barents Sea (Ajiad *et al.*, 1992). Cod feeds on fish and crustaceans and its food habits vary with size (age). At onset of feeding, phytoplankton is included in the larval food, but various stages of *Calanus* are the most important food items for cod larvae at all stages. The importance of euphausiids in the diet increases towards the end of the pelagic stage of the 0-group, and euphausiids, amphipods and various size groups of shrimps continue to be important prey for fish up to considerable sizes (30–50

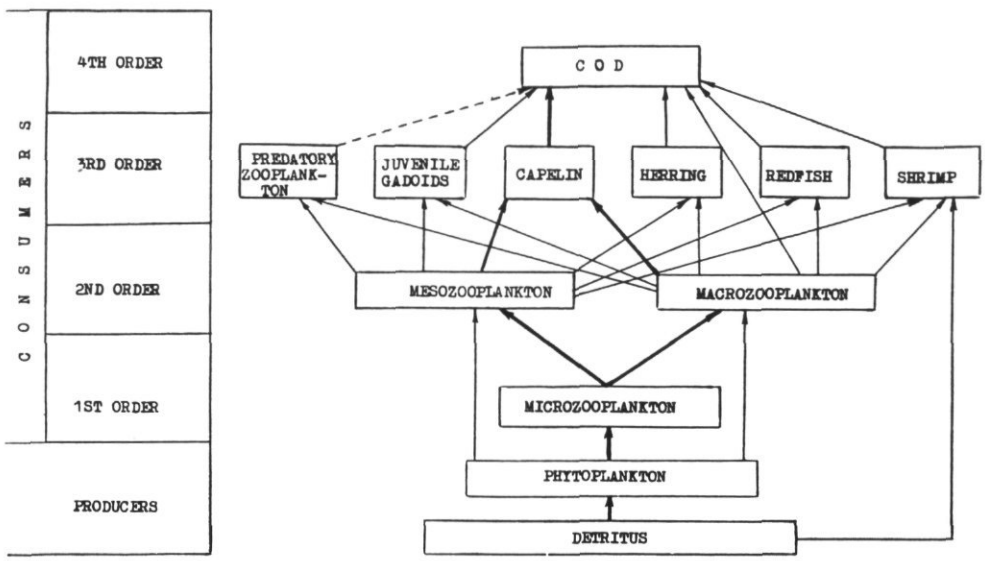


Figure 7. Main food webs in the Barents sea ecosystem (after Ajiad *et al.* (1992)).

cm). Ponomarenko (1984) considered the abundance of euphausiids prior to the first wintering season of the cod as an important factor for cod survival. For cod between 30 and 70–80 cm in length fish (capelin, herring, polar cod, sandeel, young gadoids) on the average make up about 70% of the food. Capelin and juvenile herring are the most important prey species. Cod above 80 cm in length eats almost exclusively fish including young cod up to 30–34 cm in length. Since the stock of Norwegian spring spawning herring collapsed in the 1960s capelin has been the major food resource for cod.

Table 2 gives the stock's consumption of the main prey species during the period 1984–1989 (Bogstad and Mehl, 1992). Capelin and amphipods were predominant and a shift from capelin to amphipods appeared along with the collapse in the capelin stock in 1986–1987 (Mehl, 1989; Hamre, 1988, 1991; Jakobsson, 1992). Herring and young gadoids amounted to only a few percent of the total biomass consumed, but the mortality of these groups due to cod predation increased in 1985–1986 and led to a pronounced reduction in the 1984–1986 year classes of cod, as well as in the 1984 and 1985 year classes of herring (Mehl, 1989; Hamre, 1991; Jakobsson, 1992). As early as in the mid-1970s Ponomarenko and Ponomarenko (1975) anticipated the circumstances that had become apparent by the mid-1980s from Table 2. On the basis of estimates of the cod and haddock stock's food demand and the production capacity of the capelin stock they concluded that if the two gadoid stocks were to recover, the capelin stock and fishery would decline and the cod would have to change to other food. In the event, the capelin stock was heavily reduced from 1984 to 1986 and fishing was banned from 1987 to 1989; the cod changed to food resources other than capelin, including increased cannibalism, in 1984–1986.

The unexpected feature of Table 2, at least to the present author, was the predominance of amphipods in the food of cod during the years when capelin was lacking (particularly 1987 and 1988). Even large cod 50–70 cm in length fed heavily on amphipods (*Parathemisto*) and although no time series of the latter's abundance exist the general impression from acoustic recordings and midwater trawl hauls is that amphipod abundance reached a peak in 1986–1988. Was the abundance of amphipods really higher in these years? If so, then was it because of less predation from capelin, as suggested by Skjoldal *et al.* (1992), or did other factors contribute to the increase?

During the last decade much effort has been put into modelling the interrelations between cod and other species in the Barents Sea, with the ultimate aim to establish interrelationships which can be used in stock assessment and predictions of stock development and catch quotas. At present a cod/capelin interrelationship (Bogstad and Tjelmeland, 1992b) that takes into account the cod stock's need for capelin as food is used when capelin quotas are estimated and advice is given by ICES. Ongoing research is focused on other main food items for cod (herring, shrimp, and redfish) as well as on cannibalism (see Bogstad and Tjelmeland (1992a) for references).

Cannibalism

Cannibalism in cod increases when other prey species are scarce compared with small cod. It was high in 1986–1988, when stocks of both capelin and juvenile herring were low (Orlova, 1992). Tables 3 and 4 give estimates of the mortality rate of young cod due to cannibalism (Ajiad *et al.*, 1992; Korzhev and Tretyak, 1992). Cannibalism of the 0-group takes place during the last quarter of the year, when the fry have descended to deeper layers and become available to the large fish. Sundby *et al.* (1989) calculated mortality rates from estimates of abundance of 0-group and three-year-olds for the year classes of 1979–1983. Depending on assumed catching

Table 2. The Northeast Arctic cod stock's consumption of main prey species in 1984–1989 (per cent of biomass). Total in million tonnes.

	1984	1985	1986	1987	1988	1989
Amphipods	1	3	25	35	44	27
Shrimp	19	5	4	8	5	5
Capelin	40	56	33	11	22	31
Herring	3	5	4	1	0	0
Cod	2	1	4	2	1	0
Haddock	2	1	3	0	0	2
Redfish	15	6	8	14	8	9
Others	17	23	19	29	20	26
Total	2.1	3.5	2.9	2.1	2.4	2.5

Source: Bogstad and Mehl (1992).

Table 3. Natural mortality rates of Northeast Arctic cod at age 0–3 years due to cannibalism in 1984–1989 (from Ajiad *et al.* (1992)).

Age	1984	1985	1986	1987	1988	1989
0	0.28	0.48	0.51	1.31	0.30	0.00
1	0.05	0.11	0.25	0.38	0.35	0.00
2	0.04	0.01	0.04	0.07	0.10	0.00
3	0.02	0.01	0.01	0.03	0.04	0.00

Table 4. Consumption of cod by cod in the Barents Sea (Ajiad *et al.*, 1992) and by harp seal during the seal invasions to the Norwegian coast in 1987–1988 (Ugland *et al.*, 1993) (millions of individuals).

	Cannibalism				
Age	0	1	2	3	Harp seal
1982	–	–	13	4	16 (at age 5+6)
1983	–	43	12	6	22 (at age 4+5)
1984	188	56	17	10	66 (at age 3+4)
1985	339	111	23	13	103 (at age 2+3)
1986	344	147	27	–	33 (at age 1+2)
1987	255	186	–	–	

efficiencies of 0-group (q = 0.1 and q = 0.25) they arrived at total instantaneous mortality rates in the range 0.5–1.0 and 0.1–0.6. The estimates of the mortality rates in Table 3 thus seem to be comparable with those which are arrived at for other year classes by using a different method.

Influence of birds and marine mammals

Birds and marine mammals can influence the stock of cod in two ways: directly by predation, or indirectly, through competition, by utilizing the same food stocks as cod (pelagic fishes and crustaceans). Their diet is probably closely related to the prey that is available at the lowest cost/benefit in terms of foraging time and effort; the predation pressure they exert on the various fish stocks (including cod) might therefore be dependent more on the relative abundance and availability of the various prey species than on their own stock sizes. A few of the species of birds in the area are highly specialized feeders (guillemot and puffin) but most species eat what is available.

The total food consumed by birds and marine mammals in the Barents Sea area is estimated at 4–8 million tonnes, depending on the biomass and energy content of the various prey species (Gabrielsen and Ryg, 1992). There exist no long-term time series of diets of birds and marine mammals which enable us to quantify their influence on stock size fluctuations of cod. Gabrielsen and Ryg (1992) estimated that marine mammals (seals and whales) in the region consumed 7–10 times more food in terms of energy equivalents than did birds. From an aerial survey in 1991, Borkin *et al.* (1992) estimated that the total population of birds in the Barents Sea is 14 million, 59% of which are fulmars and 37% kittiwakes. The total consumption of fish by fulmars and kittiwakes was estimated at ~90 000 t annually, mainly capelin.

Barrett *et al.* (1990) calculated that predation on gadoids by shags and cormorants may affect the year-class strength of saithe and cod. Their estimates would account for a substantial part of the mortality of the prerecruits of saithe and cod in the period 1985–1988, and at levels comparable to the levels of cannibalism estimated by Mehl (1989). Barrett *et al.* (1990) questioned their own estimates, pointing at the inaccuracies in the data set used; nevertheless, their results indicated that predation from birds might have a significant influence on the mortality of small-sized cod (aged 0–2 years) in some years.

The most abundant seal species in the Barents Sea is the harp seal. Bjørge *et al.* (1981) and Haug *et al.* (1991) studied the diet of harp seal caught in fishing nets along the Norwegian coast during the seal invasions (1978–1988). Their findings supported previous conclusions that harp seal are opportunistic feeders, eating what is available. In 1978–1981 when capelin was abundant, capelin and capelin roe constituted the bulk of the diet of the examined animals, while in 1986–1988, when the stock of capelin was at a minimum, various fish species including cod were predominant in the stomachs. Ugland *et al.* (1993) estimated the harp seal's consumption of various fish species as well as several year classes

of cod during the seal invasions in 1987–1988 to be at levels comparable to the levels of cannibalism (Table 4).

Observations made in recent years of the diet of minke whales in the Barents Sea region (Haug *et al.*, 1993) have revealed large differences in stomach contents between years and areas. In the summer of 1992 herring and other fish species, including cod, were observed to be the most important constituent of the diet off the coasts of Murmansk and Finnmark, while capelin was the important food item in the Bear Island–Svalbard area. Although 0-group cod dominated the biomass of the pelagic organisms in large parts of the area investigated, they were not found in whale stomachs.

Environmental influences

Periodicity in time series of temperature and yield

Loeng *et al.* (1992) used Fourier analysis to find principal periodicities (cycles) in time series of temperature at several locations in the Northeast Atlantic, including the mean temperature (0–200 m) in the Kola section (Fig. 8). In several papers, Ottestad (1986) used a similar approach searching for cycles in the time series of annual yield from the Lofoten skrei fishery. Table 5 gives the most dominant cycles found in the two studies.

Ottestad (1986) also found cycle lengths of 23, 42.2, and 57 years. The technique he used allowed for cycle lengths between 8.5 and 72 years.

There is good agreement between dominant cycle lengths in the two studies, raising the possibility that variations in yield (and thus variations in abundance) of spawning cod are related to variations in ocean climate. The mechanism of any possible causal relationship is not, however, explained by the above evidence.

The significance of temperature

The significance of temperature for the development of the stock of Northeast Arctic cod has been investigated by numerous authors (see Loeng (1989) for references). Sætersdal and Loeng (1987) assessed the relative strength of the year classes in the period 1902–1987 and compared the occurrence of year classes of high, medium, and low abundance with temperature data from the Barents Sea during the same period. They found that year classes of high abundance were either associated directly with high temperatures or occurred at the onset of a shift to a warmer regime in the area. Table 6 summarizes their findings, demonstrating clearly that medium and high year-class abundance have occurred more often in warm years than in cold years.

The average numbers of three-year-old cod in year classes of high, medium, and low abundance in the period 1943–1985 for which absolute estimates are available (Fig. 6) were approximately 400, 800, and 1400 million respectively. Applying these figures to the frequency distributions in Table 6 results in average year-class abundances in cold and warm years of 480 and 710 million individuals, respectively. The average year-class strength for 1977–1981, which is the coldest period experienced during the past 50 years, was 200 million (Fig. 6) and about one-third of an average year class (600 million) for the period 1943–1985.

Sætersdal and Loeng's (1987) observations are in agreement with results from Russian workers (see Mukhina *et al.*, 1987), who found increased larval transport (current velocity) into the Barents Sea in years when abundant year classes were formed. Variations in temperatures in the area are mainly determined by variations in inflow. Why does the production of recruits in the stock vary with temperature conditions and inflows of Atlantic waters?

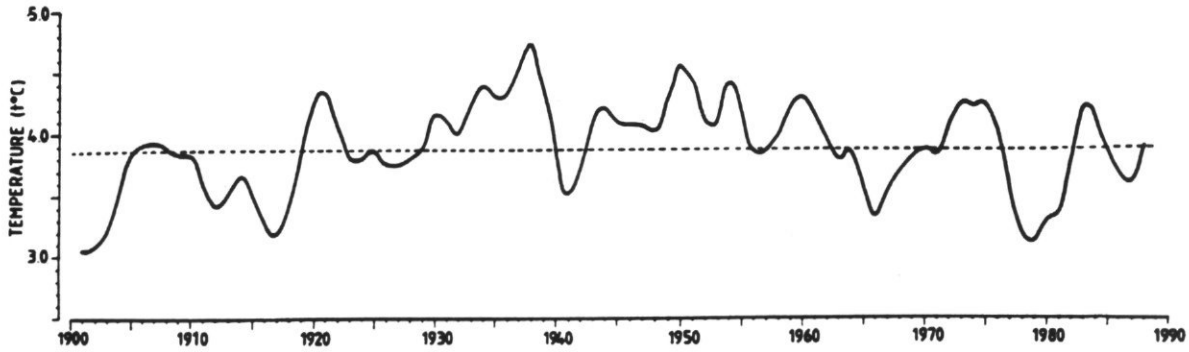


Figure 8. Three-year moving average of yearly temperature in the Kola section during the period 1900–1990 based on data from Bochkov (1982) and from PINRO, Murmansk (pers. comm.). The stippled line indicates the mean value for the period 1921–1980 (Loeng, 1991).

Table 5. Dominant periods (years) as estimated by Fourier analysis.

Temperature (Loeng *et al.*, 1992)	8.8	11.7	−13.6	17.5
Annual yield (Ottestad, 1986)	8.5	10.7	13.7	17.5

Eggs, larvae, and early juveniles

Ellertsen *et al.* (1989) reviewed the available information on spawning and distribution of eggs, distribution and feeding of early larvae as well as prey abundances. Their main findings were:

1. Year classes of high or medium abundance occur in years with medium or high temperature at the spawning grounds in March–April.
2. At the main spawning ground (Lofoten), spawning takes place during the same period each year. The date of 50% spawning varied by less then 5 days around 1 April during the 10 years of observation.
3. Egg mortality between spawning and hatching was 90% in the two years of observation (1983–1984). The causes of mortality are not well known, but predation by herring has been observed.
4. Eggs hatched after 20–35 days, depending on temperature. The peak of hatching varied by approximately two weeks between two years of extreme temperatures (1981 and 1983).
5. The cod larvae feed mainly on nauplii of *Calanus finmarchicus*.
6. Onset of *Calanus* spawning as well as maximum occurrence of *Calanus* nauplii (suitable food for larvae) varied considerably from year to year depending on temperature. In the warm year of 1960 (4.4°C), maximum abundance was 50 days earlier than in the cold year of 1981 (1.9°C), 1 April and 20 May respectively.

They concluded their discussion as follows: "In years with normal environmental temperatures, a high proportion of cod larvae will experience food concentrations high enough for growth and survival in most of the distribution area of first feeding larvae, due to the match between larvae and their prey. In years with extreme temperatures both high and low, the mismatch in time may contribute significantly to the weak year classes produced in these years."

Table 6. Occurrence percent of year classes of various abundances in cold and warm years (From Loeng, 1989).

	Year-class abundance		
	Low	Medium	High
Cold years	35	7	11
Warm years	31	14	12

Observations of reared cod larvae in closed and controlled systems have shown that shortage of food and demand for space generate extensive cannibalism (Folkvord *et al.*, 1993); the bigger ones eat the smaller ones. Lack of suitable food may take place at later stages than the first feeding period. Many workers, including Folkvord *et al.* (1993), have pointed out that the time after metamorphosis might be a critical period because of the rapidly increasing demand for food at this stage. Hence the abundance of older copepodite stages and adult *Calanus*, which are the main food items for juvenile cod at that stage, may limit growth and survival.

Post-larvae and 0-group

Loeng and Bjørke (1992) analysed mean lengths of postlarvae (July) and 0-group fish (August/September) of several species in the area and found a fairly close covariation in mean lengths of cod, haddock, and herring during the period 1965–1992. The mean length of cod and haddock in August–September seemed to depend mainly on the growth during their first three months of life (April–June), while the mean length of herring in August–September was more related to the growth during July–August. Their study indicated a weak length/temperature relationship for cod in accordance with previous findings (Loeng and Gjøsæter, 1990).

The time series (1965–1992) of abundance indices and mean lengths of 0-group cod, together with mean temperatures in the central Barents Sea, are presented in Figure 9. All data are from the 0-group surveys, 20 August–10 September each year (ICES, 1992). The curves for abundance and length appear similar; in years of low abundance of 0-group the growth has also been reduced. Low abundance and low growth also seem to occur more often in years with low temperatures.

Sundby *et al.*, 1989 found density-dependence of the mortality rate of cod between the postlarvae (early juveniles) and 0-group stages. This may indicate that lack of suitable food (starvation) rather than predation is the primary cause of the reduction in numbers at this stage too. Reduced growth would be an indicator of starvation but can hardly be measured in practice since predators will preferentially remove the weak (small) specimens. If for instance cannibalism within a cohort occurs at this stage in nature, as it does in controlled systems, reduced growth can only be expected when cod densities and abundances become low.

Age group 1 and older fish

Figure 10 shows the mean ambient bottom temperature for various age groups of cod in February. The temperatures were calculated from survey data using fish density

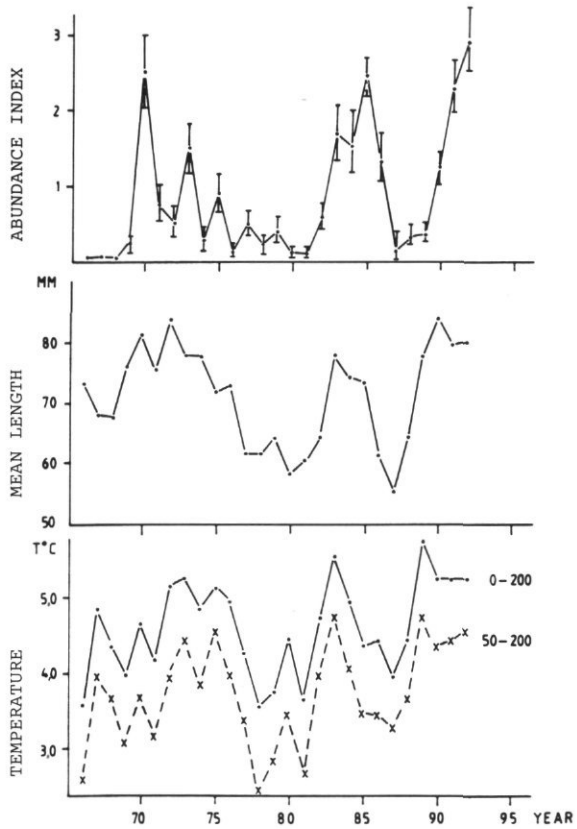


Figure 9. Indices of abundance (upper) and mean lengths (middle) of 0-group cod, and mean temperature in the Kola section in August–September 1965–1992. (*Source:* ICES, 1965–1992.)

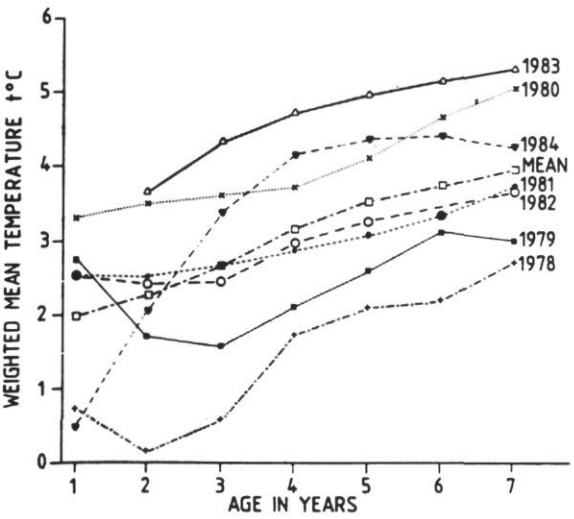


Figure 10. Weighted mean values of bottom temperatures for the various age groups of cod in February for the years 1978–1984. MEAN is the arithmetic mean for the whole period (Nakken and Raknes, 1987).

as weight in the calculation. Young fish were distributed in colder waters farther east than older age groups. For all age groups the mean temperature in February varied within a range of about 3°C over the years of observation. Ranges in temperature at fixed sections within the distribution area were also large, 1.5–2.5°C during the same period (Nakken and Raknes, 1987, Fig. 2; Skjoldal *et al.*, 1992, Fig. 3), but significantly less than the variations in the temperature of the environment of the fish. Variations in environmental parameters at fixed stations and/or sections do not necessarily represent the variations in the environment of the stock or certain age groups (see also Nilssen and Hopkins (1992)).

Figure 10 shows a systematic increase in ambient temperature by age of ~0.35°C per year for fish aged three years and older, indicating that these age groups maintain their distributions within the temperature field relative to each other and independent of the absolute temperature. Shevelev *et al.* (1987) suggested that cod year classes migrated westward at an average of 80 nautical miles per year. Independent of fish age, westward displacements of cod also coincide with decreasing temperatures in the area (Eggvin, 1938; Konstantinov, 1967, 1969; Nakken and Raknes, 1984). These temperature-related displacements have brought about great changes from year to year in the availability of fish at the various fishing grounds in the spring cod fisheries. Similar west/east and south/north displacements have also been observed for several other species (Loeng, 1989; Nilssen and Hopkins, 1992) some of which are important food items for the cod (capelin, shrimps). Hence, temperature-related migrations of cod might partly be the result of the fish adjusting its feeding area to suitable prey distributions as well as a direct response to temperature.

Other factors affecting year-class strength

As pointed out above the biomass of the spawning stock, i.e. the number of eggs spawned, has reached levels insufficient to maintain full recruitment. Recently, increased attention has been given to the quality and size of eggs (Kjesbu *et al.*, 1992). Large old fish, having already spawned several times, spawn eggs of varying size and varying specific gravity (buoyancy), while first-time spawners (small fish) and fish in poor condition spawn small eggs with quite stable specific gravity. Hence the eggs from established spawners are more widely vertically distributed and thus subjected to greater horizontal spreading, factors that are considered favourable for larval survival. In addition, bigger eggs give the larvae bigger yolks and widen the window for adaptation to first feeding.

Another factor of importance for larvae survival is turbulence (Rothschild and Osborn, 1988; Sundby and Fossum, 1990). Turbulence favours larval feeding by increasing the contact rate between larvae and their food particles.

Changes in growth and maturation

Long-term changes in length-at-age and age at sexual maturity of Northeast Arctic cod are described by Jørgensen (1990 and 1992). Figure 11 shows the time series of mean length-at-age of first-time spawners. There is a trend towards increased length-at-age over the period 1932–1987, which is more pronounced for the older age groups. At the end of the 1930s and the beginning of the 1940s a marked reduction in mean length-at-age occurred for all age groups. It coincided with the fall in temperature in 1939–1941 (Fig. 8) and with a complete disappearance of spawning capelin at the coast of Finnmark in the years 1938–1942 (Olsen, 1968).

From 1945 to 1980 an overall increase in length-at-age of 5–10 cm is seen (Fig. 11), most markedly for the older fish (9 and 10 years). Jørgensen (1990) interpreted this as a possible density-dependent effect, but in his more comprehensive later study on growth (1992) he found neither a significant relationship between length increment and stock size nor an overall trend in length-at-age throughout the period of investigation (1953–1989). Length-at-age showed marked short-term variations (1–5 years) with amplitudes of 10–15 cm. Growth-in-length was positively related to increasing ratio of capelin to cod stock abundance and also to increasing water temperature.

The pronounced increase in length-at-age of seven and eight-year-olds from 1982/1983 to 1987 (Fig. 10) (year classes 1975–1980), was also observed for the immatures of these year classes (Nakken and Raknes, 1987). It was explained as an effect of increasing environmental temperatures in the period (Fig. 10), although it occurred during a period (1978–1983) when both total stock size (Fig. 4) and the number of immatures in the stock declined rapidly.

The large changes in growth of cod observed during the years 1985–1989 when the stock of capelin collapsed are shown in Figure 12. Growth was particularly low in 1986 and 1987; the mean weight of five-year-olds by 1988 being two to three times less than that of five-year-olds in 1985 and 1991. At the end of the 1980s, when the stock of capelin recovered and capelin again became important as food (Table 2), the mean weights increased to the levels observed in 1985 and preceding years. The consequences of the dramatic reduction in cod growth were also dramatic (Mehl and Sunnanå, 1991); the 1986 predictions from ICES of stock biomass development in 1987 and 1988 were too high and so also were the recommended catch quotas for 1987 and 1988. Hence fishing mortality rates which were expected to decrease in these years stayed at a record high level (Fig. 4).

Jørgensen (1990) observed considerable reductions in age-at-maturity for the postwar period (Fig. 13); the median age-at-maturity decreased from about 10 years in 1945–1950 to 7–8 years in the early 1980s. Over these years the range of age covered by the maturity ogive also decreased. Jørgensen discussed his findings in relation to

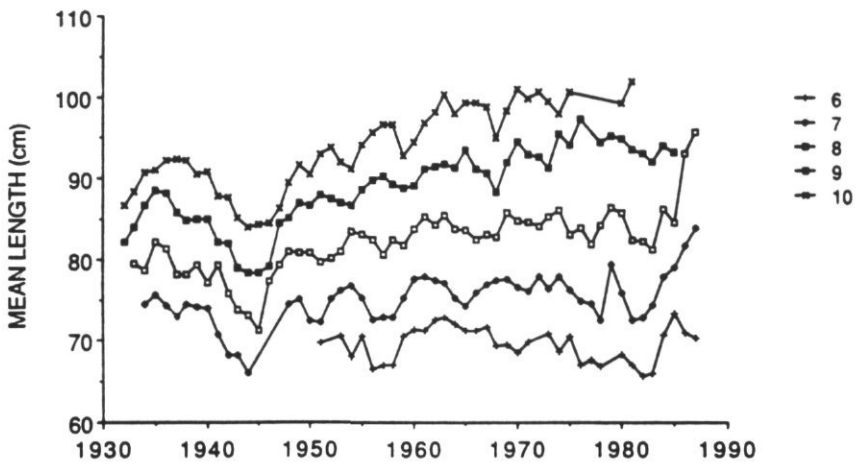


Figure 11. Mean length-at-age of first-time spawners of ages 6 through 10 caught by long-line at Lofoten. All means are based on a minimum of 10 observations (Jørgensen, 1990).

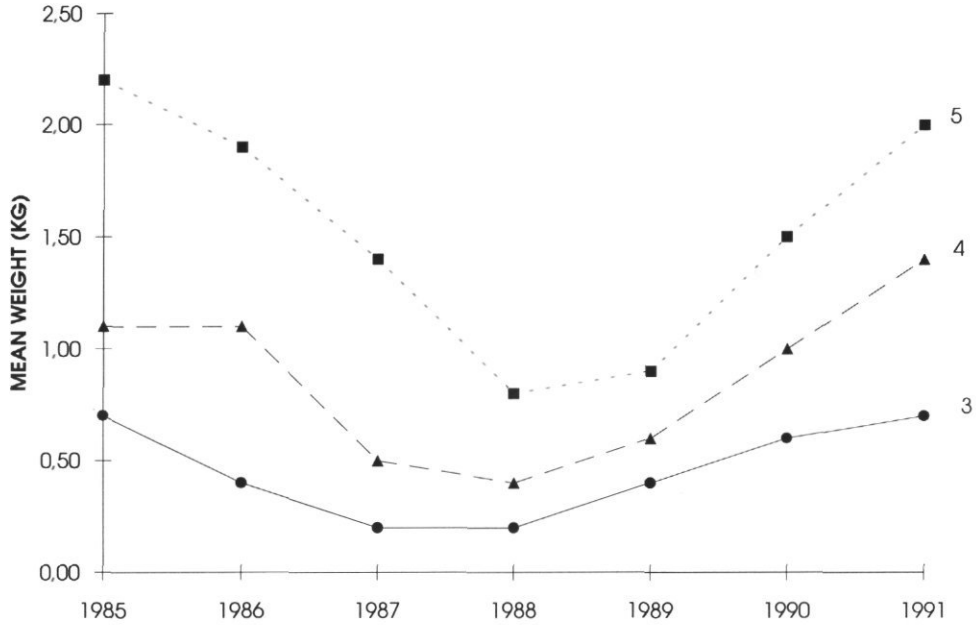


Figure 12. Mean weights (kg) of cod, age groups 3–5 years, as observed during surveys in February each year (data from Korsbrekke *et al.*, 1993).

genetic changes due to selective fishing, as had been suggested by other authors, and concluded: "Since the changes predicted by life history theory as a result of intensified exploitation and reduced abundance are exactly the same as those expected from phenotypic compensatory mechanisms, observed changes in length and/or age at maturity are *per se* no proof of genetic changes." He further concluded that the response of the stock, i.e. the general trend to mature at younger ages (Fig. 13), was probably an adaptation to the increased mortality.

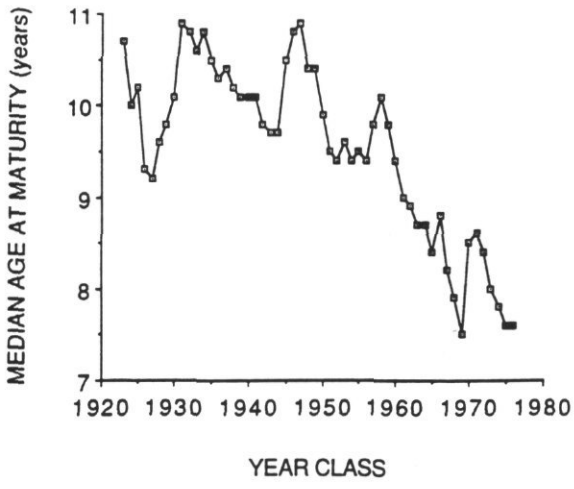


Figure 13. Median age at maturity for the year classes 1923 to 1976 (Jørgensen, 1990).

Concluding remarks

Owing to environmental factors and interactions North-east Arctic cod show a 20-fold range of year-class abundance at age 3 (100 million to 1900 million fish), with an average of 600–700 millions. The fish is recruited to the directed fisheries at age 3–5 years and appears as by-catch in small-meshed fisheries as young as 0-group. Measures taken to protect small-sized fish (increased mesh size, increased minimum catching size, and closed areas) have largely reduced the influence of fisheries on year-class abundance at age <4 years during past decades. The development of year-class abundance from age 4–5 onwards depends heavily on the fishing pressure to which it is exposed, and the declining trend of stock biomass from 1955 to 1988 was caused mainly by fishing; the number of fish removed from the stock by fisheries and by natural mortality exceeded by far the number recruited to the fishable stock in these years. The stock responded to the decline in abundance by shorter generation time (maturation at earlier age). Fisheries may also have had an adverse effect on recruitment by reducing the spawning stock and along with that the abundance of established spawners (large fish) to

low levels. Other man-made activities, such as pollution, seismic exploration, and modification of freshwater runoff, have had no detectable effect on stock abundance.

Year classes of high and medium abundance occur more frequently in warm climatic periods than in cold periods, and the recruitment to the stock is positively related to the inflow of Atlantic water to the area. A temperature-related degree of synchrony between early larval abundance and *Calanus* spawning and development seems to affect larval survival and thus year-class abundance at later stages. The observation that 0-group size and abundance in August–September are positively related and also related to temperature indicates that inflows of Atlantic water prior to and during the larval drift offer favourable conditions for growth and survival of cod juveniles during their first 5–6 months of life. Variation in the abundance at age 3 is also strongly dependent on interactions between species and size groups beyond the larval and 0-group stages. Predation from birds and marine mammals as well as cannibalism have caused year-to-year variations in juvenile cod mortality depending on the abundance of other prey items (capelin, herring). Unless such variations are foreseen and quantified by utilizing knowledge of trends in the most important prey and predator stocks in the area, predictions of year-class abundance at age 3 from estimates of 0-group abundance are of limited value.

Growth studies have revealed large short-term variations in length and weight-at-age for all age groups caused by varying availability (abundance and distribution) of prey. Neither an overall trend in length-at-age nor a significant relationship between length increment and stock size were found for the period 1953–1989, when stock size declined. The growth of cod increases with increasing temperature. However, a growth–temperature relation based on field data includes the effect of interrelations and depends on the availability of prey under various temperature regimes.

The importance of capelin as a major food resource has been clearly demonstrated and the significance of herring as another main prey item is pointed at by many authors (Øiestad, 1994).

The reliability of the conclusions arrived at on the causes which have influenced the development of the stock have been discussed in many of the papers referred to. Besides the need for improvement in observations, sampling, and analytical tools (models), there is a need to improve the fishery statistics. In earlier periods, as well as in recent years, the official statistics do not fully reflect the actual landings. According to a press release from the Norwegian Ministry of Fisheries in April 1993 the total international landings of Northeast Arctic cod in 1992 were 90 000–120 000 t higher than the official ones. Since such unreported landings as well as discards were not corrected for when annual stock estimates were established, the time series of stock size, fishing mortalities, and year-class abundance at age 3 do not fully reflect the actual development over the 50 years' period considered. These discrepancies do not, however, affect the main conclusion that the stock during a period of 40 years suffered from overfishing and declined to very low levels. The present increase in stock size and yield is a combined effect of moderate fishing pressure since 1989 and improved recruitment and growth in recent years.

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ICES mar. Sci. Symp., 198: 229–243. 1994

Changes in the North Sea cod stock during the twentieth century

Niels Daan, Henk J. L. Heessen, and John G. Pope

Daan, N., Heessen, H. J. L., and Pope, J. G. 1994. Changes in the North Sea cod stock during the twentieth century. – ICES mar. Sci. Symp., 198: 229–243.

The development of the North Sea cod stock since the beginning of the last century is described on the basis of available yield and catch-per-unit-of-effort data. Given the data limitations, the analysis is not based on a strictly formal model, but rather is an attempt to capture the main trends in stock sizes and recruitment levels to match the realized catches and estimated fishing mortalities. The data indicate a very marked increase in recruitment during the period 1960–1990 which cannot be explained by density-dependent effects. Also, there is as yet no clue in any environmental signal providing a likely explanation. The hypothesis that the apparent increase in the carrying capacity of the North Sea for juvenile cod is caused by overexploitation of the pelagic fish species cannot be discounted. The recruitment pulse has had only a minor effect on stock biomass, because the expected increase has been counteracted by increased exploitation of the cod stock. The data suggest that the present spawning stock is at an all-time low.

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Introduction

The North Sea cod stock is heavily overfished and is considered to have reached the stage of recruitment overfishing (ICES, 1993a). In the last few years, the Advisory Committee on Fishery Management of ICES has been advising that fishing effort on cod be sharply reduced. Although TACs have been reduced accordingly, there is as yet no sign that fishing mortality is decreasing. Additional measures are being considered, but the main management problem is that cod is largely taken in mixed trawl fisheries, which would have to be closed altogether if the cod is to be saved.

The recent history of the cod stock is well documented. Since 1963, estimates of fishing mortality, recruitment, and biomass have been available on an annual basis (Fig. 1). Despite problems with the reliability of catch statistics and uncertainties about the effect of discarding of juvenile cod, the marked increase in fishing mortality is well established and leaves little doubt that fishing is responsible for the gradual reduction in spawning-stock biomass (SSB) since the late 1960s (ICES, 1993b). Moreover, the most recent five years have been characterized by below average recruitment and SSB is steadily decreasing further. Although the coincidence of a low SSB and low recruitment is a major reason for concern, recruitment has been fairly variable throughout the last 30 years, and the significance of another factor contributing to the poor recruitment cannot be ruled out. The situation is particularly difficult to interpret, because the catches increased steeply during the 1960s from a level of approximately 100 000 t to over 200 000 t. This was caused by a sharp increase in the average recruitment level (Daan, 1978) associated with large-scale changes in the system during that period (the "gadoid outburst"; Cushing, 1984). However, the causes of these major system changes have remained obscure (Hempel, 1978). The collapse of the pelagic fish stocks as a consequence of overfishing has been suggested as the primary cause of a shift to a system dominated by demersal species (e.g. Andersen and Ursin, 1978), but changes in zooplankton production, possibly related to variations in atmospheric circulation, have also been considered responsible (Cushing, 1984). The available evidence is not entirely convincing in either direction, but whatever the cause it seems not impossible that the recent drop in recruitment level reflects a reversal of the system back to "normal".

In the context of this Symposium, it is appropriate to consider the cod stock over a somewhat longer time

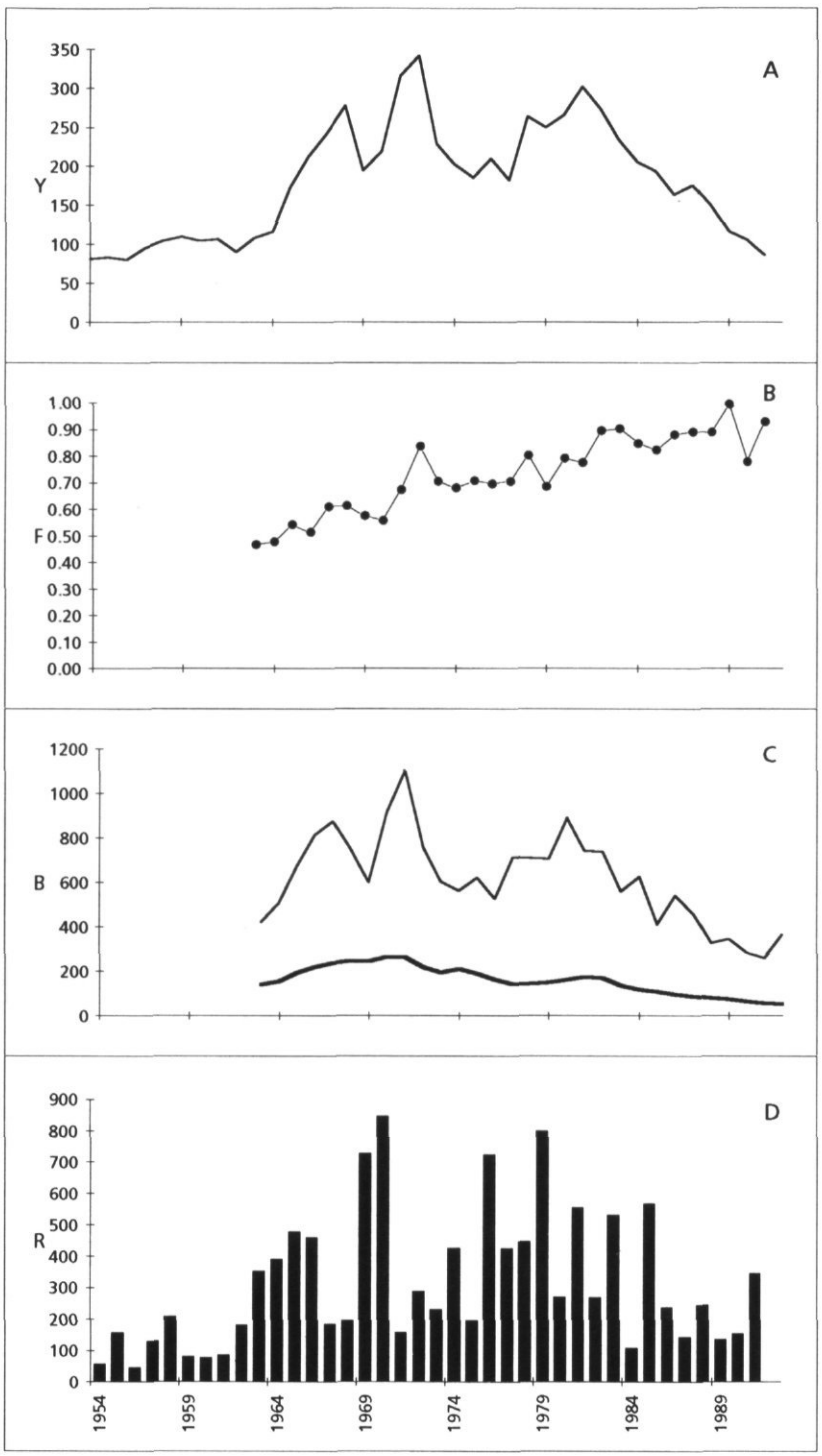


Figure 1. Summary of annual assessment parameters for North Sea cod, 1963–1991 (from ICES, 1993b). A. Yield (Y in '000 tonnes). B. Fishing mortality rate (F). C. Total stock (upper line) and spawning-stock (lower line) biomasses (B in '000 tonnes). D. Recruitment (R in millions at age 1).

scale. However, backward extension of the assessment is hampered by a lack of detailed information on catch composition. Daan (1978) reviewed the available historic data and tried to compare population parameters during different periods. Although in the subsequent 15 years much new information has been collected (e.g., Rijnsdorp *et al.*, 1991), very little has been done towards developing a clearer picture of the stock during earlier years. ICES (1992) has provided estimates of fishing mortalities since 1914 based on old catch-per-unit-effort (c.p.u.e.) series, which were tuned to recent results from virtual population analysis (VPA). This method is developed further here and is used in connection with data on yield in drawing inferences about the development of stock biomass and recruitment levels throughout most of the century.

The purposes of this paper are thus: (1) to provide an overview of the changes in the cod stock, and (2) to comment on the results in relation to evidence on changes in the abiotic environment.

Methods

For the period 1963–1991, assessment data for cod (Fig. 1) are directly available from ICES (1993b). Additional estimates of year-class strength for the years 1955–1962 are based on c.p.u.e. data (Daan, 1978). Data on nominal catches (Fig. 2) are taken from ICES (1969, 1993b).

ICES (1969) also provides c.p.u.e. data series for a number of North Sea fish species, including cod. The most extensive series for cod is that of Scottish trawlers (motor and steam combined) extending over the period 1914 to 1966. In addition, English c.p.u.e. data are available for steam trawlers and motor trawlers separately. These c.p.u.e. series were used in combination with the reported annual landings of cod to estimate the total international effort (in varying units) using the following simple approach. The effort series just overlap by a few years the period after 1963 for which available catch-at-age data allow VPA to be carried out (ICES, 1993b). The fishing mortality rates by age estimated by VPA were condensed to provide an estimate of average (unweighted) fishing mortality rate (F) on ages 2 to 8 for each year (suffix y). The results from VPA in relation to those from the total effort series (E) can be used to compute an average catchability (q) for each fleet during the period of overlap (a to b) as:

$$q = \sum_{y=a}^{b} F_y \Big/ \sum_{y=a}^{b} E_y$$

The value of q is used to convert the effort series of earlier years to estimates of F. The approach outlined above for a single c.p.u.e. series sufficed for the relatively inexacting purpose of placing current levels of fishing in their historic context in ICES (1992). In the present paper a more exacting use of the results is made, and it was therefore appropriate to question the validity more closely. A validation of the estimated F values against different individual c.p.u.e. sets is given in Appendix A.

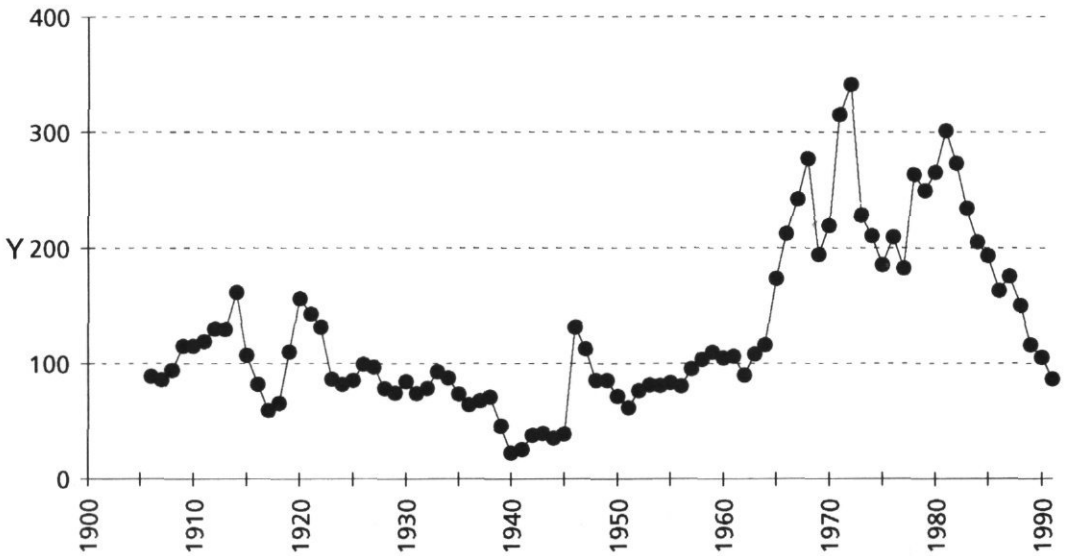


Figure 2. Nominal catches (Y in '000 tonnes) of cod in Subarea IV, 1903–1992 (ICES, 1969, 1993b).

Although the period of overlap between c.p.u.e. series and the VPA is relatively short, the estimated fishing mortalities over the entire period concur reasonably well between independent series, if allowance is made for reasonable changes in catchability for some of them. They also agree well with estimates from average catch-at-age data for the prewar period (see Appendix A). Therefore, the average values per year (Fig. 3) of the estimated Fs obtained from the individual fleets were used in the present analysis as a reliable index of the long-term trend in fishing effort.

In recent years, North Sea cod fully recruit to the fishery during the summer of their second year of life. Because it is not unlikely that age at recruitment has changed over time as a consequence of fleet changes and the introduction of mesh size and minimum landing size regulations, the total-stock biomass (TSB) of one year and older cod at 1 January from VPA has been taken as an approximation of the exploited biomass. According to the VPA, the fraction of the TSB taken each year as yield (Y) is directly related to the fishing mortality (Fig. 4). The fairly wide scatter is probably caused by the recruiting year class, because the variance appears to increase with fishing mortality. Based on an assumed linear relationship passing through zero and the centre of the cluster, the estimated TSB (TSB = 2.16 × Y/F) appears to provide a reasonable estimate of the "observed" biomass in the VPA over a wide range of biomass values (Fig. 5). Obviously, other estimators of TSB based on a more formal relationship between F and Y or on the c.p.u.e. series are possible. Appendix B provides a comparison of different estimators and the rationale for selecting the "empirical" relationship described above for estimating TSB for the years before 1963.

Recruitment may be estimated from the yield using appropriate values of the yield per recruit (Y/R) for the estimated F-level. However, estimates for individual years are not very reliable, because the Y/R concept applies to an equilibrium situation. In Figure 6, the average yield divided by the average recruitment per five-year period is given by black dots from 1955 onwards, for which annual recruitment estimates are available. This can also be regarded as an "empirical" relationship. Because of uncertainties about changes in exploitation pattern over time and because the exploitation pattern estimated for recent years is biased anyway, due to the fact that discards are not included in the assessment, we prefer to use an empirical relationship rather than the values calculated from a formal Y/R model. Given that F_{max} should be somewhere in the order of 0.2 (cf. ICES, 1992), a rough curve can be drawn from which the appropriate Y/R values for previous periods can be read (circles). In this case, only two values must be considered as representing extrapolations. The others are interpolations, suggesting that the possible bias is limited.

Estimating the SSB is more problematic. Not only is there one data point less than in the Y/R curve, but also the extrapolation in this case follows an exponential curve. Consequently, any estimates for the lower exploitation levels must be regarded as fairly uncertain. However, there are some boundary conditions: (1) SSB can never be higher than total biomass and (2) SSB must

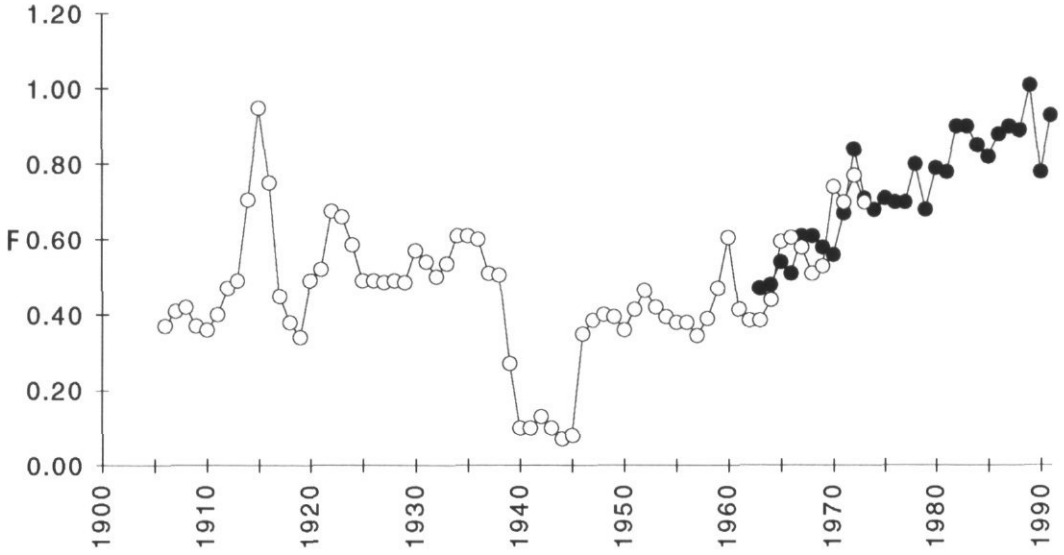


Figure 3. Estimated fishing mortality rate (F), 1906–1991. Dots represent VPA estimates, circles averages based on c.p.u.e. in Scottish and English fleets.

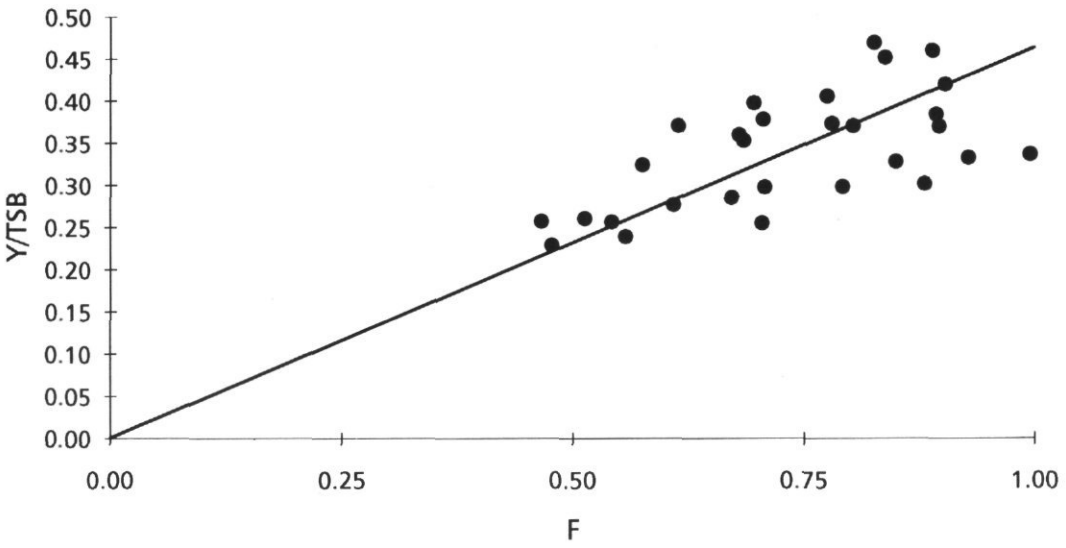


Figure 4. Relationship between yield over total stock biomass ratio (Y/TSB) and fishing mortality rate (F), 1963–1991.

represent an increasing proportion of the total biomass with decreasing fishing mortalities. The latter would only be true if there are no strong density dependent effects in the adult phase. This is supported by available data for North Sea cod, which do not indicate that variability in reproductive parameters is related to population density (Rijnsdorp *et al.*, 1991). Based on SSB/R values of 2 kg at an F of 0.3 and a value of 6 kg at an F of 0.1 (ICES, 1993a), we used the relationship provided in Figure 7 as a reasonable approximation for estimating SSB from average recruitment.

In view of the fact that the estimated population parameters are heavily dependent on a limited source, which is probably characterized by a high variance, and because both Y/R and SSB/R are based on equilibrium situations, the calculations were carried through for each five-year period rather than for individual years.

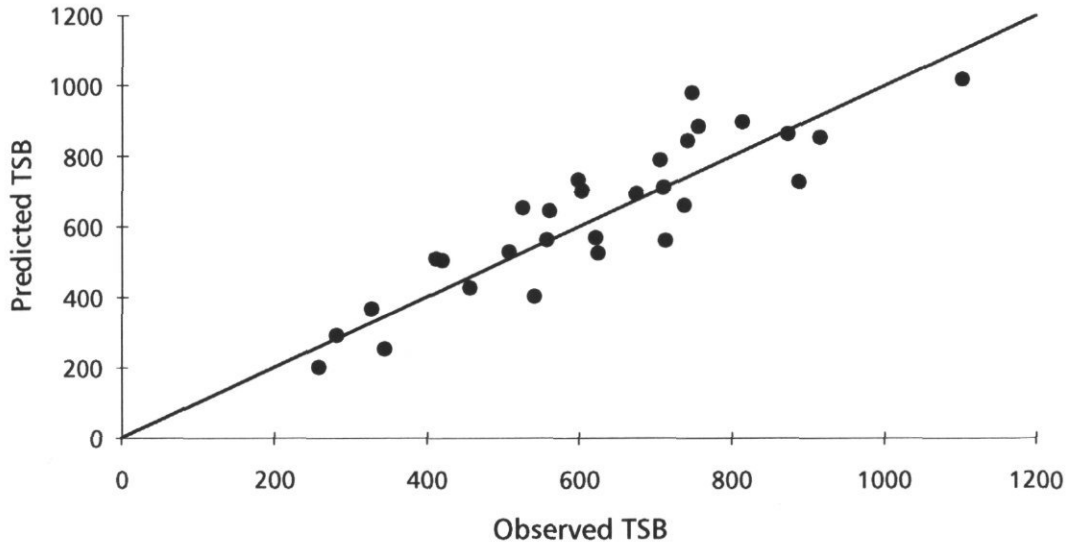


Figure 5. Predicted versus observed spawning-stock biomass (TSB in '000 tonnes) 1963–1991 based on the relationship in Figure 3.

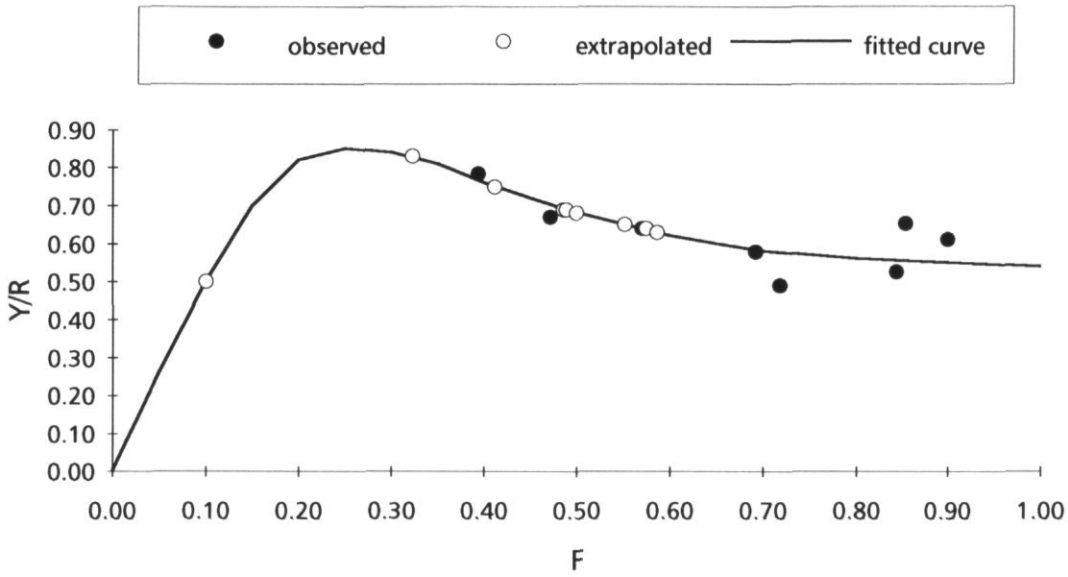


Figure 6. Yield per recruit (Y/R in kg) vs fishing mortality (F) curve used (fitted by eye, see text).

Results

The integrated picture (Fig. 1) emerging from the VPA for recent years (ICES, 1993b) exhibits a strongly dome-shaped landings curve (Fig. 1A), a steadily increasing fishing mortality (Fig. 1B), an increase in recruitment in the 1960s followed by a reduction in recruitment in the late 1980s (Fig. 1D), and a steady decline in SSB after a peak value in the early 1970s (Fig. 1C). Recent recruitment is still higher than in the 1950s, but SSB has dropped significantly below the 1963 value, representing the situation before recruitment increased.

Figure 8A–D provides results for the entire century in five-year periods. The yield (Fig. 8A) reflects a gradually decreasing trend in the prewar years, reaching an

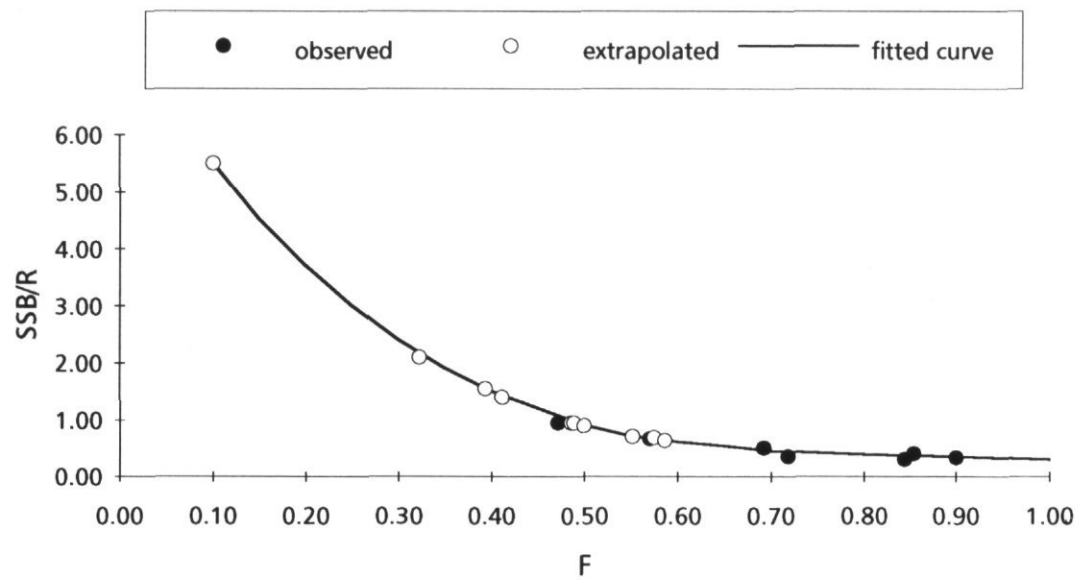


Figure 7. Spawning-stock biomass per recruit (SSB/R in kg) vs fishing mortality (F) curve used (fitted by eye, see text).

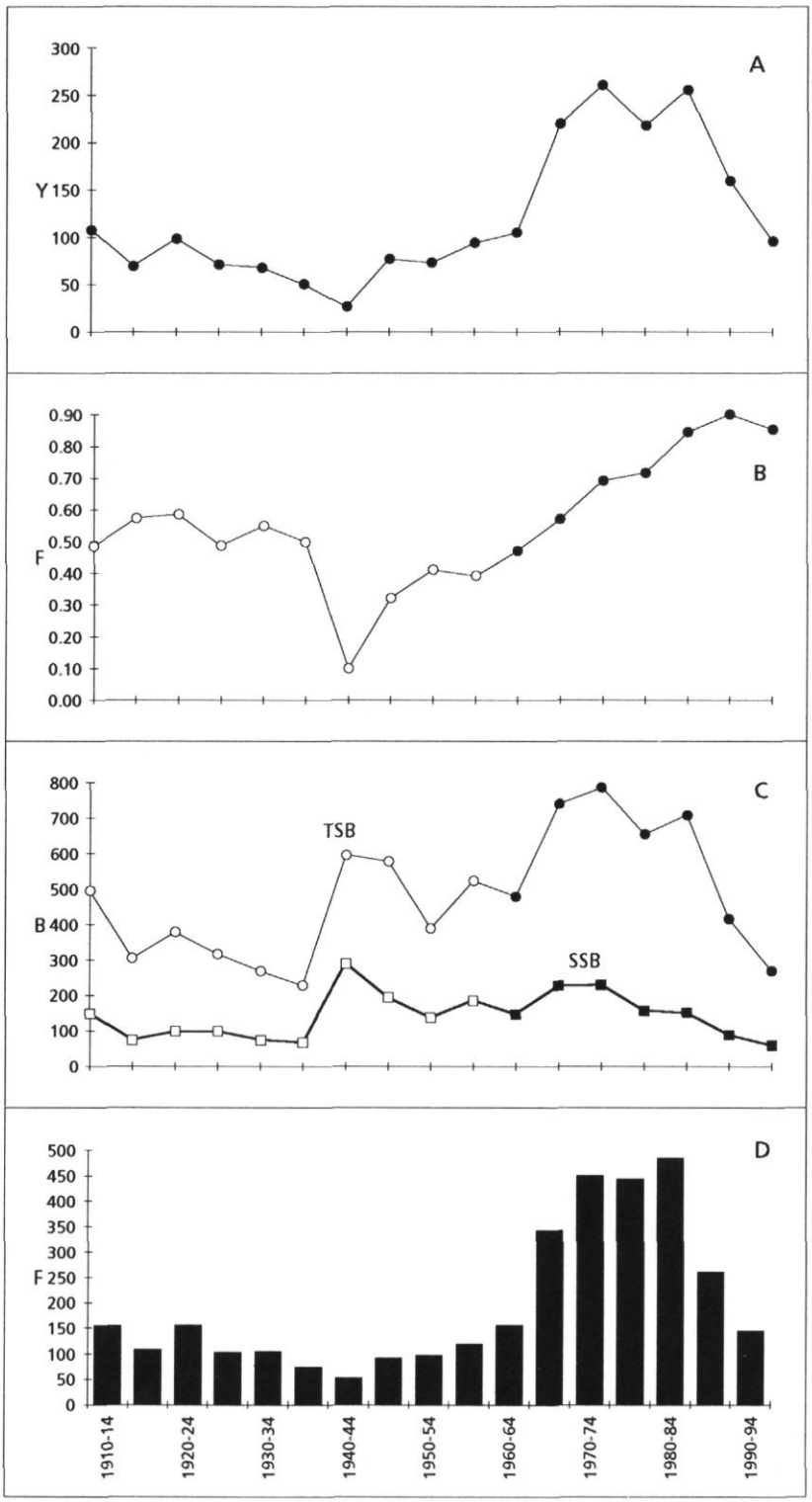


Figure 8. Summary of 5-yearly assessment parameters for the period 1914–1990. A. Yield (Y in '000 tonnes). B. Fishing mortality rate (F); dots represent VPA estimates, circles based on c.p.u.e. analysis. C. Total-stock (upper line) and spawning-stock (lower line) biomass (B in '000 tonnes); dots represent VPA estimates, open symbols based on c.p.u.e. analysis. D. Recruitment (R in millions at age 1).

all-time low during World War II with the cessation of fishing. After the war, yield increased fairly steadily up to 1965, when there was a sharp increase associated with the gadoid outburst. In recent years, yield has declined to a level comparable to the postwar years. The estimated fishing mortality (Fig. 8B) exhibits quite a different pattern. Exploitation during the prewar period was relatively high compared to the postwar years. After the marked drop during the war, fishing mortality built up slowly but very consistently to the late 1980s. The analysis indicates that average recruitment per five-year period was very stable (Fig. 8D) up to 1965, followed by a threefold increase in the 1970s. Although recruitment has dropped significantly in recent years, in an historic perspective it is still at the same level as it was during the early part of the century. The total biomass (Fig. 8C) has fluctuated markedly over the period. The biomass dropped gradually from the beginning of the century until World War II. Even though recruitment is estimated to have been low during the war, the biomass increased sharply, which can only be explained by improved survival as a result of the marked reduction in fishing activity. After the war the biomass remained at a relatively high level, but did not profit nearly as much as the catch from the increased recruitment, as a consequence of the steadily increasing fishing mortality. Since 1985, biomass has dropped to almost the lowest prewar level. Finally, the SSB (Fig. 8C) follows essentially the same trend as the TSB, but at a lower level. The increased recruitment has barely affected the spawning stock. Apparently, the cod did not mature during the 1970s because of the extremely high fishing mortalities. The recent SSB value appears to be the lowest on record.

Discussion

There is of course considerable uncertainty about the true values of the various population parameters over time owing to the data limitations and the rough nature of the assessment carried out. It is understood that the results cannot be interpreted in terms of confidence limits. In the future, more work has to be done to quantify the possible range of the various estimates based on border conditions for some of the relationships involved. This would make the interpretation of the long-term trends more reliable than the point estimates given here. Nevertheless, in a qualitative sense the assessment highlights significant changes in the population parameters and a consistent picture appears to emerge of the history of the North Sea cod stock in relation to fishing activity.

The most reliable source of information underlying this assessment is undoubtedly the landings statistics. All countries around the North Sea have gone to great lengths to provide reliable catch statistics, at least up to the 1980s. Since the introduction of the Common Fisheries Policy of the European Union, which relies heavily on a TAC management scheme, this source of information has deteriorated, as is evident from the unallocated landings used in various assessments (ICES, 1993a). This may have led to bias, particularly when extrapolating established relationships from the recent period backwards in time. The second most important source of information is the estimated fishing mortality for the entire period. The values are based on different sets of c.p.u.e. data, but data from independent fleets gave essentially the same results (Appendix A). The trend in fishing mortality shown must therefore be considered fairly reliable.

Data on yield on the one hand and on fishing mortality on the other impose clear constraints on the biomass and recruitment levels that might have existed. Essentially, the approach followed here is quite different from the existing age structured population models and can be considered as "empirical" rather than formal. The problem is that the existing formal models of for example the relationship between yield, biomass, and fishing mortality appear to be inadequate when the parameters are averaged over age groups and exhibit a bias when applied to the data from which they were estimated (see Appendix B). In a way, the results from this empirical approach can be interpreted as representing logical deductions from our detailed knowledge about the recent interactions between the cod fishery and the cod stock when applied to the limited information available for earlier years. Only if there is a severe bias in the recent assessment, in the long-term catch data, or in the c.p.u.e. data, is the emerging picture likely to change significantly.

Thus, even though the type of assessment presented might be considerably improved by incorporating confidence limits for the "empirical" relationship based on a thorough statistical analysis, it would seem unlikely that this would affect the basic trends observed.

The outstanding feature in the North Sea cod stock appears to be the recruitment explosion in the 1960s. This inference has been made previously (Daan, 1978), but the present analysis provides a much firmer basis for evaluating the significance of this feature over a longer time scale. In an historic perspective, the higher recruitment has had only a minor effect on the TSB and much less, for instance, than the cessation of fishing during World War II. Nevertheless, the net effect must certainly have been that biomass remained relatively high even at extremely high levels of fishing mortality.

Figure 9 provides a plot of recruitment against SSB based on the two analyses available. The VPA estimates for individual years since 1963 have led to the argument

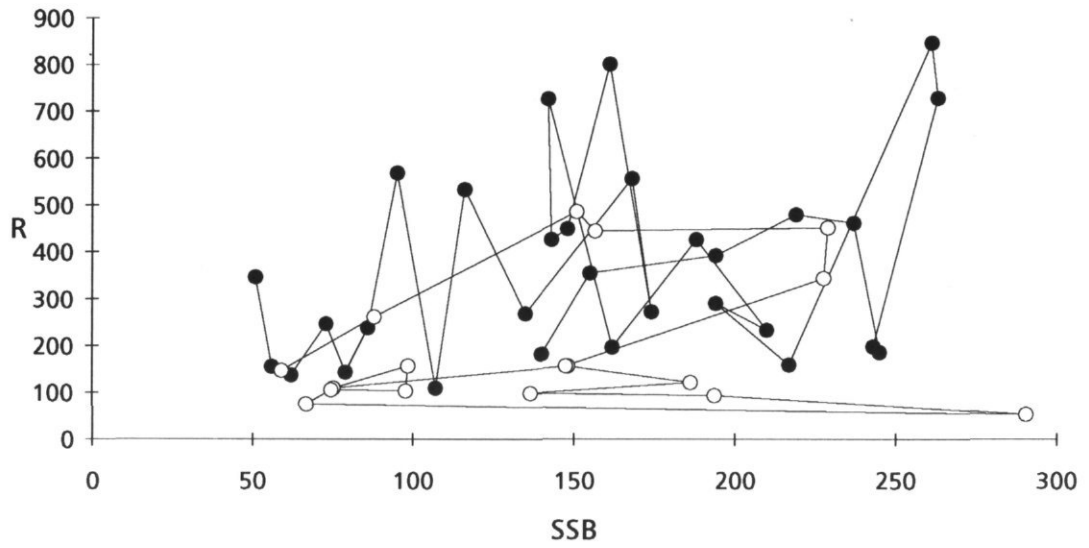


Figure 9. Stock recruitment relationship for cod (R in millions at age 1; SSB in '000 tonnes). Open circles represent the 5-year means given in this paper. Black dots are for individual years (from ICES, 1993b).

that the cod stock is at present recruitment overfished, and that SSB should be increased above the Minimum Biologically Acceptable Level (ICES, 1993a) of 150 000 t in order to ensure average recruitment. Based on this detailed analytical assessment, this conclusion would seem justified. However, a different picture emerges when the relationship based on five-year averages over a much longer time span is considered. In this case, the stock–recruitment relationship shows clearly that overall on an historic basis such a conclusion would hardly be justified. Average recruitment has always been very much lower than in the years after 1963, independent of whether the stock was below 100 000 t or above. This does not necessarily mean that there is no stock–recruitment relationship involved, because it may well be that the relationship has changed. In any case, consistently more juvenile cod have been surviving in recent years at the same level of SSB as previously. One might conclude that the 'carrying capacity' for young cod appears to have changed.

Whether the reduced recruitment in recent years represents a sign of recruitment overfishing or marks a reversal of the carrying capacity to the level observed before the 1960s is open to debate. However, this may not be the important issue, because if recruitment were to return to the original level, the SSB associated with the present level of exploitation would be bound to drop far below any historically observed level. This would obviously still introduce serious risks of recruitment overfishing. Therefore, the clear message from this picture, in combination with Figure 8, is that the present level of exploitation of the cod stock is above any level which can be considered biologically or scientifically safe. Strong protection measures are required, if not to maintain a viable cod population in the North Sea then at least to maintain a viable cod fishery.

Daan (1978) did not find any evidence of significant changes in the growth of North Sea cod since prewar years, although the maturity ogive had shifted to smaller sizes for both sexes. Since stock biomass has increased according to the assessment given here, this phenomenon cannot be explained by density dependent processes. Figures 8 and 9 indicate how unlikely it is that the difference in recruitment level is caused by density-dependent processes in the juvenile or adult phase, because there is no corresponding signal in the SSB.

Since the sudden jump in recruitment cannot be related to events within the cod stock itself, the cause must be sought in an environment factor resulting in improved survival during the first year of life. Whether this change is caused more by natural (hydrographic) changes (Cushing, 1984) than by anthropogenic changes in the North Sea ecosystem, either environmental (e.g., climate change, eutrophication) or in response to overexploitation of the entire system (Andersen and Ursin, 1978), has not yet been resolved (Hempel, 1978). However, in our view the prolonged period of increased recruitment must point to some marked and consistent change in the environment.

So far, the signal for such a marked change has not yet shown up in any of the available meteorological or hydrographical data sets. Brander (1992) re-examined

Cushing's (1984) hypothesis that cod recruitment was related to changes in timing and peak occurrence of *Calanus finmarchicus*, but concluded that the Continuous Plankton Recorder data do not reveal marked trends in the latter which correlate with cod recruitment. A salinity anomaly in the North Atlantic hit the North Sea in the early 1970s (Dickson *et al.*, 1988), but this anomaly occurred after cod recruitment had already increased, and lasted for some five or six years only.

The total collapse of the pelagic stocks of herring and mackerel in the late 1960s which was caused by overexploitation (Burd, 1978; Hamre, 1978), coincided roughly with the gadoid outburst. The herring stock started to rebuild in the early 1980s, after a period of recruitment failure which has been attributed to the salinity anomaly (Corten, 1986). The North Sea mackerel stock, once in the order of 2 million tonnes, has never recovered from its collapse and is still at an extremely low level (ICES, 1993c). However, the main feeding and overwintering areas of the stock of Western mackerel have shifted to the northern North Sea during the 1980s (ICES, 1990). Therefore, in practice the biomass of herring and mackerel exploiting the North Sea is probably not dissimilar to the situation that existed before the 1960s. Without underestimating the impact of overexploitation of the cod stock, the recent decrease in cod recruitment might signify the end of a period when the North Sea ecosystem has been dominated by demersal species. Although eggs of cod have been reported from herring stomachs (Daan *et al.*, 1985) and mackerel feeds on 0-group gadoids (Mehl and Westgård, 1983), the quantitative extent of the interactions during the early life phase is still largely unknown. Yet, in our view the overexploitation of the pelagic system cannot be discounted as a major causal factor in relation to the gadoid outburst, even if this hypothesis may be very difficult to prove.

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Appendix A

Validation of fishing mortality on North Sea cod prior to 1963

ICES (1969) provides c.p.u.e. data for the Scottish fleet (1914–1966), a somewhat shorter c.p.u.e. series for English steam trawlers (1924–1938; 1946–1966), and a short series for English motor trawlers (1958–1966). The basic data are copied in Table A.1. As noted by ICES (1969), the results for the English steam trawlers are unreliable for the last few years, because the catch rates were based on the last few steam trawlers working the North Sea from English ports. Unfortunately, these are the years that overlap in time with the VPA results and this precludes using them in a similar fashion to that adopted for the Scottish data. However, the English motor trawler time series can be used. Moreover, this series can be expanded to span the years 1924 to 1938 and from 1946 to 1972 using results published in the MAFF Sea Fisheries Statistical Tables and their appendices (MAFF, 1924 through 1973).

Table A.1. C.p.u.e. series for Scottish steam + motor trawlers, English steam trawlers, English motor trawlers, and English first-class steam trawlers with the corresponding estimates of fishing mortality. The annual efficiency increase applied in each series is indicated.

	Total VPA, Int. av. 2–8		q = 1 Scottish steam + motor trawlers		q = 1.02 English steam trawlers		q = 1.04 English motor trawlers		q = 1.02 English 1st class		Comp. English	Comp. English + Scottish
Year	Catch	F	C.p.u.e.	F	C.p.u.e.	F	C.p.u.e	F	C.p.u.e.	F	av. F	av. F
1906	88.7								35	0.37	0.37	0.37
1907	85.5								31	0.41	0.41	0.41
1908	94.0								34	0.42	0.42	0.42
1909	114.7								48	0.37	0.37	0.37
1910	114.9								50	0.36	0.36	0.36
1911	119.0								48	0.40	0.40	0.40
1912	129.6								45	0.47	0.47	0.47
1913	129.2								44	0.49	0.49	0.49
1914	161.4		47.0	0.80					45	0.61	0.61	0.71
1915	106.8		26.4	0.95								0.95
1916	81.6		25.5	0.75								0.75
1917	59.1		31.0	0.45								0.45
1918	65.2		40.4	0.38								0.38
1919	109.7		91.7	0.28					52	0.40	0.40	0.34
1920	155.8		86.8	0.42					53	0.56	0.56	0.49
1921	142.7		68.4	0.49					51	0.55	0.55	0.52
1922	131.3		45.2	0.68					39	0.67	0.67	0.68
1923	86.4		32.7	0.62					25	0.70	0.70	0.66
1924	81.7		35.5	0.54	20.6	0.63	0.3		26	0.65	0.63	0.59
1925	85.3		43.9	0.45	26.2	0.53	0.6		35	0.52	0.53	0.49
1926	99.1		49.0	0.47	32.1	0.51	1.8		42	0.51	0.51	0.49
1927	96.8		50.8	0.45	31.0	0.52	0.4		42	0.51	0.52	0.49
1928	78.5		41.4	0.44	24.8	0.54	0.6		32	0.55	0.54	0.49
1929	74.6		37.2	0.47	26.1	0.50	0.9		34	0.50	0.50	0.49
1930	84.4		31.4	0.63	29.4	0.51	1.0		39	0.50	0.51	0.57
1931	73.9		32.2	0.54	24.7	0.54	0.9				0.54	0.54
1932	78.3		36.0	0.51	29.8	0.49	1.8				0.49	0.50
1933	92.7		36.4	0.60	37.4	0.47	1.9	2.06			0.47	0.54
1934	87.0		31.1	0.65	29.2	0.57	3.2	1.19			0.57	0.61
1935	73.5		28.0	0.61	23.6	0.61	4.7	0.75			0.61	0.61
1936	64.0		25.9	0.58	20.8	0.62	5.5	0.55			0.62	0.60
1937	67.4		35.8	0.44	23.9	0.68	5.5	0.60			0.58	0.51
1938	71.1		35.9	0.46	27.0	0.55	9.0	0.40			0.55	0.51
1939	45.5		40.0	0.27								0.27
1940	22.7		51.0	0.10								0.10
1941	25.4		60.9	0.10								0.10
1942	37.7		69.2	0.13								0.13
1943	39.3		96.4	0.10								0.10
1944	35.5		120.6	0.07								0.07
1945	38.9		119.0	0.08								0.08
1946	131.1		122.5	0.25	108.2	0.30	15.1	0.60			0.45	0.35
1947	112.4		70.9	0.37	71.7	0.39	20.2	0.40			0.40	0.39
1948	85.0		45.8	0.43	62.6	0.35	16.0	0.40			0.37	0.40
1949	85.4		48.5	0.41	57.0	0.39	17.6	0.38			0.38	0.40
1950	71.5		55.4	0.30	51.3	0.37	12.2	0.48			0.42	0.36
1951	61.4		42.2	0.34	48.9	0.34	8.0	0.65			0.49	0.42
1952	76.4		49.2	0.36	48.9	0.43	9.5	0.71			0.57	0.47
1953	81.1		62.2	0.31	47.1	0.48	12.7	0.58			0.53	0.42
1954	80.6		61.1	0.31	46.4	0.50	16.6	0.46			0.48	0.40
1955	83.5		60.0	0.33	55.7	0.44	19.2	0.43			0.43	0.38
1956	80.3		54.1	0.35	56.8	0.42	20.8	0.40			0.41	0.38
1957	95.0		71.3	0.31	63.1	0.46	33.1	0.31			0.38	0.35
1958	103.7		66.7	0.36	63.6	0.51	34.3	0.34			0.42	0.39
1959	109.5		64.5	0.40	46.7	0.74	38.0	0.33			0.54	0.47
1960	104.4		55.3	0.44	27.2	1.24	42.3	0.30			0.77	0.61
1961	105.8		50.5	0.49	53.0	0.66	39.1	0.34			0.34	0.42
1962	89.6		54.7	0.38	94.6	0.32	29.8	0.39			0.39	0.39

(*continued overleaf*)

Table A.1. (continued)

	Total VPA, Int. av. 2–8		q = 1 Scottish steam + motor trawlers		q = 1.02 English steam trawlers		q = 1.04 English motor trawlers		q = 1.02 English 1st class		Comp. English	Comp. English + Scottish
Year	Catch	F	C.p.u.e.	F	C.p.u.e.	F	C.p.u.e	F	C.p.u.e.	F	av. F	av. F
1963	108	0.47	81.3	0.31			31.8	0.46			0.46	0.39
1964	116	0.48	78.4	0.35			31.0	0.53			0.53	0.44
1965	173	0.54	63.3	0.64	178.2	0.35	46.5	0.55			0.55	0.60
1966	212	0.51	70.7	0.70	516.0	0.15	44.3	0.51			0.51	0.61
1967	242	0.61			225.2		66.1	0.58			0.58	0.58
1968	277	0.61			97.6		89.9	0.51			0.51	0.51
1969	194	0.58					63.5	0.53			0.53	0.53
1970	219	0.56					52.8	0.74			0.74	0.74
1971	315	0.67					83.1	0.70			0.70	0.70
1972	341	0.84			627.2		86.1	0.77			0.77	0.77
1973	228	0.71			413.0		65.6	0.70			0.70	0.70
1974	210	0.68										
1975	185	0.71										
1976	209	0.70										
1977	182	0.70										
1978	263	0.80										
1979	249	0.68										
1980	265	0.79										
1981	301	0.78										
1982	273	0.90										
1983	234	0.90										
1984	205	0.85										
1985	193	0.82										
1986	163	0.88										
1987	175	0.90										
1988	150	0.89										
1989	116	1.01										
1990	105	0.78										
1991	86	0.93										

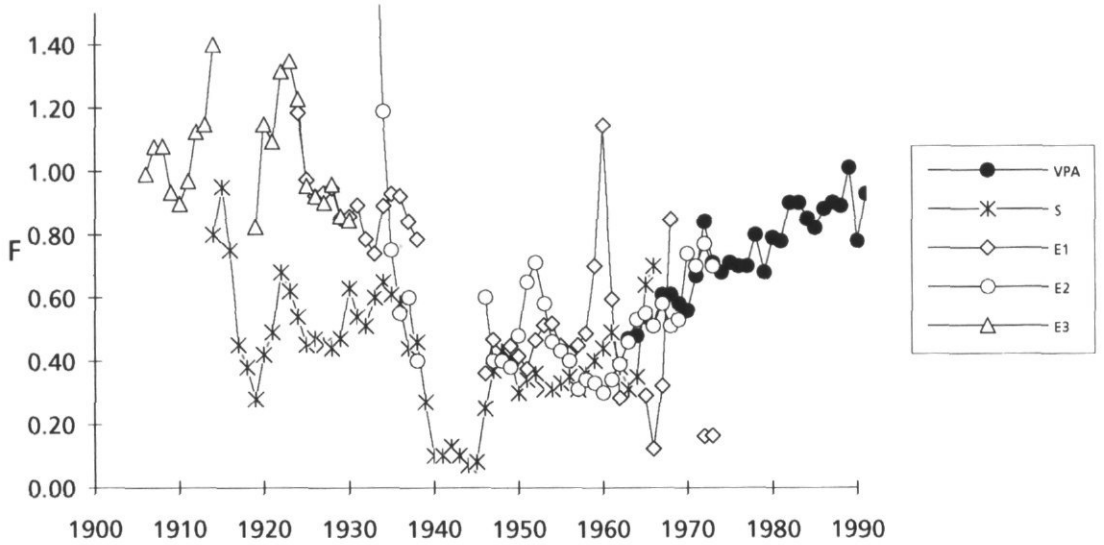


Figure A.1. Estimates of average fishing mortality rate (age 2–8) based on c.p.u.e. data from various fleets (S = Scottish steam + motor trawlers; E1 = English steam trawlers; E2 = English motor trawlers; E3 = English first-class steam trawlers) in comparison with VPA estimates.

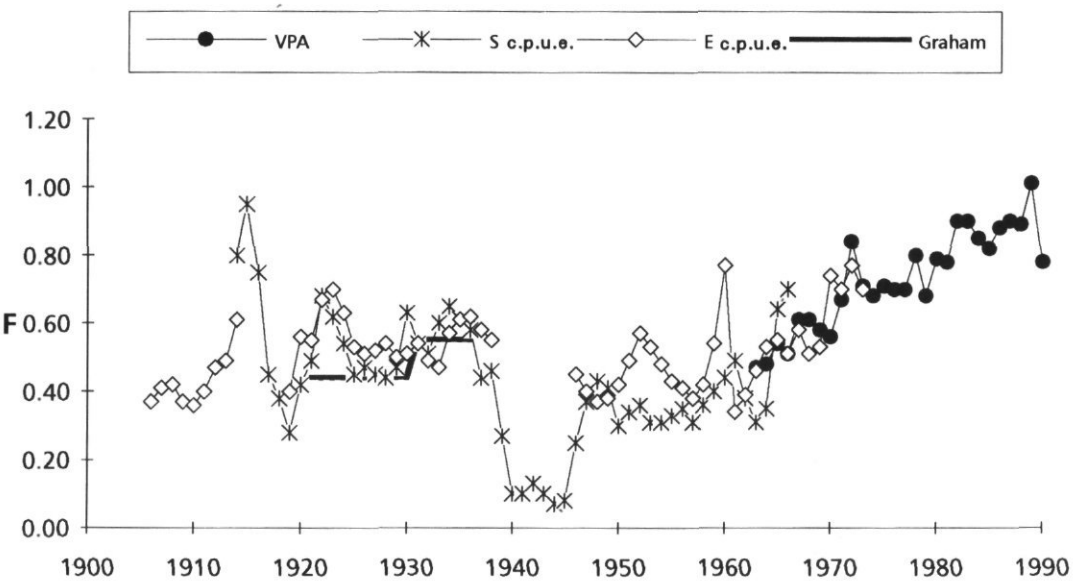


Figure A.2. Estimates of average fishing mortality (age 2–8) based on c.p.u.e. data from the Scottish and English fleets in comparison with VPA estimates and estimates based on Graham (1938). The estimates for the Scottish fleet are not corrected for increases in efficiency. The estimates for the English fleet represent a composite estimate based on a 2% annual increase in efficiency for steam trawlers and a 4% increase for motor trawlers.

The longer period of overlap provided by the total international effort based on English motor trawler days' absence with the VPA results enables the assumption of constant catchability to be questioned for this effort index. Regression of the logarithm of the annual catchability on time for the years 1963 to 1973 gave a R^2 value of 0.54 ($df = 9$; $p < 0.01$). The slope indicates that during this period the efficiency of this fleet increased by 4% per year. This efficiency factor was then applied to the total effort estimates for the years 1924 to 1973. With the corrected effort data, the average q and corresponding F were then calculated, using the same approach as described in the main paper, but now based on the years 1963 to 1973.

The F estimates for the years since World War II correspond fairly closely with the F series based on Scottish data, but in the pre-war period the English series rapidly reach unbelievably high values (higher than in the most recent years) as they go back in time (Fig. A.1).

The English motor trawler estimates of F were now used to estimate a value of q for the total international effort, based on English steam trawler c.p.u.e., since the results for this fleet appeared less variable in these series. The F estimates after conversion of the rest of the effort series are also shown in Figure A.1.

It is possible to extend the F series still further back in time, using the catch rates for English first-class steam trawlers, given in Graham (1934; Table 43). His data span the years 1906 to 1914 and 1919 to 1930. A similar procedure was applied now based on English steam trawlers for the years 1924 to 1930 and the results are given in Figure A.1.

The three series of F estimates based on the different English c.p.u.e. series are all calibrated against each other but independently of the Scottish series. This allows a proper comparison to be made. It is clear from Figure A.1 that F estimates based on the Scottish series are more coherent than those based on the English series. Moreover, the extremely high pre-war values justify a suspicion that the English series are biased upwards.

It is possible to reconcile the English steam trawler-based F with the Scottish trawler-based series by giving the former an annual efficiency increase factor of 2%. In addition, the F results based on the English series (with steam and first-class steam trawlers being modified by an annual 2% efficiency change) can be simplified by forming a composite series from the three sets. This set (Figure A.2) is based on first-class steam trawlers (1906–1914; 1919–1924), steam trawlers (1924–1938), the average of steam and motor trawler-based F values (1946–1960), and motor trawlers (1961–1973).

The use of efficiency changes to reconcile the Scottish and English series begs the question of which series, if any, is correct. It seems likely that efficiency changes resulting from new technology and increased knowledge are positive. Therefore, the English fleets would be expected to show increasing efficiency, resulting in overestimates of F in earlier years. The Scottish trawl c.p.u.e., however, is a composite of steam trawler and motor trawler catch rates. At least for the English fleets, the latter, being of smaller size, have lower c.p.u.e. It seems therefore possible that a progressive move to the use of motor trawlers in the Scottish fleet might have offset or even reversed any tendency for catchability to rise due to increased efficiency. Thus the F results for the Scottish fleet might be either too high or too low in earlier years. To decide which, if either, series is more correct thus requires some independent evidence of the value of F in the past.

To provide this independent evidence, a new analysis is made of data on numbers by age group, caught per day by Grimsby steam trawlers (Graham, 1938; Table III). These were used to provide estimates of total mortality rate at age for the periods 1921 to 1930 and 1931 to 1936. Estimates of F at age were obtained by subtracting the earliest available (1963–1967) esti-

mates of predation mortality at age on cod (Pope and Macer, 1991) and the 0.2 level of "other" natural mortality, from the total mortality rate. The average Fs over the age range 2 to 6 obtained from this exercise were 0.44 for the period 1921–1930 and 0.55 for 1931–1936. These values compare closely with the F estimated for the same years using the Scottish c.p.u.e. series and the corrected English steam trawler series (Fig. A.2). We conclude, therefore, that although either of these series might be used with reasonable confidence to provide estimates of F for years before 1963, it is appropriate to use the average of the two for further analysis.

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Appendix B

Comparison of different estimates of total stock biomass

The formal relationship between catch in numbers in a particular year (C), number of fish in the population at the beginning of the year (N), and fishing mortality (F) and total mortality (Z) is given by:

$$C = \frac{F}{Z} N(1 - e^{-Z})$$

Disregarding growth, one might postulate a similar model for yield (Y) in relation to biomass (B):

$$Y = \frac{F}{Z} B(1 - e^{-Z})$$

Since yield and fishing mortality are known for each year, this allows the biomass to be estimated, assuming $Z = F + M$ and a natural mortality rate (M) of 0.2.

Another estimator of the biomass is given by the c.p.u.e. series, tuned against the total-stock biomass (TSB) values from

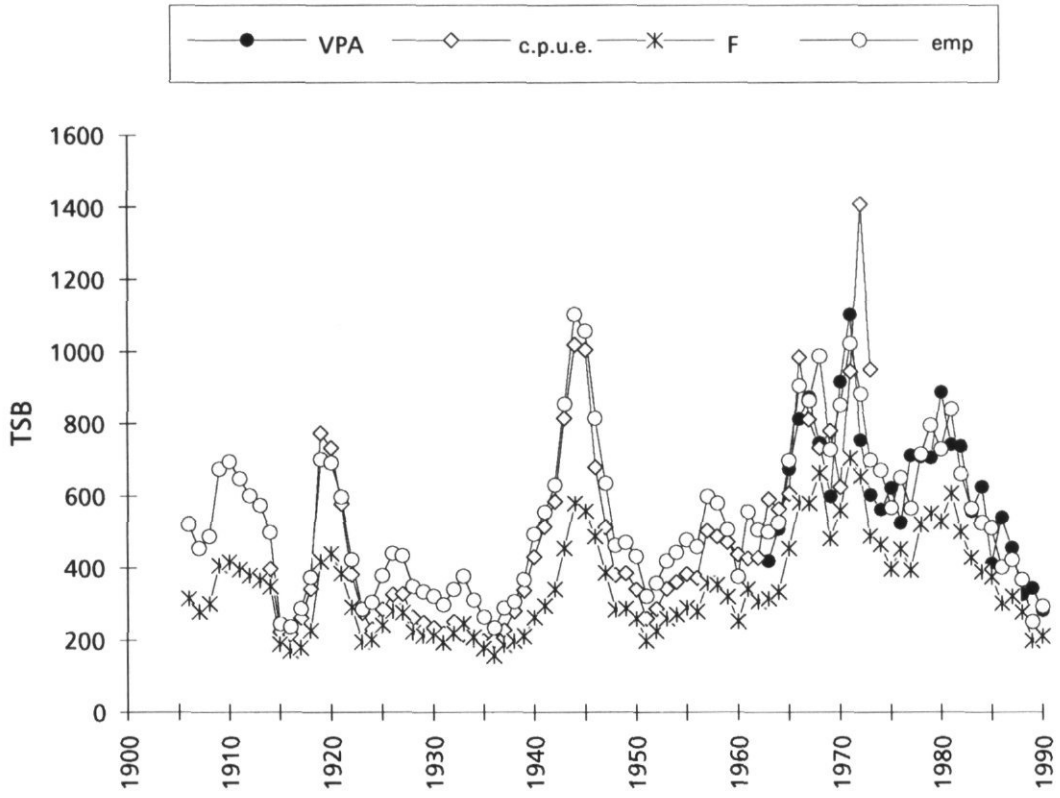


Figure B.1. Comparison of three estimators of total-stock biomass (c.p.u.e. = based on average Scottish and English series; F = formal model; emp = empirical model; see Appendix B) with VPA estimates.

VPA for the period of overlap. The English first-class steam trawlers were excluded because they have no period of overlap with VPA estimates. We thus obtain independent estimates from three fleets. Ideally, a composite estimator should be weighted by the relative catches taken by each fleet, but since these data were lacking TSB was estimated as a straight average of the values obtained from the Scottish and English c.p.u.e. series, where the English data were corrected for a change in efficiency (c.f. Appendix A).

Lastly, we used the "empirical" relationship between F and TSB for the years for which VPA data were available, described in the main body of the paper: $TSB = 2.16 \times Y/F$.

Figure B.1 shows a comparison of the three series in combination with the VPA estimates. For the recent VPA years, the formal relationship appears to underestimate the TSB rather consistently by ca. 30%. The reason for this is probably that (1) growth during the year is not taken into account and (2) the average fishing mortality over 2–8 years old and weighted by numbers gives relatively too much weight to younger age groups when applied to biomass.

The "empirical" TSB estimates agree, of course, much better with the VPA data, because they were tuned directly against these. Moreover, they also agree closely with the c.p.u.e. estimates, although the latter appear to be somewhat lower during the pre-war years. Although the differences between the two appear to be marginal, we have chosen to use the "empirical" model above the average c.p.u.e. data, because (1) a bias may be expected in the latter due to the fact that the estimates could not be weighted by the relative catches of each fleet, and (2) the c.p.u.e. estimates extended backwards only to 1914.

ICES mar. Sci. Symp., 198: 244–253. 1994

Cod distribution and temperature in the North Sea

Henk Heessen and Niels Daan

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Survey data on the distribution of individual age groups of cod in the North Sea exhibit marked annual differences in the ambient temperature. There is no indication that these differences are related to a certain preferred temperature, not at least for the juveniles. Juvenile cod are exposed to the highest water temperatures in late summer and autumn, and the lowest temperatures in winter. This analysis may provide a better basis for the study of annual growth differences and the effect of temperature on digestion rates.

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Introduction

One approach to the cod and climate problem is provided by the behaviour of the cod population in relation to annual variations in water temperature, with particular reference to distribution patterns. Mountain and Murawski (1992), for example, attributed changes in the distribution of several fish species on the northeast continental shelf of the USA to changes in temperature. In the North Sea, young herring surveys were initiated in February 1965, which have evolved over the years to highly standardized and internationally coordinated surveys (now called International Bottom Trawl Surveys, IBTS), aimed at estimating the year-class strength of a variety of species, including cod. Although preliminary analyses of the effect of water temperature on the distribution of cod have been presented earlier (Buijsse and Daan, 1986; Heessen, 1993), an in-depth analysis is hampered by the fact that the hydrographical data collected during these surveys are entered in a different database at ICES than the fish data, and so far it has not been possible to link the stations properly. Analyses have therefore been limited to subsets of stations, for which temperature data have been made available on a national basis. Consequently these studies covered only some of the stations. However, upon request from the Multispecies Assessment Working Group, ICES has now made available a comprehensive data set giving the range, average, and standard deviations of the recorded temperatures in the database by statistical rectangle, quarter, and year. Although this set includes sources of information other than just the IBTS, it provides an excellent opportunity to study the relationship between the average cod catches during the surveys and the temperature regime in each year. The objective of this paper is to relate annual changes in distribution to variations in temperature.

Methods

The data available include the catches per hour fishing by age group by statistical rectangle for the IBTS in February 1977–1991. In addition to these data on the winter distribution of cod, quarterly surveys were carried out in 1981 and 1991 in connection with large-scale stomach sampling projects. During these additional surveys a variety of other gears was used, although in 1991 most of the countries involved employed the GOV trawl, which was also the standard gear for the February surveys (ICES, 1992). The catch data from the February surveys were made available through ICES; for the other surveys, data from the individual countries were sent directly to the Netherlands Institute for Fisheries Research. No corrections were made for possible differences in catchability between gears.

Although information on hydrographic parameters could be included in the exchange format for the survey data, this is not done as a matter of routine, largely because such information is stored within ICES in a

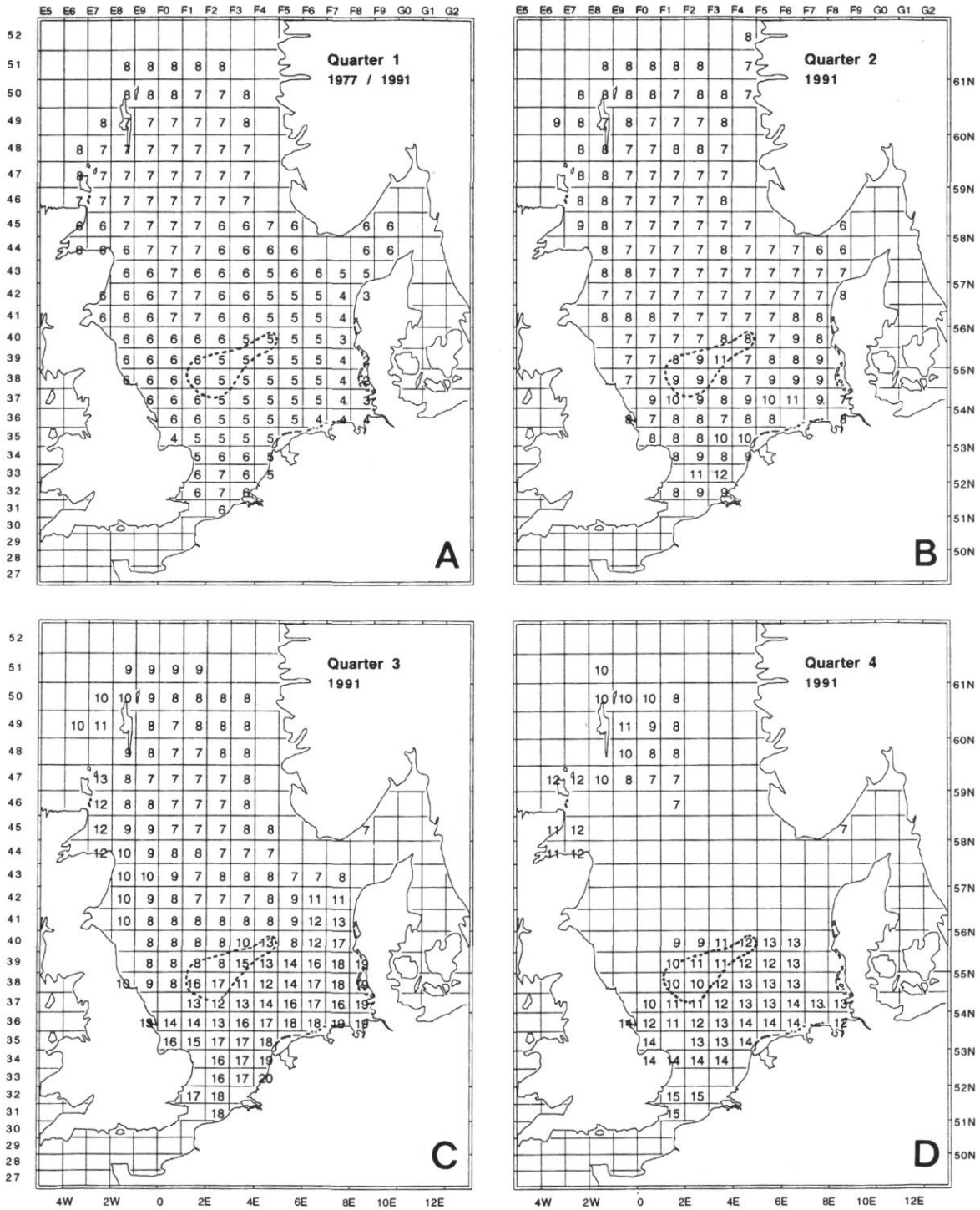


Figure 1. Quarterly distribution charts of mean bottom temperature by rectangle, based on data from the ICES Oceanographic Data Bank. The position of the Dogger Bank is indicated. A. Winter 1977–1991; B. Spring 1991; C. Summer 1991; D. Autumn 1991.

separate database. These two databases cannot be directly linked and consequently temperature information is not available for all individual hauls. However, the ICES Oceanographic Data Bank can export mean quarterly bottom temperatures by statistical rectangle with the associated ranges of observed temperatures and standard deviations. In order to meet the objective of this study, we replaced all temperature data in the IBTS database with the mean temperature data from the Oceanographic Data Bank. The winter temperature data cover almost the entire North Sea, but in other quarters there are considerable gaps, particularly for 1981 and the last quarter of 1991. In cases of missing values, we interpolated temperature data if data were available for at least two neighbouring rectangles. Nevertheless, a large component of the cod population could not be associated with the ambient temperature and therefore the results for quarters other than the first one may be unreliable.

In the subsequent analysis, the rectangles were classified in 1°C temperature bands. All observations of temperatures below 0°C were pooled in the temperature band of −1°C. Subsequently, the number of rectangles in each temperature band and the average catch-at-age per hour per temperature band were calculated. The results were analysed in two ways: as densities in relation to temperature, and as percentages of the total population, relative to the surface area covered by each temperature band.

Results

Temperature

In order to interpret the results, the quarterly temperature regime is indicated in Figure 1A–D. The data for the first quarter cover 15 years and therefore can be taken to describe the average situation fairly well. For the other quarters, only 1991 data have been used, because of the even larger gaps in the 1981 set. During the winter season (Fig. 1A), the average temperature in the northwestern North Sea is between 6 and 7°C, and the Dogger Bank marks the border of the colder waters found along the continental coast. The Shetland area, where Atlantic Water enters the North Sea, is characterized by the highest temperatures, and an inflow of slightly higher temperatures can also be observed through the Channel.

The average bottom temperature in the North Sea during winter (Fig. 2) varies between 4.5 and 7.5°C, with notably high average values during the period 1988–1990. The years 1979 and 1986 were relatively cold. For the entire North Sea, however, the temperature signal is weak.

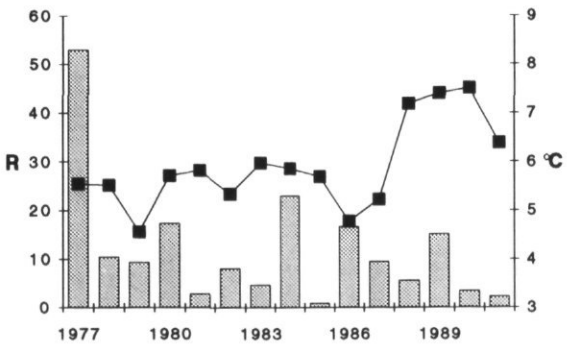


Figure 2. Indices (R) of abundance of 1-group cod (bars) and average North Sea bottom temperature in °C (squares) during winter 1977–1991.

The winter of 1991 was fairly mild and probably affected the temperatures recorded in the later seasons (shown in Figure 1B–D) compared to the average winter situation (shown in Figure 1A). The southeastern North Sea has started to warm up in the second quarter. The available data indicate major differences between neighbouring squares, which is undoubtedly caused by the fact that the ICES Oceanographic Data Bank is based not just on bottom trawl survey data but also on other sources, and the data are integrated over three months of observation. Depending on the actual date on which the data have been collected, considerable differences can be expected. In the third quarter there is a small strip of higher temperatures along the Scottish coast running southwards. Southeast of the Dogger Bank, temperatures above 10°C are recorded throughout. As far as temperature data are concerned, nothing has changed very much in the fourth quarter compared to the third. Altogether, these data imply only minor seasonal differences in temperature over a large central area north of the Dogger Bank.

Distribution

There is a marked overall age dependent relationship between cod density and temperature during the February surveys (Fig. 3). On average, the highest densities of 1-group cod are found at the lower end of the range, even below 0°C. The highest density of 2-group cod is at somewhat higher temperatures, whereas the older part of the population has its highest densities at the upper end of the temperature range. The general pattern appears to be consistent from year to year, although there are annual variations (Fig. 4). These observations are obviously strongly related to the general observations that 1- and 2-group cod are found predominantly

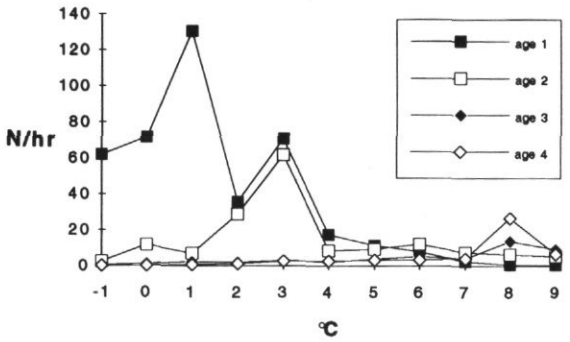


Figure 3. Average numbers-at-age of cod per hour fishing by 1°C temperature bands in February 1977–1991.

in the southeastern North Sea, particularly along the continental coast, where temperatures are lowest. It has to be borne in mind when interpreting these data that fish are not free in selecting preferred temperatures, because the temperature range depends on the severity of the winter. In addition, the distance over which cod usually migrates is restricted (Daan, 1978).

To circumvent this problem, we compared the fraction of the North Sea characterized by the different temperatures with the proportion of the population found at each temperature for the years 1977–1991 (Fig. 5). The percentage of surface area of the North Sea within each 1°C temperature band is based on the number of rectangles within that band. The percentage of the total population of each age group is given for ages 1–4+. This provides a better indication of the importance of a particular temperature in relation to the total distribution of the fish than the observed densities, because a large catch could be restricted to a single square. In that case, the particular temperature of that square would be overemphasized. Figure 5 shows that the largest fraction of 1-group cod is consistently found at the lower end of the range. To a lesser extent this is also true for 2-group fish, whereas the distribution of the older age groups is more variable. In general, however, the older age groups seem to be found towards the high side of the available temperature distribution.

These pictures can be summarized by plotting the mean ambient temperature of the population by age group in each year against the mean North Sea temperature (Fig. 6). The ambient temperature of 1-group fish is indeed consistently below the average, and to a lesser extent this appears to be true also for 2-group fish. In contrast, 3-group and 4+ cod have always been found in a slightly higher ambient temperature than the average.

Figures 7 and 8 provide similar data for all quarters in 1981 and 1991. Note that the temperature data for the

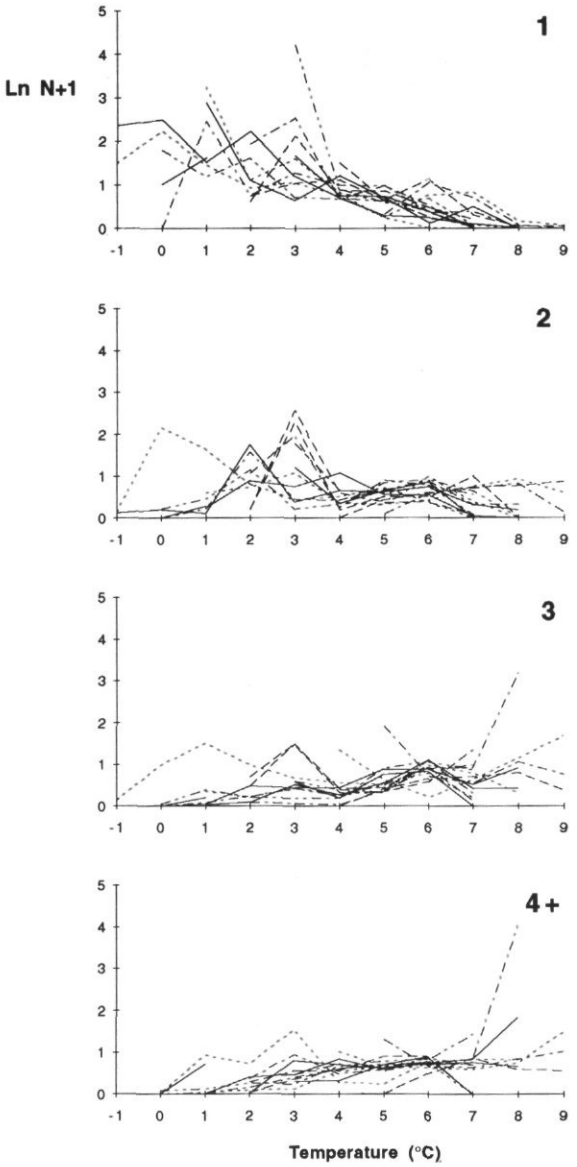


Figure 4. Numbers-at-age of cod per hour fishing (log scale) by 1°C temperature bands in individual years, February 1977–1991.

2nd, 3rd, and 4th quarters of 1981 and the 4th quarter of 1991 are far from complete and may be biased. Nevertheless, the picture emerging here is that the pattern of ambient vs. average temperature (Fig. 8) shifts markedly during the year. In autumn, 0- and 1-group cod live at higher ambient temperatures than the average North Sea values, whereas for the oldest age groups the opposite is the case.

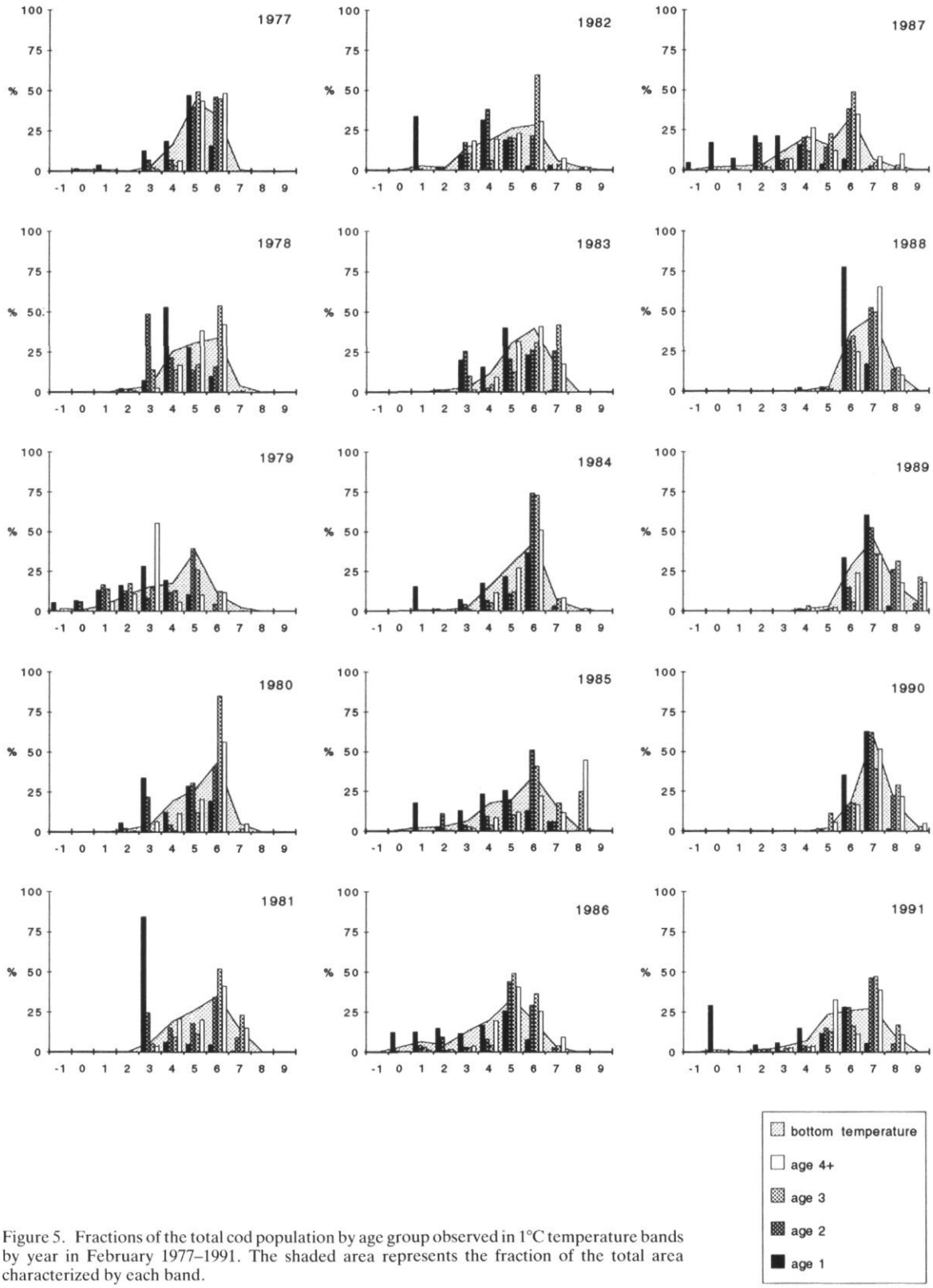


Figure 5. Fractions of the total cod population by age group observed in 1°C temperature bands by year in February 1977–1991. The shaded area represents the fraction of the total area characterized by each band.

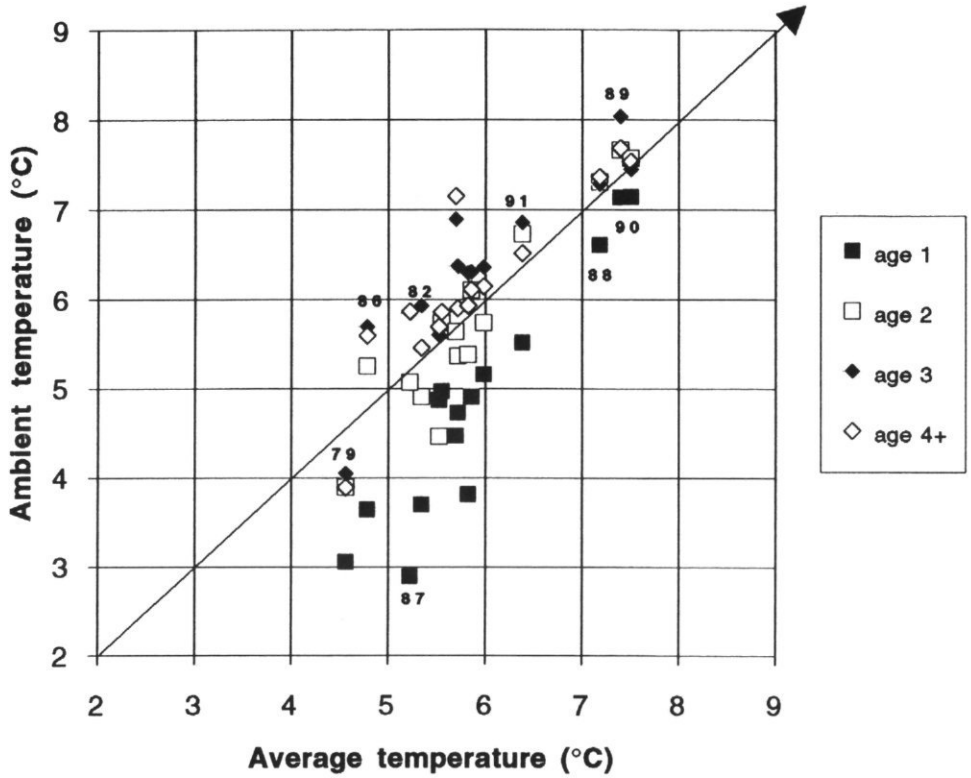


Figure 6. Average ambient temperature of different age groups of cod in relation to the average North Sea bottom temperature by year in February 1977–1991.

Discussion

The available data strongly suggest that there are marked differences in the temperatures at which the different age groups of cod live in the North Sea. However, it is unlikely that there is a specific preference involved for lower or higher temperatures, not at least in the case of the juveniles because of their exposure to the lowest temperatures in winter and to the highest temperatures in late summer and autumn. The older fish seem to avoid areas where temperatures fluctuate strongly and to buffer themselves against these by staying in those areas where the annual fluctuation in temperature is minimal. This suggestion is supported by the average distribution patterns of the different age groups (Fig. 9). This, of course, need not be a direct cause and effect relationship, because there are other parameters related to temperature, such as depth and the availability of food, which are more likely to be responsible. Also, for fish aged 3 and older the distribution will be affected by spatial differences in exploitation rate. When comparing the situation in different regions, it is difficult to detect general patterns in the relation between distribution of cod and temperature. For example, Sinclair (1991) found that in summer on the Eastern Scotian Shelf ambient temperature decreased with increasing age, just as we found in the North Sea, whereas Rose *et al.* (1994) found older Labrador cod occurring in relatively warmer water. Observations in the fall in the Southern Gulf of St Lawrence showed distribution to be independent of age (Swain, 1991), as did Rose *et al.* (1994) for the Northeast Newfoundland Shelf.

In studies of cod distribution in relation to temperature, conclusions are often drawn about the 'preferences' involved without the annual and seasonal variations in possibilities for selecting the 'preferred' temperature being taken into account (Sinclair, 1991; Swain, 1991). Even if the density of 1-group cod in relation to temperature (Fig. 3) suggests that, in winter, these fish prefer the 1–2°C temperature band, it must be taken into account that in warm winters their choice is restricted to a minimum of 6°C. Moreover, if 1-group fish prefer to remain close to the continental coast

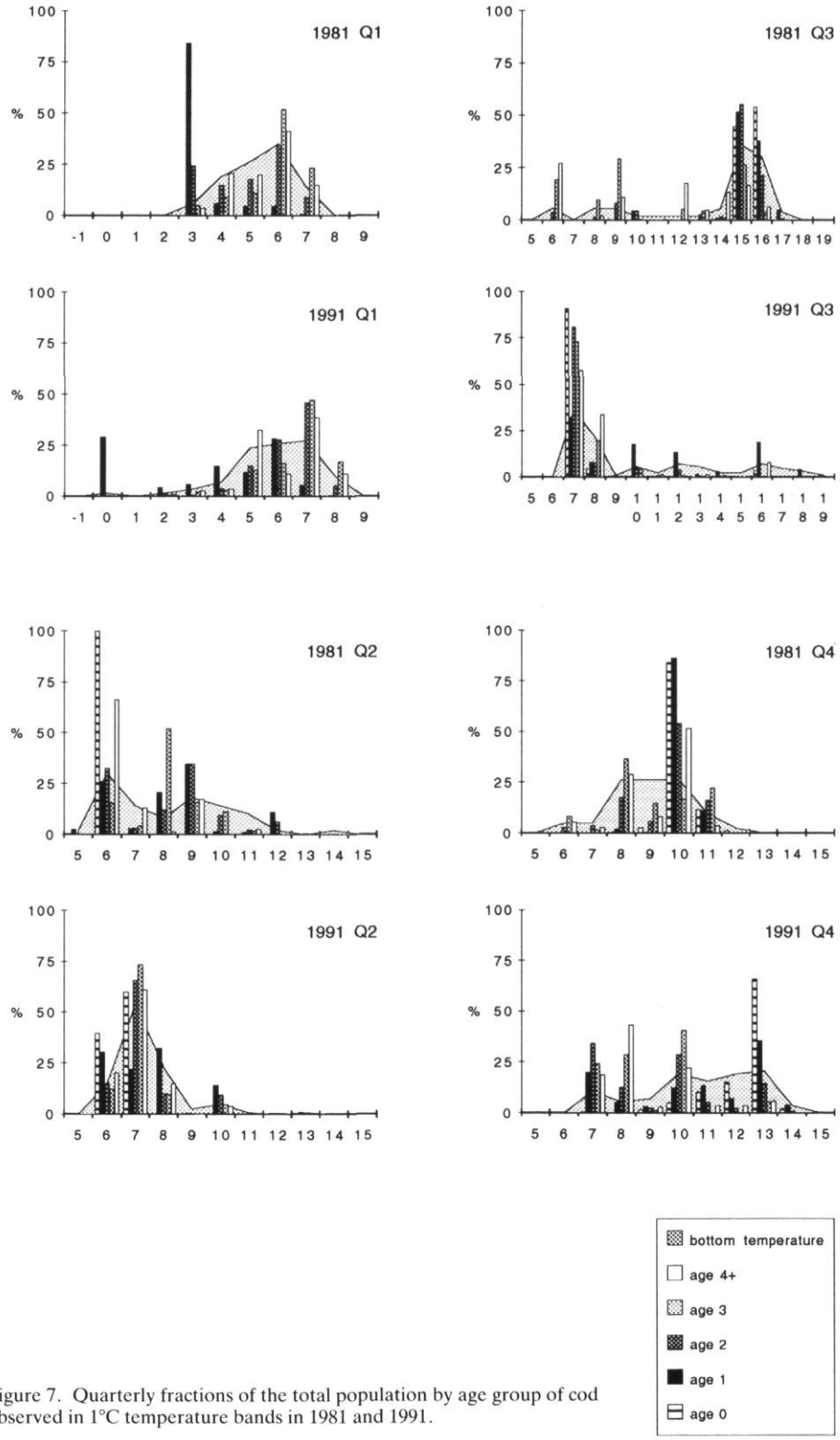


Figure 7. Quarterly fractions of the total population by age group of cod observed in 1°C temperature bands in 1981 and 1991.

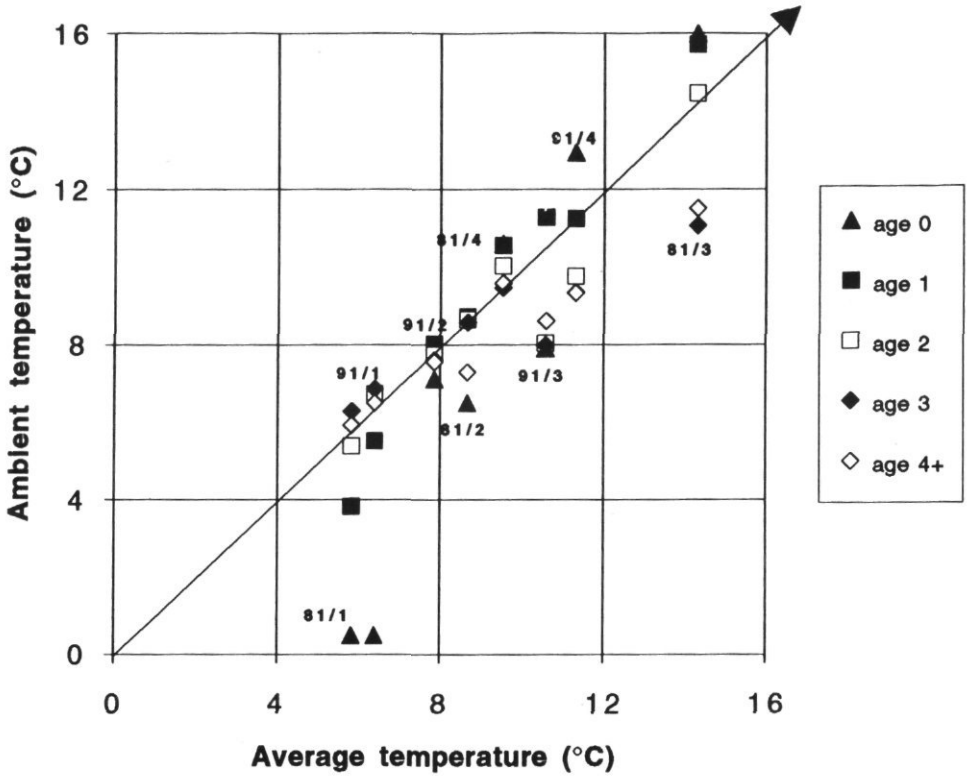


Figure 8. Average ambient temperature of different age groups of cod in relation to the average North Sea bottom temperature by quarter in 1981 and 1991.

irrespective of the type of winter, the apparent effect will be high densities in cold waters, because these are necessarily restricted to the coastal area at these latitudes. Because the warmer waters encompass a large area, where 1-group fish are not found, the average density in those is reduced. Therefore, differences in ambient temperature between age groups or years are not necessarily explained by differences in preference in the true sense of the word; much more intricate analyses are required if we are to arrive at any firm conclusions in this respect.

The approach presented in this paper may be useful also because it provides a better basis for studying annual growth differences or effects of temperatures on digestion rates than a point estimate for the average temperature in the sea. The ambient temperatures of the individual age groups deviate quite unpredictably from the average. If the winter is cold, 1-group fish are exposed to much lower average values than when the winter is relatively warm. The physiological effect is thus much stronger than indicated by the average.

Within the context of "cod and climate change", it would seem unlikely that the distribution of cod in the North Sea would be very much affected by a gradual increase in temperature, because there is no direct evidence that the cod actively avoid high temperatures, at least not in the range observed so far. This contrasts with the findings for several fish species, including cod, on the northeast continental shelf of the USA; these were shown to compensate, at least partly, for the interannual temperature changes by migration (Mountain and Murawski, 1992).

Water temperature may of course have other effects on the population dynamics of cod, particularly on recruitment, and in this context it is worth noting that the mature cod population (4+) appears to perceive a very limited temperature signal during spawning (January/February). Since the North Sea is well mixed at this time of the year, the surface and bottom temperatures are not that different and therefore it is unlikely that a severe winter will directly affect egg mortality to any large extent. If there is an effect, it is more likely to be found in the larval and early 0-group phase. However, the remarkable change in recruitment during the 1960s to 1980s (see Daan *et al.*, this volume) would seem very much stronger than could ever be explained by

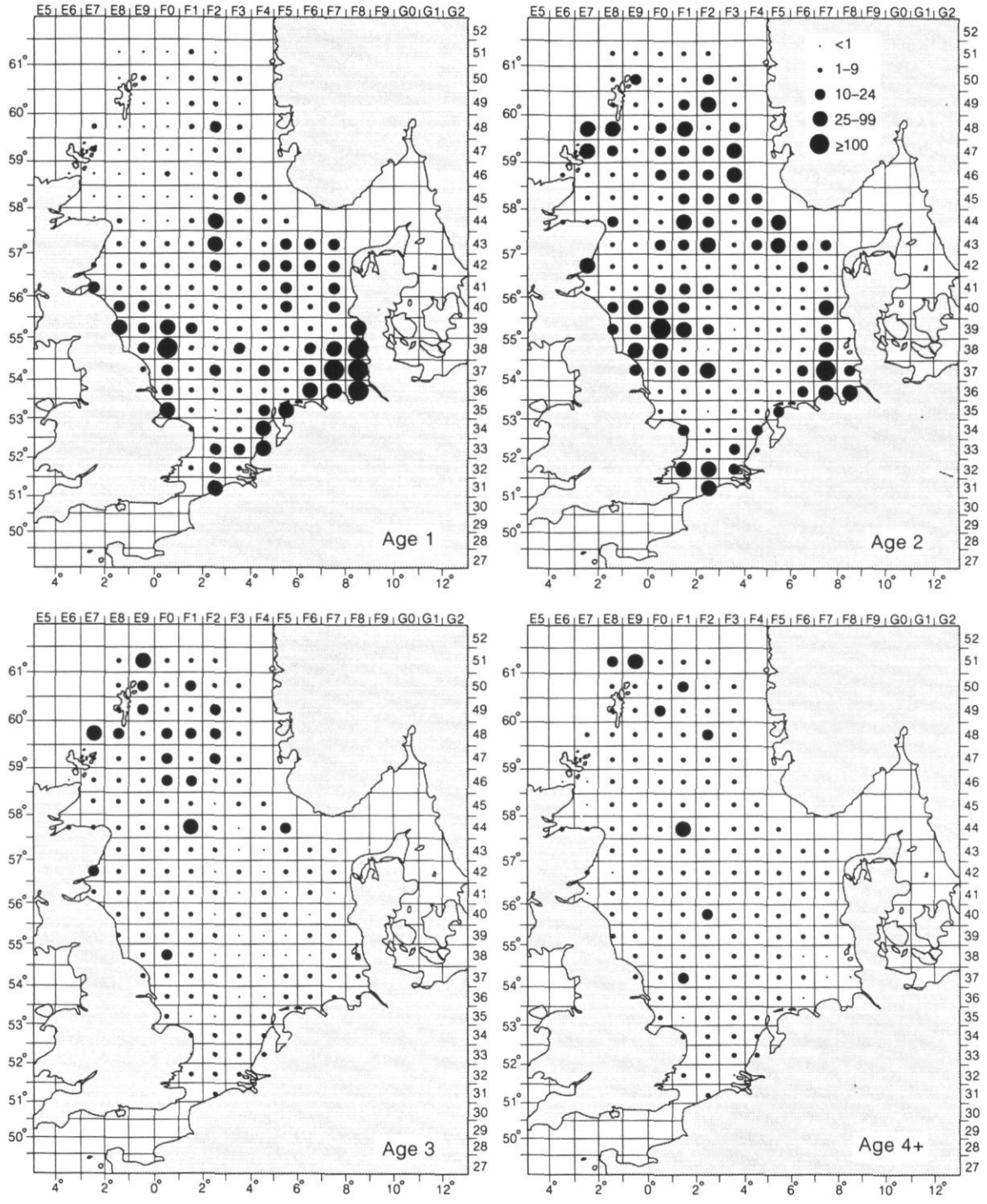


Figure 9. Average distribution of age groups 1, 2, 3, and 4+ of cod for the period 1983–1987 (from Heessen, 1993).

any temperature signal, and to that extent the effect of climate change on the North Sea cod can be expected to be subordinate to other much more important factors.

Acknowledgments

We are grateful to Dr Harry Dooley and Garry Hopwood from the ICES Secretariat for providing us with pre-processed temperature data from the ICES Oceanographic Data Bank and to various colleagues from national laboratories around the North Sea participating in the International Bottom Trawl Survey for providing us with the necessary data.

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The Baltic cod stock: fluctuations and possible causes

Ole Bagge and Fritz Thurow

Bagge, O., and Thurow, F. 1994. The Baltic cod stock: fluctuations and possible causes. – ICES mar. Sci. Symp., 198: 254–268.

The yield of cod in the Baltic has fluctuated owing to varying fishing effort and to varying strengths of year classes. The success of reproduction is closely related to the salinity and the oxygen conditions in the depth strata where the cod eggs are able to float (a salinity of 10–11). A peak in abundance and a maximum yield in historical time were registered in the mid-1980s, followed by a drastic decline. The fluctuations in abundance are discussed in the light of fishing effort, inflow of saline water from the North Sea, eutrophication, and predation.

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Introduction

The highest abundance of cod (*Gadus morhua*) in the recent history of the fishery was in the late-1970s to mid-1980s, followed by a dramatic decline (ICES, 1993). The yield has fluctuated owing to varying fishing effort and to varying strengths of year classes (ICES, 1988, 1991, 1993, and Thurow, 1974). The success of reproduction and hence the year-class strength is closely related to the salinity and the oxygen conditions in the depth strata where cod eggs are able to float (Wieland and Zuzarte, 1991). In this article the fluctuations in abundance of the Baltic cod stock are discussed in the light of fishing effort, inflow of saline water, and eutrophication and predation.

The Baltic Area

The Baltic Sea is the largest brackish water body in the world covering an area of 375 000 km^3 with a volume of 22 000 km^3. The mean depth is 34 m and the maximum depth 459 m (Landsort Deep). The drainage basin covers an area of 1 750 000 km^2, yielding about 470 km^3 of fresh water per year.

The Danish straits and the Kattegat form a transition area to the North Sea (Fig. 1). Precipitation and evaporation are of the same order of magnitude, which means that the net outflow from the Baltic Sea is equal to the run-off from the drainage basin. The water exchange through the Danish straits is, however, 6–10 times larger and dependent on differences between the surface level in the Kattegat and the western and central parts of the Baltic caused by the barometric situation. This means that inflow of saline water is generated by a preceding outflow creating a lower sea surface level in the Baltic, compared with the Kattegat, followed by strong westerly winds (Kändler, 1951 and Matthäus and Franck, 1992). A deep water current generated by the horizontal salinity gradient between the North Sea and the Baltic Sea makes a further minor contribution to inflows.

Salinity

The Kattegat, the Danish straits, and the westernmost part of the Baltic are meeting points for the high-salinity water masses from the North Sea (35), and the brackish water masses from the Baltic (8–10‰ at the surface). Because of the difference in the specific gravity of the two water masses, a stratification occurs with the brackish Baltic water on the surface.

In the transition areas there are two sills, one in the southern Sound at Drogden (depth 6 m) and another at Dars (depth 18 m), (Fig. 1), over which 20% and 80%, respectively, of the inflows had to pass (Wyrtki, 1954). The inflow of January 1993 was found to have entered both entrances in almost equal proportions (Håkansson *et al.*, 1993). The sills prevent the inflow of high saline water under average weather conditions and cause a mixing of bottom and surface water very much reducing the salinity of the inflowing water. Only under extreme

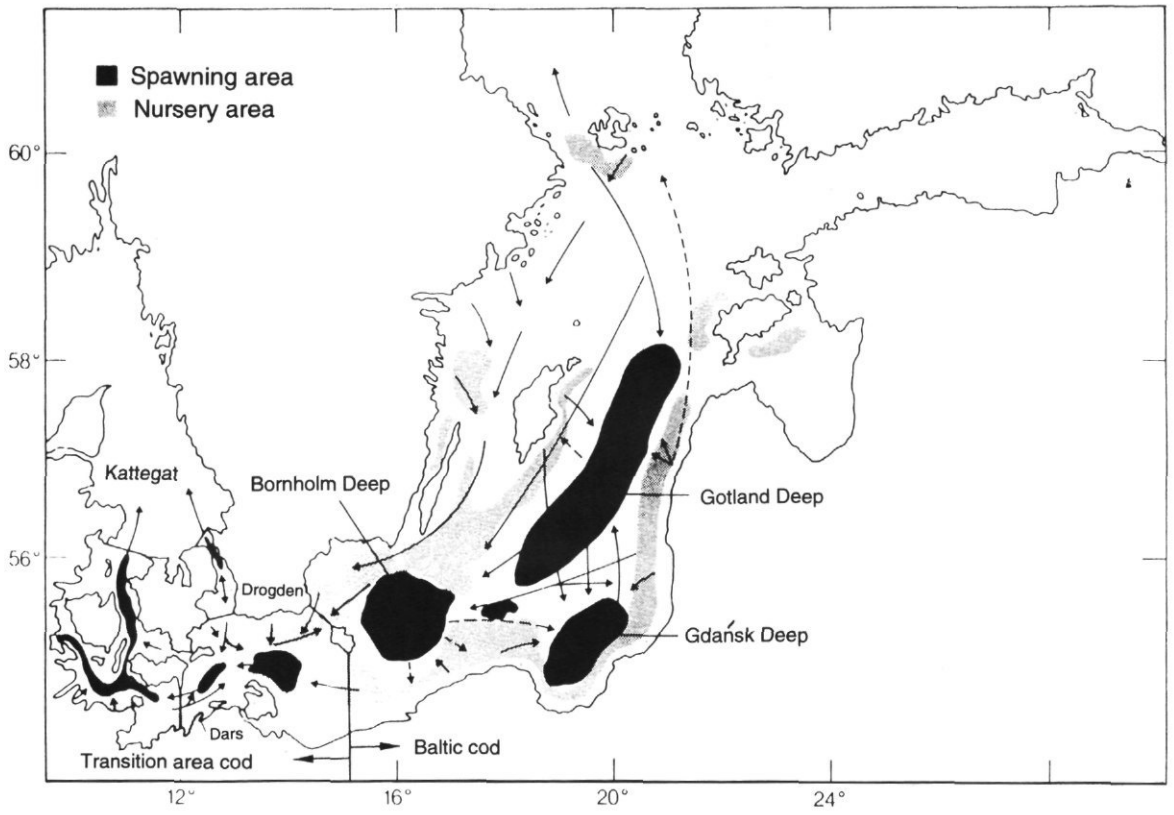


Figure 1. Spawning and nursery areas in the Baltic. Full drawn arrows indicate spawning migrations, dashed arrows drift of young fish. (ICES, 1978, appendix; with some additions).

weather conditions is high saline water forced over the sills. The effect on salinity is that three strata are found in the Baltic: a fairly saline bottom layer, an intermediate layer with lower salinity, and a brackish surface layer. Big inflows of high saline water occur very irregularly, and sometimes at several years' intervals. The average salinity in the bottom layer in the Bornholm Deep, in the Gdańsk Deep, and the Gotland Deep may be 18, 14 and 11‰, respectively, but these will decrease in periods with no inflow. The surface layer, which is almost isohaline vertically, is separated from the deep water by the primary halocline. This transition layer is about 10–20 m thick. The depth of the halocline increased from 50–60 m in the Bornholm Deep to 80 m in the Gotland Deep. The salinity in the surface layer is about 7 in the Gotland Deep and 8‰ in the Bornholm Deep.

Oxygen

The surface layer above the halocline is supplied with oxygen by thermal convection, but the halocline forms an effective barrier to convection, which means that the main oxygen supply below the halocline is dependent on inflow through the Danish straits. Owing to sedimentation of organic matter there is a persistent oxygen consumption and, if not made up for by inflow, results in an extended but varying oxygen deficiency in the deeps, depending on the frequencies of inflows. Since 1977, no major inflow has occurred (Fonselius *et al.*, 1984; Fonselius, pers. comm.) and the situation has been that of a decreasing salinity, a decreasing oxygen concentration, and the development of hydrogen sulphide in the eastern deeps (Matthäus, 1992; Juhlin, 1990). An increasing eutrophication producing an increasing sedimentation of organic matter may further contribute (Rosenberg *et al.*, 1990).

The fish fauna

The biomass of the fish has been dominated by a small number of species, the most important of which are herring, cod, sprat, and flounder, in that order. The total biomass of these in 1990 was about 7.4 million

tonnes. Other species are salmon and sea trout with a biomass of about 5000 t and turbot about 1000 t in 1990. The biomass of some other commercially caught species may be of the same order of magnitude, recent catches being: eel 2000–4000 t and smelt 4000 t. The yields of other species fluctuated widely: stickleback 100–19 000 t and eelpout 100–9000 t (ICES Fisheries Statistics; Thurow, 1993). Some species are not listed in the catch statistics although they are caught in considerable quantities, e.g., four-bearded rockling, lumpsucker, and others. In the western part of the Baltic, there is an increased species diversity because of a higher salinity and a shorter distance to the Kattegat.

The Baltic Cod

The stocks

There are two stocks of cod in the Baltic Sea which are quite well separated by a border along longitude 14°30′E, immediately west of Bornholm (Fig. 1). On the eastern side, the true Baltic cod stock extends to about 63°N latitude. On the western side, the transition area cod stock extends to the southernmost Kattegat. The separation of these two stocks has been shown by meristic characters (Schmidt, 1930), by electrophoresis (Sick, 1965; Jamieson and Otterlind, 1971), and by numerous tagging experiments (Aro, 1989). A review of stock identification in the Baltic has been given by Bagge and Steffensen (1989). The total stock size of the western and eastern stock in 1989 was estimated at 40 000 t and 350 000 t, respectively (ICES, 1991). In the following, only the cod stock east of longitude 14°30′E, i.e., in the Baltic Proper, is considered.

Landings

Figure 2 compares the landings of cod, herring, and sprat since 1903. The cod fishery was the first to develop in open sea. The yields of cod from ICES division IIId are given in Table 1 as means for 10-year periods. The statistics stem from ICES (1990), ICES *Bulletin Statistique*, its Advance Release, and Thurow (1974). This Division IIId is almost identical to ICES Subdivisions 24–32. Thus, it should be noted that as Subdivision 24 is included, part of the western stock is included as well, but only amounting to 3–5% of the total. It appears that until 1938 total landings were below 30 000 t. During the Second World War, landings increased to over 80 000 t. Following a drop just after the war, they increased to the range 112 000–197 000 t during the period 1948–1974. Since then landings increased substantially to a maximum of 413 000 t in 1984 before declining in 1992 to the level of the 1940s, i.e., 58 000 t. The reasons for the increasing yield may be attributed either to an increase in fishing effort or stock size or to a combination of both.

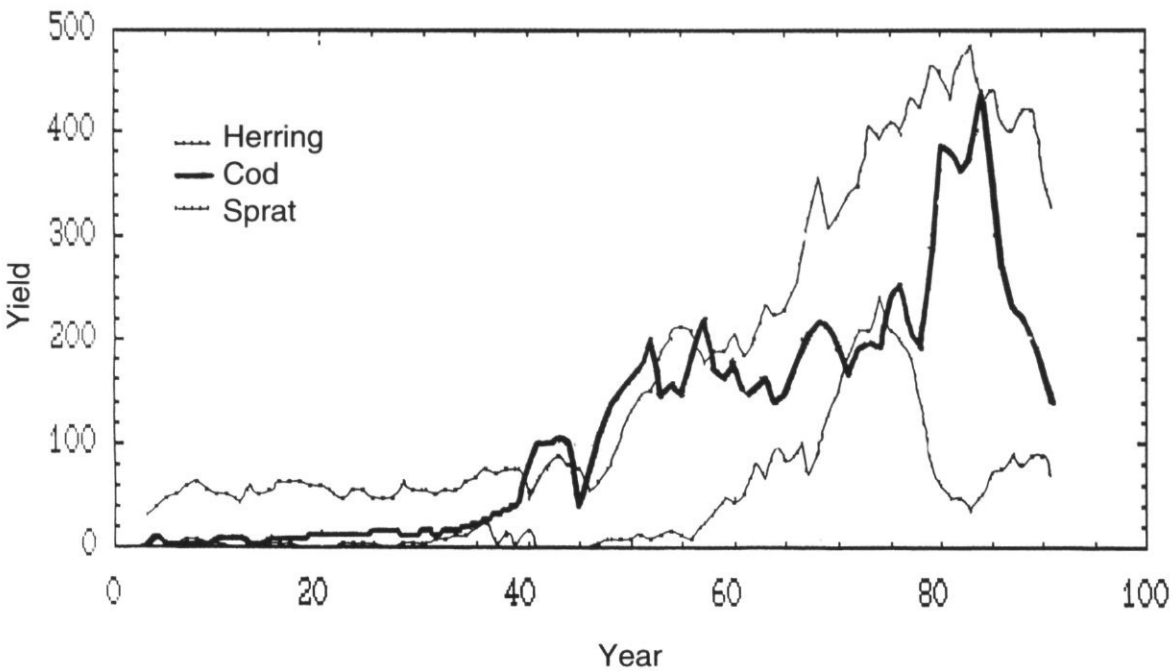


Figure 2. Yield of herring, cod, sprat, 1903–1991, 1000 t.

Table 1. Landings of cod by countries from the Baltic (Division IIId; Subdivisions 24–32).

	Denmark	Faroe Islands	Finland	Germany FRG	Germany GDR	Poland	Sweden	USSR	Estonia	Latvia	Lithuania	Total (Bull. Stat.)	Grand total
1911–1920	0.8	–	–	0.9		–	1.2	–	–	–	–	2.9	–
1921–1930	1.0	–	–	1.6		0.1	2.2	1.2	–	–	–	5.8	6.1
1931–1940	2.3	–	–	7.9		0.9	4.6	3.1	–	–	–	17.4	18.7
1941–1950	9.8	–	–	29.9		17.4	14.2	12.8	–	–	–	47.1	83.0
1951–1960	14.6	–	0.1	6.0	13.7	47.4	22.1	45.9	–	–	–	98.7	149.7
1961–1970	25.0	–	0.0	5.1	11.2	51.1	22.4	34.3	–	–	–	138.9	148.8
1971–1980	45.0	2.6	1.2	11.2	8.6	66.5	19.3	47.4	–	–	–	–	199.6
1981–1990	78.3	5.0	5.5	16.6	5.8	62.5	52.4	59.4	–	–	–	–	285.5
1991	43.6	2.6	1.7	7.8		25.7	39.2	3.3	1.8	2.6	1.9	–	130.0
1992	19.2	0.6	0.5	4.1		13.3	15.7	1.8	1.4	1.2	1.3	–	57.1

Abundance as indicated by catch and effort

Up to the second half of the 1930s the fishing effort on cod was low. The main fishery was on flounder and in the western part plaice as well (Jensen, 1954). It was not possible for the German fleet to work in the North Sea during the Second World War and 85 steam trawlers, a vessel type up until then never used in the Baltic, were transferred to this region (Meyer, 1952). Their catches amounted to almost 50 000 t (mean for 1941–1944). The increase in the landings depicted in Figure 2 is therefore thought to be due to this additional effort.

Thurow (1974) has evaluated the early development of effort and abundance based on density and reported landings. The density data are from several authors (Alander, 1948, 1950; Dementjeva, 1959; Jensen, 1954; Kändler, 1944; Sahlin, 1959). For Denmark, Germany, and the USSR they concern catch rates of cod, and the effort calculated from c.p.u.e. and yield would be directed on cod. The Swedish data refer to the number of fishing vessels fishing for both herring and cod. From this the increases in effort are thought to be as follows: Germany between 1931–1935 and 1937–1938 – 2.6 times; Denmark between 1931–1935 and 1936–1939 – 2.5 times; Denmark between 1936–1939 and 1950–1953 – 2.7 times; Denmark between 1931–1935 and 1950–1953 – 7.0 times; USSR between 1948 and 1951 – 4.0 times; Sweden between 1933 and 1957 – 3.6 times.

During the same period the catch-per-unit-effort data seemed to have increased slightly, but as the data were scattered, partly obtained by research vessels in different areas and not comparable, they are probably not good indices of abundance. However, some more reliable data are available in the published literature. Thus Dementjeva (1959) gives yearly mean catch/hour of USSR commercial vessels during 1948–1956, which show a decrease from 1948 to 1953 followed by an increase to the same level as in 1948.

Tiews (1974) compared the catch-per-hour of cod made by the German steam trawlers (1934–1944) with the catch-per-hour made by the research vessel "Anton Dohrn" (1962–1970) in the Bornholm Deep, the Gdańsk Bay, and the southern Gotland Deep. The catch rates in the Bornholm Deep in 1966, 1969, and 1970 were similar to those from 1939–1944, but in the Gdańsk Deep and the Gotland Deep the catch rates in 1969 and 1970 were much higher. Because of varying oxygen conditions near the bottom in the Baltic, one would assume catch-per-unit-effort data from research vessels with bottom trawl not to be reliable. These vessels worked in short periods, and consequently the choice of period may have been the main influence on the catch. However, Thurow and Weber (1992) have shown that research vessel catches with bottom trawl in the Bornholm Deep (Subdivision 25) are highly significantly related to biomass 1975–1992 as estimated by the Working Group on the Assessment of Demersal Stocks in the Baltic (ICES, 1991, 1992). The same is true for data of commercial USSR vessels (1974–1988) which have been submitted to the ICES Working Group on Demersal Species in the Baltic. This relationship is depicted in Figure 3. An additional data series of Dementjeva (1959) for the period 1948–1956 is given together with the recent USSR series in Table 2. These presentations suggest that the stock in the period 1948–1956 was on a lower level than in the period 1974–1986. Since 1986 the stock has declined to the level of the former period. The maximum catch/day was observed in 1979 and 1980.

Abundance estimated from VPA

The first VPA on the Baltic stocks based on age compositions of national landings was run in 1975 (ICES, 1975). An attempt based on Polish age data only was made in 1972 (ICES, 1973). Since 1975 the VPA has been updated yearly by the Working Group on the Assessment of Demersal Stocks in the Baltic.

Until 1987, the natural mortality was set at 0.3, but in

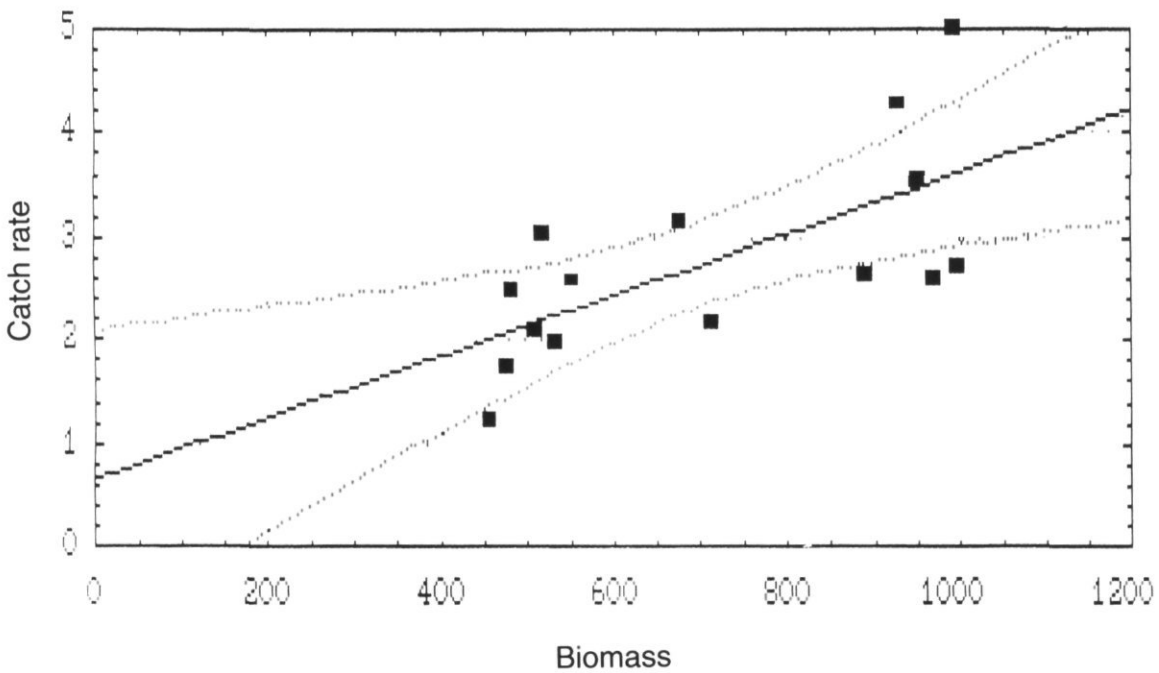


Figure 3. USSR trawlers, cod catch/day, t.v. biomass (ICES, 1992), 1000 t.

1988 it was reduced to 0.2. The effect of this measure was that biomass at the beginning of the year was reduced by about 30%. At the same time the maturity ogive was changed. Therefore, the 1988 and 1993 VPAs were used to cover the period 1966–1992. The recruitment, spawning-stock size, the fishing mortality, and the yield for the period 1966–1992 are shown in Figure 4 (ICES, 1988 and 1993).

Recruitment in the 1960s was about 300 million cod of age 2. Some ten years later a series of good and very rich year classes followed. Subsequently, a decreasing trend became obvious, and since 1986 recruitment has been the lowest on record, less than 100 million in 1989–1992. The yield increased to a maximum of about 400 000 t in 1984, before declining to about 58 000 t in 1992. Fishing mortality has had an increasing trend since 1979, reflecting a heavy increase in effort due to the transfer of fishing vessels from the North Sea, a transition to larger vessels, and the introduction of pelagic trawling for cod. The maximum fishing mortality on record (F=1.4) was found in 1991 (Fig. 4).

Table 2. Mean daily catch by USSR trawlers in the Eastern Gotland Deep (1948–1956) Dementjeva 1959. 120 hp trawlers, 1974–1988. Unpublished USSR data, 150 hp trawlers).

	Catch (t)		Catch (t)
1948	1.82	1976	3.06
1949	1.45	1977	2.10
1950	1.36	1978	3.18
1951	1.29	1979	4.29
1952	1.39	1980	5.00
1953	1.14	1981	3.56
1954	1.24	1982	2.73
1955	1.27	1983	2.62
1956	1.66	1984	2.66
		1985	2.18
		1986	1.98
1974	2.50	1987	1.75
1975	2.60	1988	1.24

The development of pelagic single-boat trawling, which was introduced by German vessels, made it possible to fish continually day and night in contrast to bottom trawling. Bottom trawling is only practical in areas with sufficient oxygen near the bottom and only from sun-up to sun-down, because the cod leave the bottom when it gets dark. Consequently, effective effort increased by about threefold when they switched over to the pelagic method.

It can be seen from Figure 4 that fishing mortality in the 1960s was almost as high as in the late 1980s. This coefficient, as evaluated by the Working Group on the Assessment of Demersal Stocks in the Baltic (ICES, 1988 and 1993), is the weighted average F of age groups 4 to 7 and is thought to have a linear relationship with fishing effort.

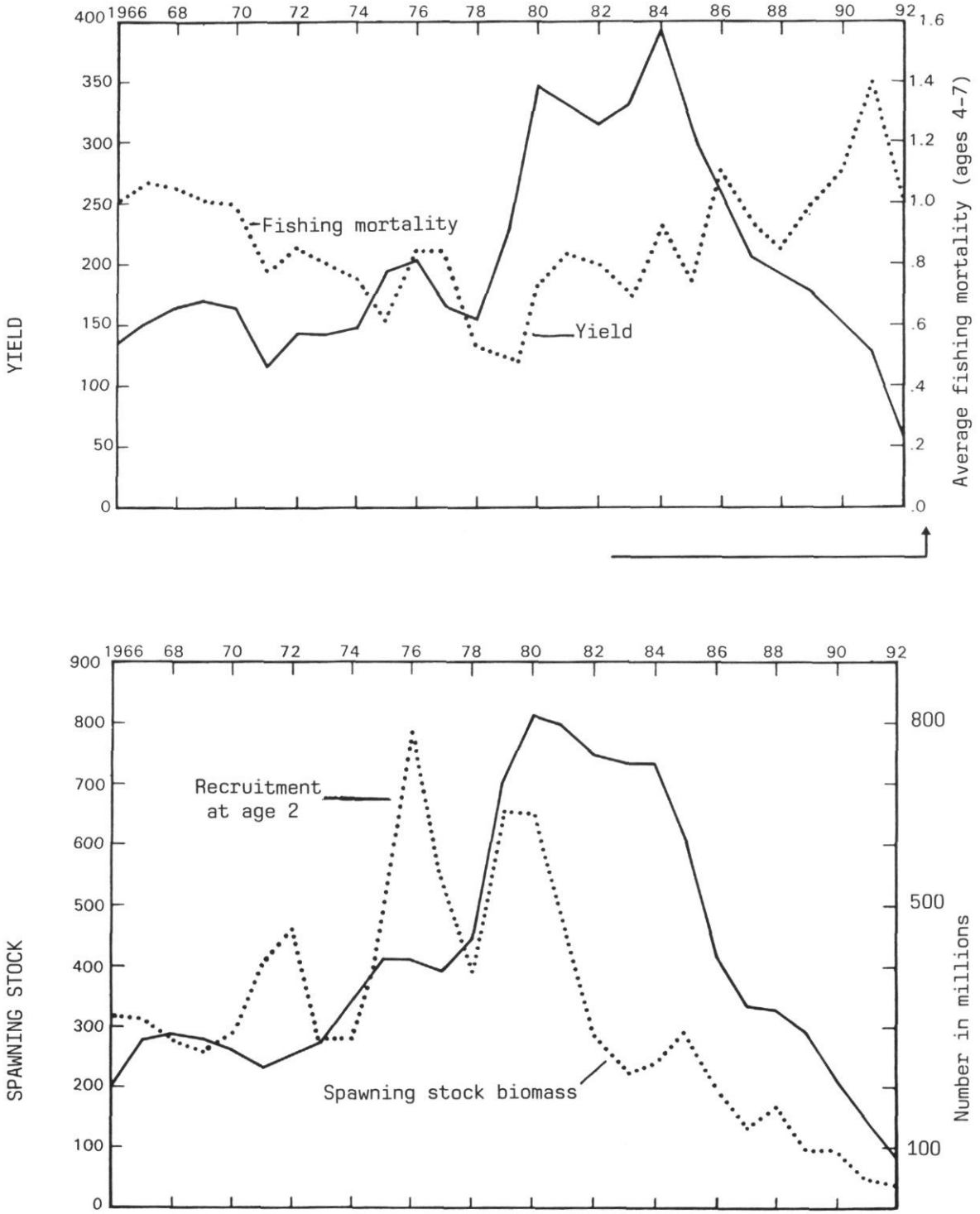


Figure 4. Baltic cod. Subdivisions 25–32. Yield (1000 t). Average fishing mortality (ages 4–7), spawning-stock biomass (1000 t) at 1 January and recruitment at age 2 (no. in millions). (ICES, 1993).

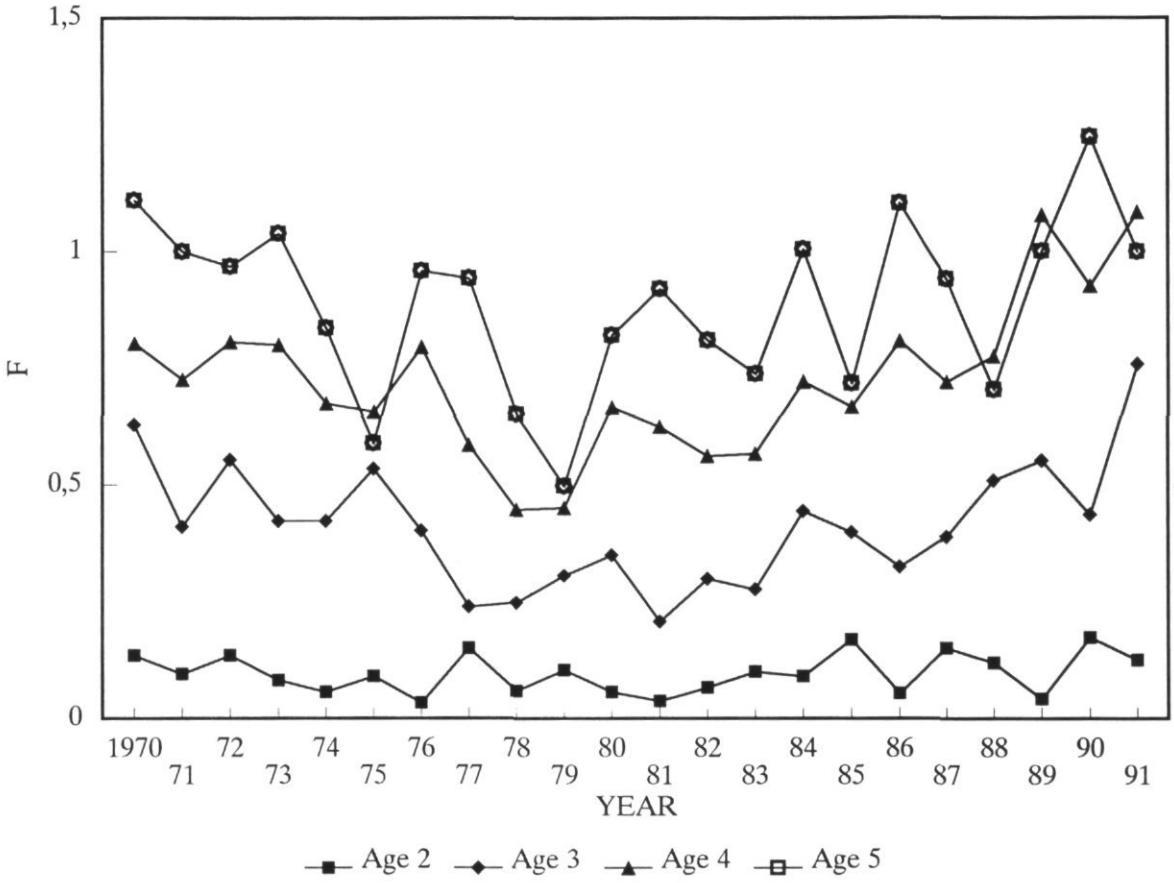


Figure 5. F per year at ages 2 to 5. (ICES, 1992, p. 60).

The indication is therefore that effective effort decreased until the late 1970s and inclined thereafter. The proportion of ages >6 in the total biomass was relatively small, in the period 1970–1980 amounting to <15%. During the following years it increased to within the range 14–22% (except for 1986 when it was as high as 30%). This change indicates that more old fish survived because fishing mortality decreased. Because of the relatively low proportion of old fish we will now look at the course of F at ages 2–5.

Figure 5 shows essentially the same picture as Figure 4 and suggests little clue about a change in fishing pattern. Figure 6 shows the average exploitation pattern for three periods. The early and late phases hardly differ with regard to ages 2–5. Some differences concerning their older ages are present, but not consistently so. A distinction can be made, however, between the middle stage and the other two, but this does not imply a change in exploitation pattern, it simply shows an overall decrease in fishing effort.

An increase in fishing mortality in the 1980s, as shown in Figures 4 and 5, was caused by a corresponding rise in effort (ICES, 1993). The declining effective effort and fishing mortality in the 1970s is not understandable at first sight. How can it be explained?

The overall analysis, so far, has determined that cod and the fishery are evenly distributed. If this were not so, the conclusions might be different. To investigate, we examine the distributions of catches by subdivisions. Unfortunately, Denmark and Finland did not split their catches accordingly, but the data of the remaining five countries can be used, their catches amounting to 63% to 83% of the total of all countries.

Figure 7 shows these catches in Subdivisions 25 + 26 and 27–32 as a percentage of the totals of the five countries. The development of the catches in the two areas is in opposite directions. A clearly declining trend is seen for Subdivisions 25 + 26 until about 1980, when the proportion of Subdivisions 27–32 increases. A highly significant correlation between the catch in Subdivisions 27–32 and total biomass is depicted in Figure 8. The essential point is that its intercept is also highly signifi-

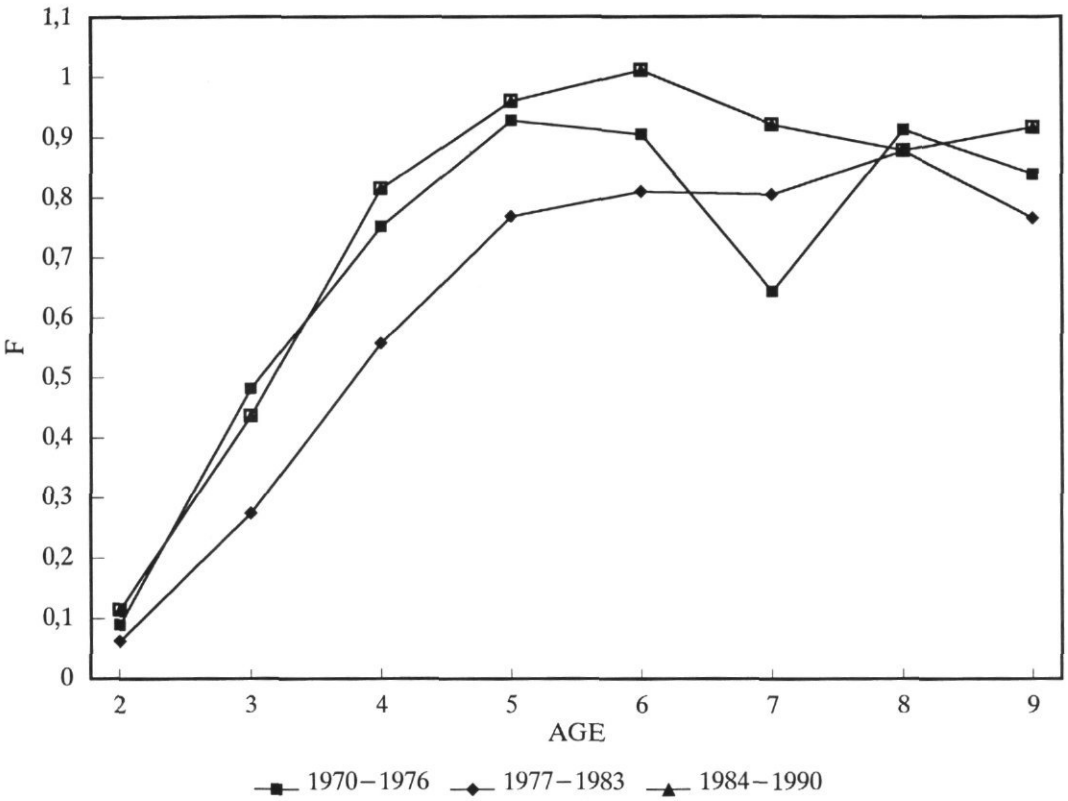


Figure 6. Mean F over three periods: 1984–1990, 1970–1976, 1977–1983.

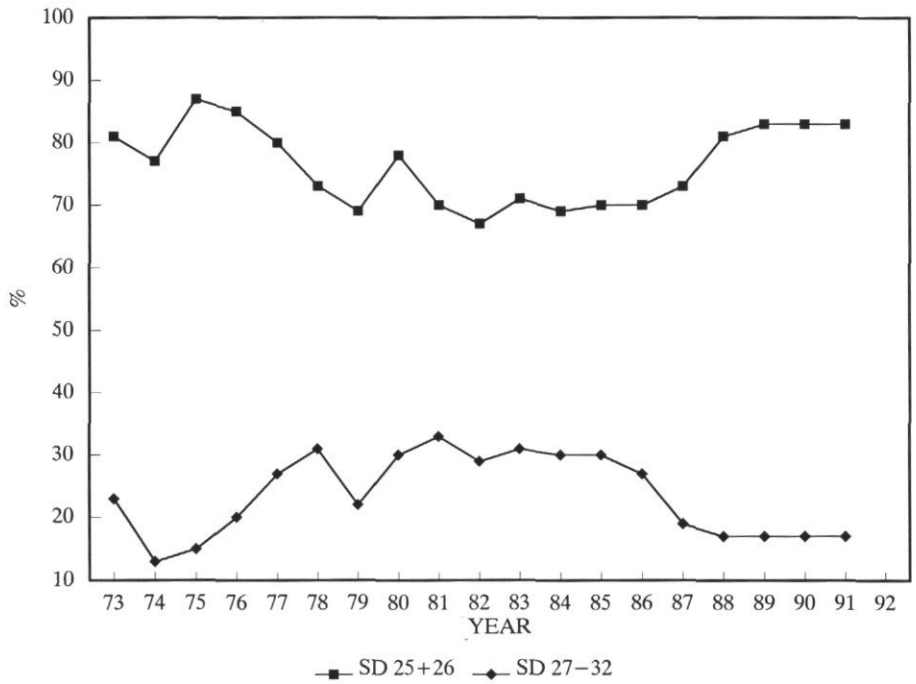


Figure 7. Distribution of catches (%) on Subdivisions 25+26 and 27–32, 1970–1991.

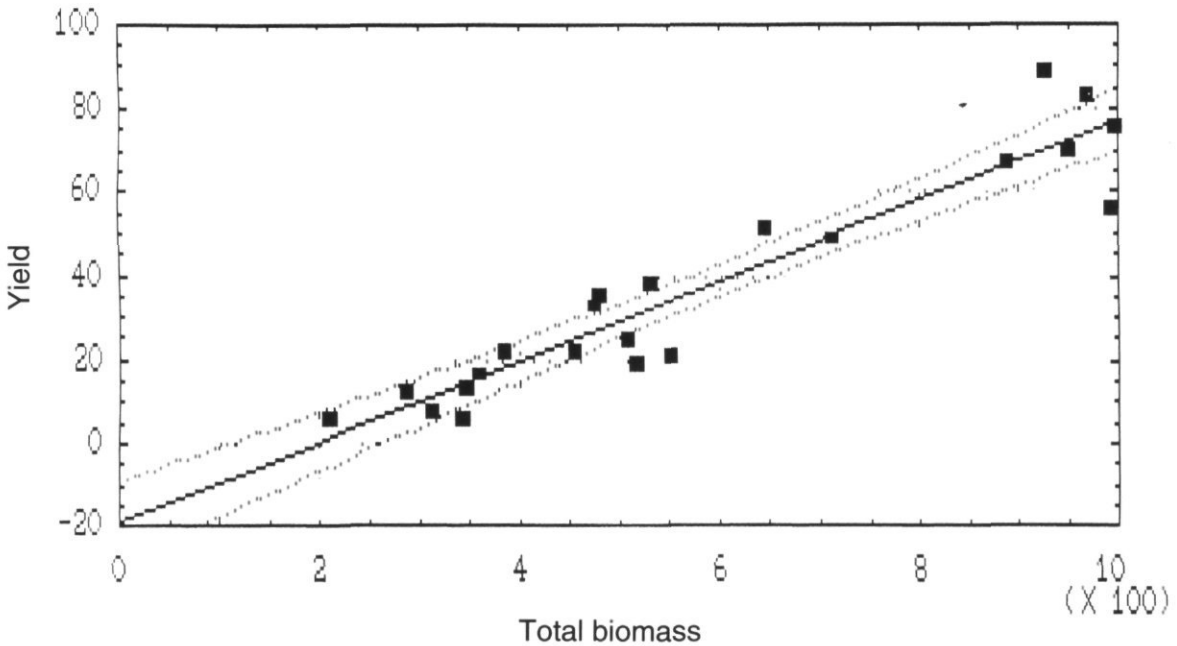


Figure 8. Catch in Subdivisions 27–32. Biomass, 1000 t.

cantly different from zero. Catches in the northern subdivisions are obtained on the condition that total biomass exceeds a certain level.

It is suggested from the foregoing that in about 1980 the cod inhabited additional northern regions for spawning and nursery. As a result, biomass more than doubled. At the beginning of the period, the fishery was essentially concentrated in the southern Baltic before increasingly extending to northern subdivisions. The assumption is that this occurred with a time-lag, the delay leading to an uneven distribution of the fishery and to a decrease in effective effort. One of the likely reasons for the interlude was the introduction of economic zones in 1978. This would have brought about, or contributed to, the low fishing mortalities in 1978 and 1979 (Figs. 3, 4), the lowest on record.

It could be argued that the introduction of the pelagic and gillnet fishery against bottom trawl could have contributed to the changes in fishing mortality. ICES (1993) gives length distributions of cod in catches with these gears (Figs. 9.1–9.3). They do actually differ between tackles. However, the samples are not comparable because different seasons are compared. Also, the fishery for cod in Subdivisions 25–32 is largely an exploitation of spawning shoals. Catches in the second half of the year have the smallest impact on the size of the yield. Finally, it is important that the pelagic trawl is used on the bottom as well as in open water layers as conditions permit.

Spawning of the Baltic Cod

Spawning area

There are three main spawning areas for Baltic cod: the Bornholm Deep, the Gdańsk Deep, and the Gotland Deep (Fig. 1). Spawning usually begins in March, reaches a maximum in May–June, and finishes in September–October.

Salinity and oxygen

In the spawning areas, a salinity of not less than 10 is necessary if the eggs are to remain afloat (Kändler, 1938, 1944; Grauman, 1973). At less salinity the eggs are deposited on the bottom and do not develop, but even if the salinity does allow the eggs to float, the oxygen content is a determining factor for development. Fertilization of the eggs is possible at salinities lower than 10, but with a reduced percentage of fertilization and a cessation of further development (Westin and Nissling, 1991).

The cod eggs are found below the halocline in the Bornholm Deep between 60 and 75 m at salinities of 11–13 (Müller and Pomerantz, 1984); in the Gotland Deep they are at depths of 80–100 m or where the salinity allows them to float. The oxygen content in the strata where the eggs are concentrated may vary from 0.5 to 6.0 ml/l, varying between months and years depending

on the inflow of saline and oxygenated water from the North Sea. The lower limit of oxygen content at which development of cod eggs is possible is 1.0 ml, but at this level egg mortality is very high (Grauman, 1973). Experiments on cod eggs from the Bornholm Deep indicate that below 0_2 of 2.3 ml/l development of the eggs does not proceed beyond stage III (Wieland and Zuzarte, 1991). Hence a combination of salinity of not less than 11 and oxygen content of not less than about 2.3 ml/l is very important for the survival of cod eggs. As salinity and oxygen content below the halocline are dependent on inflow from the North Sea, stagnant periods which reduce the salinity and the oxygen content might be expected to have a negative effect on the year-class strengths in the Baltic.

Inflows and stagnant periods

Long-term trends of salinity below the halocline in the Gotland Deep in 1895–1983 and 1977–1990 (Fonselius *et al.*, 1984; Matthäus 1992) are shown in Figures 9 and 10. Long periods with continuously decreasing salinity values were observed from 1922 to 1933 and from 1952 to 1962. Both began with very high salinities caused by heavy inflows. A big inflow into the Gotland Deep also began in 1935 but, because of the war, there was no further information between 1940 and 1947. Four smaller inflows occurred after the 1952 inflow, interspersed with stagnant periods. The last major inflows occurred in 1970, 1974, 1976, and in 1979 (Matthäus, 1992; Matthäus and Franck, 1992). An inflow of medium size occurred in January 1993. Figure 11 shows the salinity, temperature, and oxygen content in March 1991 on stations in the central Gotland Deep in a line from the central east coast of Gotland to off Libau at the Latvian coast. It appears that a salinity of 11 is found at a depth of 120–130 m, at which the oxygen content is 0.5 ml/l or less, which means that cod eggs are unable to develop. Dahlin *et al.* (1993) present a similar but monthly set of data (1990–1993) from Station By 15, which is situated in the centre of transect 1 (shown in Figure 11). In 1990 the 11 contour is at a depth of 150 m and the corresponding oxygen content less than 0.5 ml/l. In 1991 the depth of the 11 contour and the oxygen content there in March corresponds to that shown in Figure 11, but in the last part of the year and in 1992 the 11 contour is situated at a depth of 180 m, where H_2S is found. In 1993 the depth of the 11 salinity decreases rapidly to about 150 m, because of the inflow in January (Dahlin *et al.*, 1993, Fig. 9).

Reproduction of cod in the Gdańsk Bay has not been possible in 1990, 1991 and 1992 as these year classes have been almost absent in the area (Netzel, 1993; Uzars *et al.*, 1991).

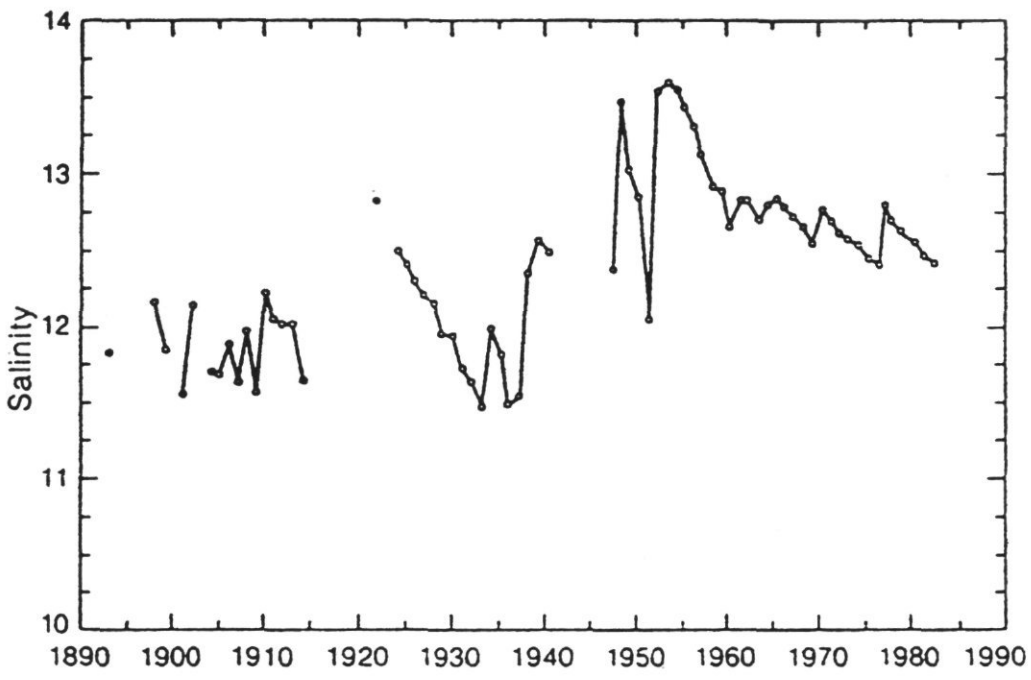


Figure 9. Annual mean values of all salinity data (200 m depth) at the Gotland Deep station from 1890 to 1982 (Fonselius *et al.*, 1984).

Discussion

Some authors have demonstrated a positive correlation between inflows and year-class strengths of cod (Berner and Borrmann, 1977; Bay, 1984; Kosior and Netzel, 1989; Bagge, 1993). In addition to increasing salinity and oxygen content, however, inflows also force nutrients from the bottom to the photic zone, stimulating primary production (Nehring, 1982), which may also be very important for the successful development of cod larvae. Around 1920 the dominance of winds from the west-southwest increased by about 25% (Jensen, 1954), and may have enhanced inflows to the Baltic. This may be a plausible reason for the subsequent increase of the stock size. In 1957 an increase in fishing effort, combined with more powerful fishing methods, brought about an increased yield of cod to nearly 200 000 t. The explosive development of the stock in the late 1970s and early-1980s, however, cannot be explained by inflow and effort alone, as inflows of the same magnitude have occurred earlier without this effect. One possibility is the increased level of nutrient input from other sources (freshwater outlets and the atmosphere, e.g., nitrogen) (Rosenberg *et al.*, 1990). The high nutrient contents together with proper salinity and oxygen regimes is believed to have produced the rich year classes of 1972, 1975, 1976, 1977, 1979, 1980, 1981, and 1985. The stagnant period since 1979, during which oxygen con-

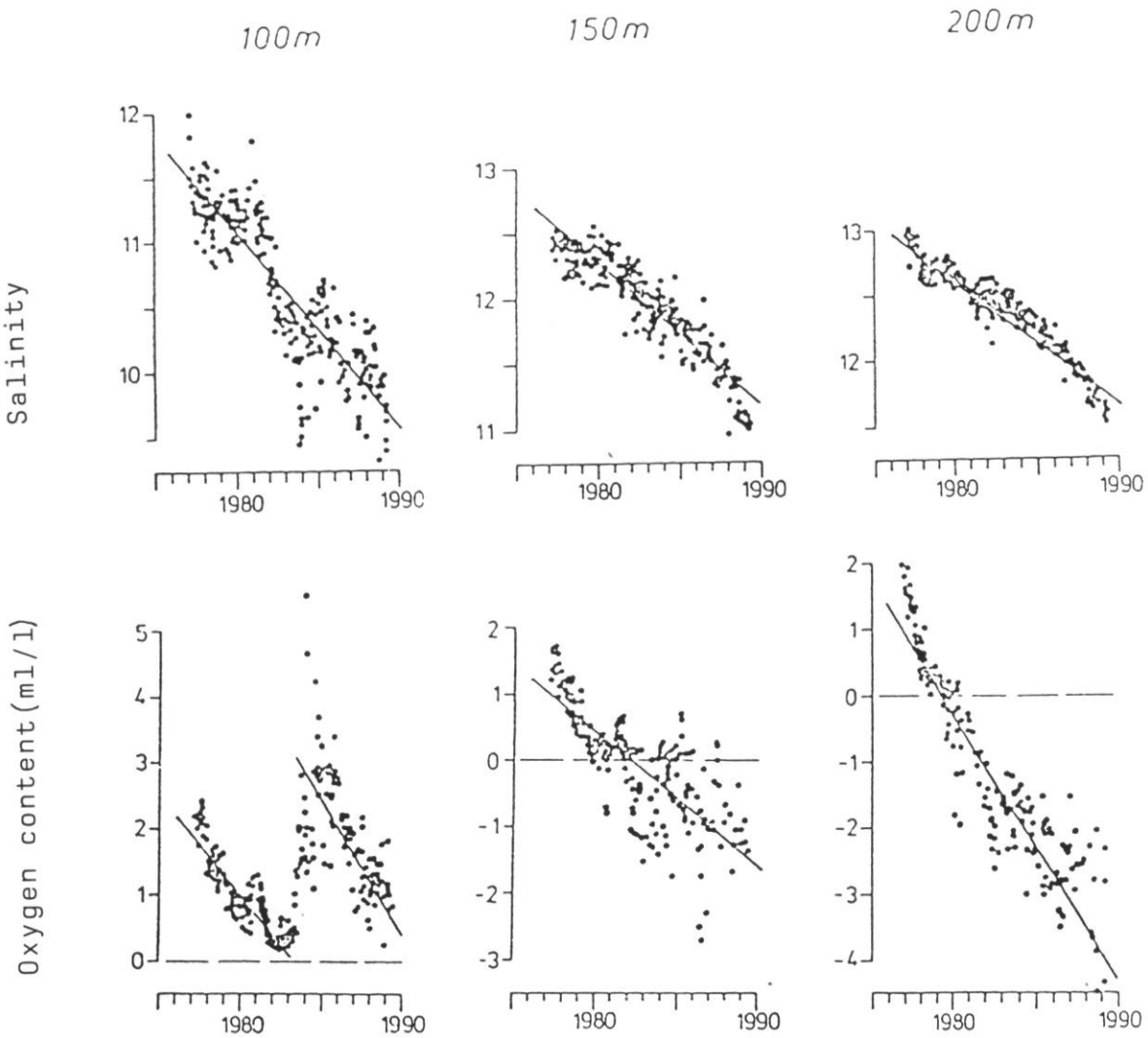
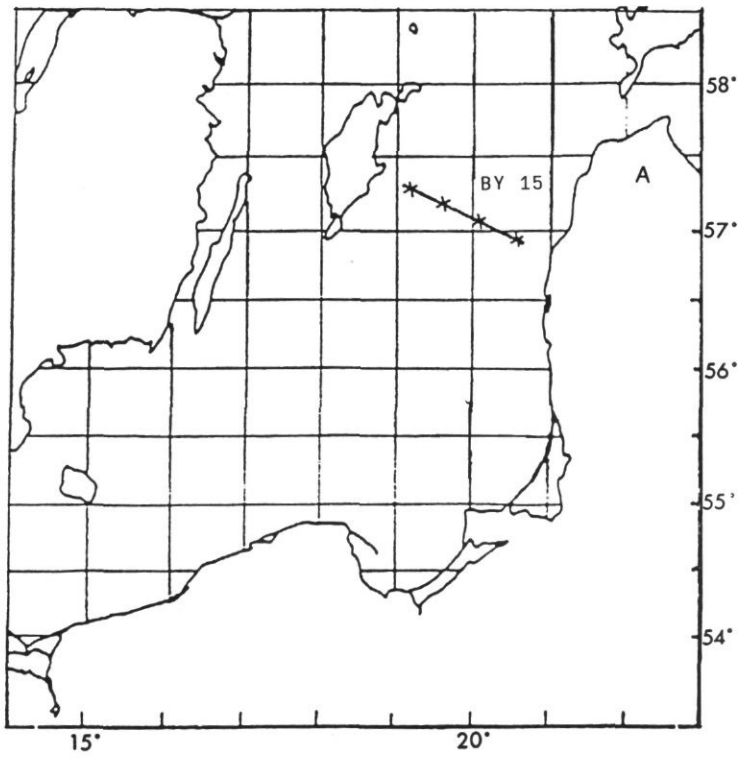


Figure 10. Annual observation of salinity and oxygen in the Gotland Deep 1977–1990 (Matthäus, 1991).

(A)



(B)

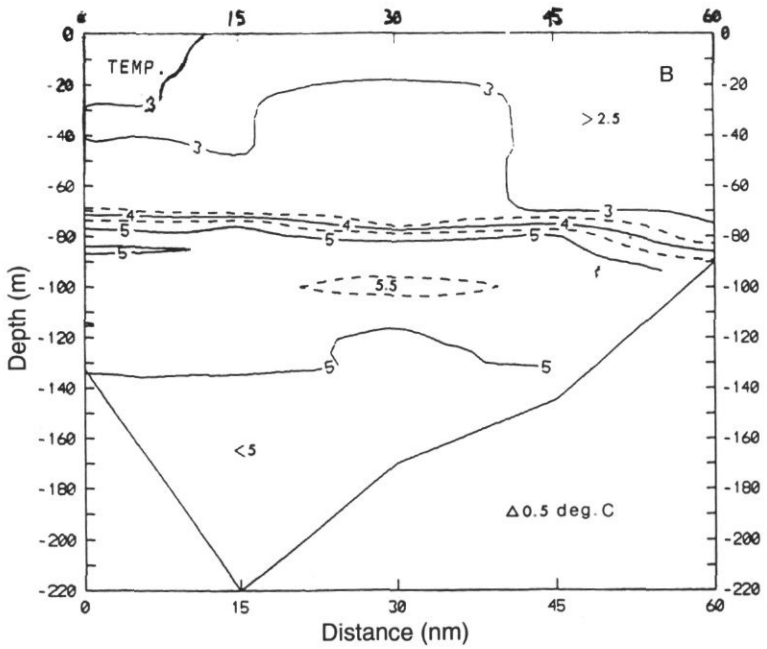
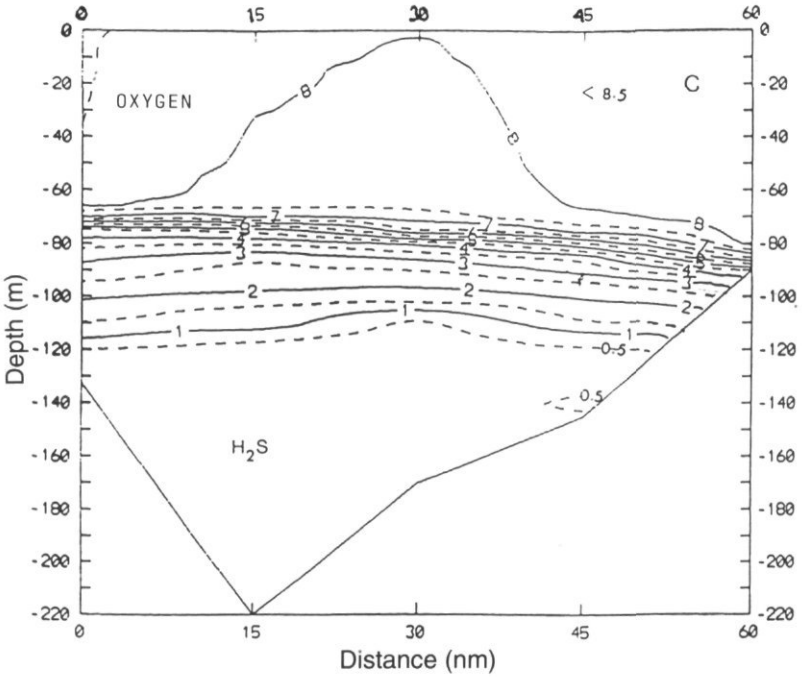


Figure 11. Measurements according to depth in a transect through (A) Station BY 15 in the Gotland Basin, of (B) temperature (°C); (*and overleaf*) (C) oxygen (ml/l); and (D) salinity.

(C)



(D)

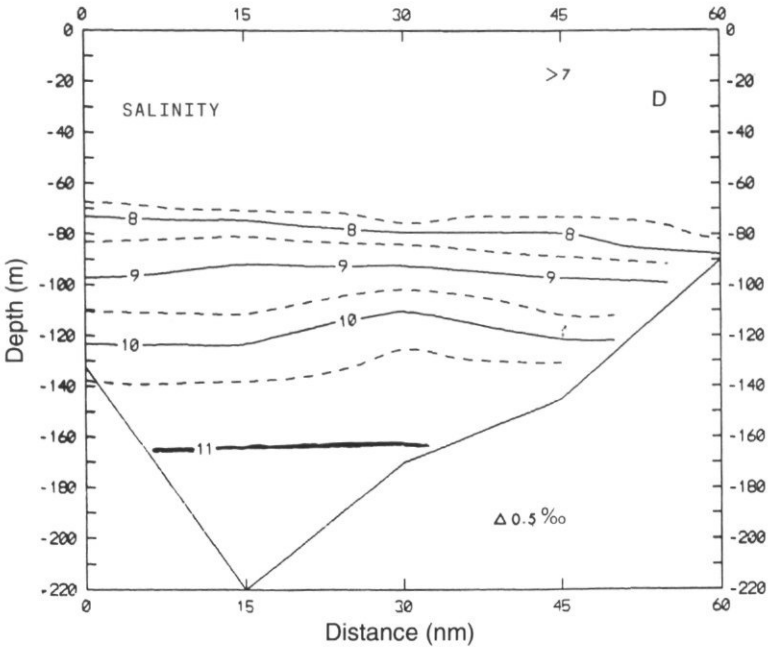


Figure 11. Continued.

sumption increased as a result of increased sedimentation of organic matter, which reduced the thickness of the water layer where it is possible for cod eggs to develop (the spawning volume), contributed to the production of a series of small year classes, especially in the Gotland and Gdańsk deeps (Uzars *et al.*, 1991). The reproduction of cod in the Baltic seems at present to be largely dependent on spawning success in the Bornholm Deep, depending on small inflows to that area only. However, even plots of recruitment on spawning volume yield a significant positive correlation; variance is high (Beverton, 1992, Fig. 4; Bagge, 1993, Figs. 2 and 3), indicating that factors other than inflows are involved, e.g. interactions with other species such as sprat, which predate on cod eggs and larvae (Köster, 1992).

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ICES mar. Sci. Symp., 198: 269–270. 1994

Trends in North Atlantic cod stocks: a critical summary

Niels Daan

Since the cod is a typical boreal species which does not invade tropical waters, climate must, in some way or another, have an influence on its distribution and also on its population dynamics. This is, of course, an open door. However, we have to be aware that climate influences not just cod, but also all other species of the Subarctic ecosystem. Therefore, any relation between climate and cod stocks will be mediated through a complex structure of abiotic and biotic processes operating in the ecosystem. As a consequence, we cannot expect simple mechanics; in fact, the effects of climate change are likely to be so complex and unpredictable that we cannot just accept without question any simple relationship which might appear to explain much of the variation observed in cod stocks. What we can hope for is that some important links between trends in temperature and cod population dynamics are revealed.

The available data series on cod landings date back several centuries in some regions. Jónsson has described extensive data series for Icelandic cod and Øiestad for Arcto-Norwegian cod, particularly in relation to the Little Ice Age. Although these studies suggest a direct relationship, it would seem likely that climate has possible effects not only on the productivity of fish stocks but also a direct effect on the extent and effectiveness of human activities. Figures on yield, even when effort is taken into account, may be related more to the catchability under different climatic regimes than to the productivity of the stock itself. Ice cover and bad weather in general probably had a much greater impact on fisheries in the old days, when the vessels were powered only by sails and oars. The technological advances made in the last century have undoubtedly reduced the sensitivity of fishing operations to meteorological circumstances. Thus, the relationship between climate and yield does not necessarily indicate a change in abundance or productivity of the stocks involved. Moreover, the economic situation in the home country of the fishermen, who even at that time spread widely over distant fishing grounds in the North Atlantic, played a crucial role in respect of total yield, as clearly indicated by the analyses made by de la Villemarqué.

Another important point to keep in mind is that the effect of climate change is not necessarily the same in all areas of the distribution. For instance, global warming might be expected to have opposite effects on the population of cod living on the northern and southern edges of its distribution. Such a pattern was indicated by the paper by Garrod and Schumacher, based on the trends in total yields from the different regions. Although they suggest that this might indicate effects of climate, the nature of the associated change remains uncertain. Moreover, fisheries have not developed entirely independently throughout the area. Some of these stocks were exploited essentially by the same distant water fleets which shifted around the North Atlantic depending on catch rates. Although others were only exploited by local fisheries, technological advances are easily transportable. Thus, timing of changes in yield in different areas may to some extent be interrelated and therefore a more elaborate analysis would be required in order to pinpoint climate as *the* responsible factor.

One obvious conclusion from the individual contributions for the different stocks is that all stocks have gradually been exposed to ever-increasing fishing mortality rates and that yields have been sharply reduced. As observed by Garrod and Schumacher, whose conclusion is supported by the more detailed analyses for individual stocks, "the very widespread decline in virtually all stocks speaks in favour of the more pervasive steadily increasing fishing mortality as the dominant factor in the most recent years". This suggests that, even if there are effects of climate throughout the North Atlantic, they are probably masked by the direct effects of fishing.

As far as our present knowledge goes, natural mortality among adult fish does not vary significantly between areas or years and in fact all cod stocks are assessed with a natural mortality coefficient of 0.2 throughout. Although the true value is not known exactly, it is undoubtedly very much lower than the present levels of fishing mortality and therefore variations herein are negligible in respect of the development of the stocks. Therefore, the important effects of climate change are more likely related to variations in recruitment. Temperature does not generally seem to correlate with year-class strength directly in any of the stocks, and in fact it may be more likely that climate affects recruitment through changes in the hydrography in the different areas. However, the processes respon-

sible for good recruitment appear to vary markedly from area to area. Thus, on the Georges Bank, retention of larvae is supposed to be the critical factor, whereas in the semi-enclosed North Sea an advective circulation would not seem important. In the Baltic, spawning success largely depends on the exchange of the deep basins with saline North Sea water, which is negatively correlated to river runoff. In the Arcto-Norwegian cod stock, the timely drift of larvae from the Lofoten area to the nurseries in the Barents Sea is probably a crucial factor. Since very different hydrographic processes appear to be involved, it would seem unlikely that climate change affects the different cod stocks in the same way, not even at the extremes of its distribution. In fact, we still do not seem to know even roughly the kind of changes that might be expected from climate change.

An important issue in relation to cod population dynamics that has not been addressed explicitly in any of the papers is the longevity of the cod under unexploited conditions. Given the estimated natural mortality of about 20% per year in the absence of any fishing, the biomass of fish older than 20 years would represent a significant contribution to the total stock. Indeed, very old and large cod have been reported frequently during the earlier periods in the history of exploitation of the different cod stocks in the North Atlantic. When the German cod fishery at Labrador started in the early 1950s, specimens up to the age of 40 years were observed regularly. The large number of year classes contributing to the virgin spawning stock biomass must have had a strong buffering effect against short-term variations in year-class strength of the age groups reaching maturity. Therefore, even if climatic events are directly related to year-class strength, the populations would have been able to survive prolonged periods of adverse conditions for juvenile survival. Longevity might even be considered an adaptation of the species to Subarctic conditions.

When the level of exploitation is increased, the number of year classes contributing to the spawning stock decreases correspondingly and at high fishing mortalities short-term variations in year-class strength are translated directly into short-term variations in spawning stock. Under these conditions, adverse climatic events of rather shorter duration could easily result in stock collapses. In other words, exploitation leads axiomatically to a reduced resilience of a stock against effects of climate.

From the different reviews presented on the individual cod stocks, it appears that, in general, levels of fishery mortality have increased in recent years to a level where approximately 70% of a year class is removed from the system annually. The concomitant drop in mean life expectancy and the associated fluctuations in spawning stock biomass may have made these stocks highly sensitive to climatic events. Still, it can be argued that the stock collapses observed in many of them, as well as the slow recoveries, are a direct consequence of overexploitation.

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Effects of a changing windfield on cod stocks of the North Atlantic (extended abstract)[1]

R. R. Dickson and K. M. Brander

This article reviews the impacts of climatic change on six North Atlantic cod stocks during the present century – at Iceland, Greenland, Labrador, the Faroes, the Barents Sea, and the Baltic.

When landings were at their individual maxima, sometime between the mid-1950s and the mid-1980s, these six cod stocks supported a total catch of around 3.5 $\times$ 10^6 t yr^{-1}. By the end of the 1980s, landings had dropped to about one-third of that total, driven down in most cases by an unsustainable degree of overfishing. That the fishing pressure was unsustainable was due in part to the impacts of a changing climate, and it is the aim of this article to identify some of the ways in which these climatic impacts have taken effect.

Climatic change can of course be described from any of a wide range of environmental variables. Here we emphasize the role of the windfield, because it is the nearest point at which we can offer a unifying context for the very different case studies we describe. Up to this point, we believe we can describe the essential changes in the windfield as pan-Atlantic in scale, and describable in terms of the long slow shifts of a few key indices. Beyond this point, the actual mechanisms by which these changes appear to have imposed their effects on cod stocks are surprisingly different in type and scale for each stock.

During the present century, the high latitudes of the Atlantic sector underwent a considerable wave of warming and salinification that included the Iceland–Greenland region, but was by no means confined to it. This change is illustrated in Figure 1 with reference to four of the longest series: the sea-surface temperature anomalies for the West Greenland Banks from 1876 to 1974 (Fig. 1a; Smed, in a succession of contributions to *Annales Biologiques*; Buch and Hansen, 1988), the salinity of the upper North Atlantic Central Water layer passing northward through the Faroe–Shetland Channel in 1902–1982 (Fig. 1b, from Dooley *et al.*, 1984), the winter sea-surface temperature (SST) at the Faroes, 1875–1969 (Fig. 1c, from Hansen and Meincke, 1984), and the temperature along the Kola Meridian (33°30′E) in the Russian Sector of the Barents Sea, 1900–1990 (Fig. 1d, from Loeng, 1991). Although long time series of salinity are less commonly available, we have sufficient glimpses of the salt record around the northern North Atlantic to suggest that the salinification was similarly pervasive, similarly protracted, and similarly extreme.

Thus, as salinities rose to unprecedented values in the Faroe–Shetland Channel in the late 1920s and 1930s (Tait, 1957; Dooley *et al.*, 1984; Fig. 1b), extreme values were also being encountered further around the subpolar gyre in the US Ice Patrol Standard Section running southwest from Cape Farewell.

In all cases, the period of peak warming and salinification occurred between the early 1930s and the late 1960s, and in a series of classic papers by Saemundsson (1934), Stephen (1938), Jensen (1939), Tåning (1943, 1949), and Fridriksson (1949), we are left in no doubt that this wave of warming and salinification was accompanied by radical northward shifts in the distributional boundaries for a wide range of marine species.

In other words, both the circulation and the ecosystem of the subpolar gyre appear to have undergone a slow evolution over large space and time scales during the present century. It is against this background that the large-scale changes in the Atlantic windfield have produced a differing regional response in six cod stocks from Labrador to the Barents Sea.

In socio-economic terms, the impact of the "warming in the North" reached a focus in the Iceland–Greenland sector, amplified through an apparent change in the effectiveness of egg and larval drift in the Irminger/West Greenland current system (Cushing, 1975, 1982). The

[1] "Cod and climate: the spatial and temporal context" by R. R. Dickson, K. R. Briffa, and T. J. Osborn (this volume) provides the descriptive background for "Effects of a changing windfield on cod stocks of the North Atlantic" which was presented at the Symposium on Cod and Climate Change but published elsewhere as part of a Festschrift in honour of Dr D. H. Cushing, FRS. The two articles were therefore intended to be complementary in content. For completeness, then, the Dickson/Brander report is represented here by an extended and illustrated abstract. For the full account, the reader is referred to *Fisheries Oceanography*, 2 (3/4): 124–153.

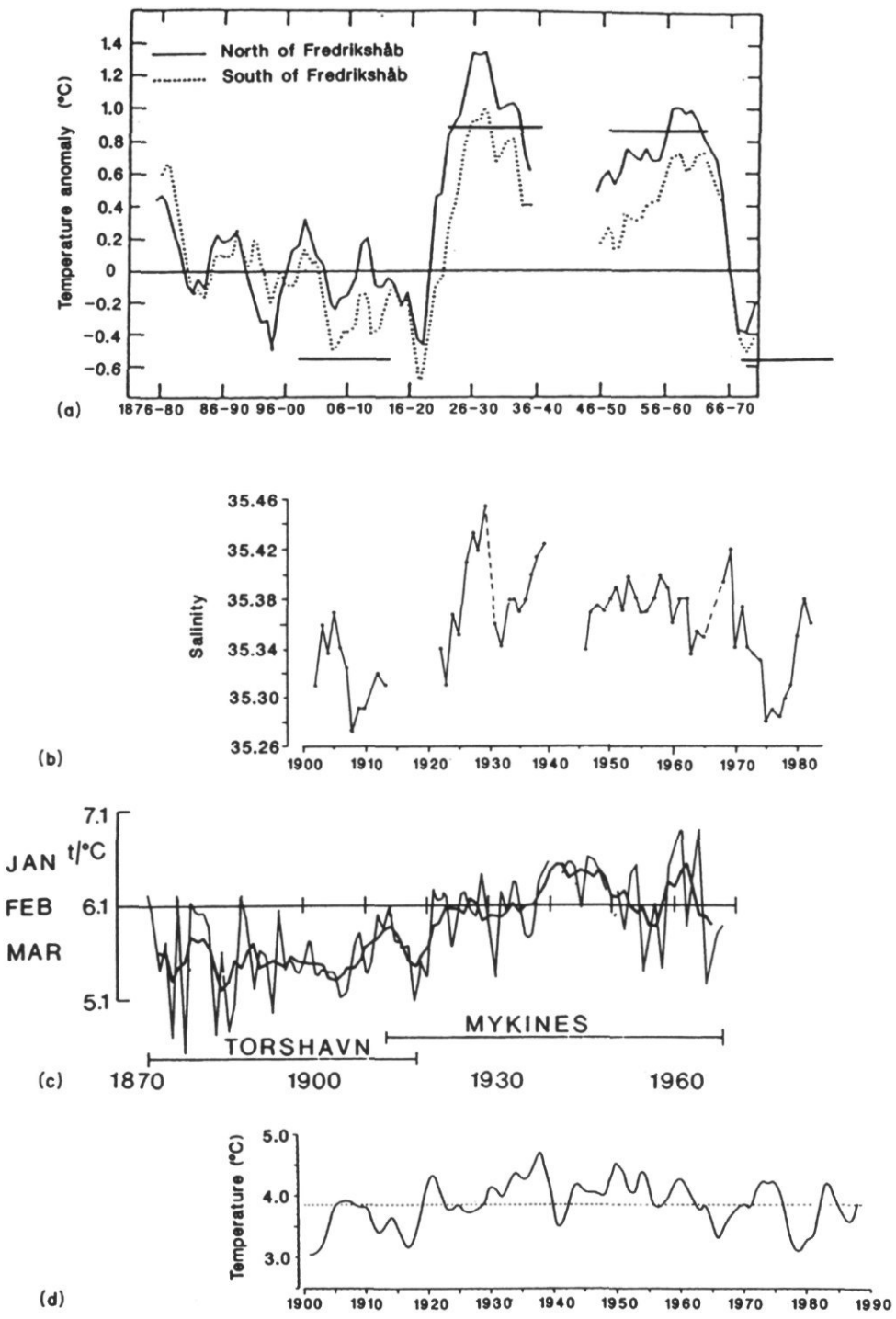


Figure 1. (a) Surface temperature anomalies for West Greenland, 1876–1974 (Smed's data, from Buch and Hansen, 1988); (b) the salinity of the North Atlantic Water in the Faroe–Shetland Channel, 1902–1982 (from Dooley *et al.*, 1984); (c) winter surface temperature at the Faroes, 1875–1969 (from Hansen and Meincke, 1984); (d) 3-year running averages of yearly temperature along the Kola Section of the Barents Sea, 1900–1990 (from Loeng, 1991), plotted to a common time base. The horizontal bars in Figure 1(a) refer to the warm and cold periods for which windfields are compared in Figure 3.

body of evidence is circumstantial but appears to be self-consistent. As Buch and Hansen (1988) indicate, the warming on the West Greenland Banks was accompanied by an explosive development of the West Greenland cod fishery, which, from a negligible tonnage in the early 1920s, rose to over 300 000 t yr^{-1} in the 1950s and 1960s, and a maximum of >450 000 t yr^{-1} before abruptly declining once again between the late 1960s and the present, as cooler conditions returned. Such "cod periods" have been documented in the past at West Greenland, in the 1820s and 1840s (Hansen, 1949), but this change represented a return of cod to West Greenland after an absence of at least 50–70 yr (Buch and Hansen, 1988; Dickson *et al.*, 1994).

The hypothesis is that this change was both initiated and maintained by an increased exchange of cod larvae from the spawning grounds off southwest Iceland during the warm decades compared with the cold periods which preceded and succeeded them. Two items of evidence sustain this theory. The first is based on the use of haddock as a tracer of larval exchange. Unlike cod, haddock do not spawn successfully at West Greenland, so if adult haddock are caught there they must have drifted there as larvae; the closest known spawning site for haddock lies upstream near the cod spawning grounds off southwest Iceland. When we compare the (small) international catch of haddock at West Greenland with the (large) international catch of cod, we find essentially similar trends of change in both species since 1952, when annual haddock catch statistics first became available (listed in Hovgård and Messtorff, 1987); there is even a qualitative similarity before that, with the first specimen of haddock reported from Greenland waters in 1929, infrequent occurrences in the 1930s, frequent catches in 1945, etc. (all from Hovgård and Messtorff, 1987).

Thus, while it is possible that the first cod colonizing the West Greenland Banks established a self-sustaining stock there, purely through the amelioration of the marine climate, the parallelism between cod and haddock catches along the western banks seems to argue that recruitment to the West Greenland cod stock was fed to a significant extent by a time-varying larval drift from Iceland.

We find confirmatory evidence in the work of Kushnir (1994) that during the period of warming off West Greenland the North Atlantic windfield was configured in such a way as to boost the warm Irminger Current. This establishment of increased easterlies over the west-going Irminger was not just a small-scale local event, however. Figures 2a and b are truncated extracts from Kushnir's North Atlantic study, showing the change in the windfield during winter (December to April) that occurred during the warming of the 1920s and the cooling of the 1960s. The sense of the change has been made comparable by subtracting the 15-year cold-year average from the 15-year warm-year average in each case. And in each case the sense of the change from cold to warm periods, during the season of egg liberation and early larval drift, has been one of increased easterly airflow overlying the westward-flowing Irminger Current.

Temporally, we suspect that this stimulation of the spread of warmth and larvae to West Greenland in the 1930s to 1960s was a most unusual event. Kushnir's U-index (Fig. 3) registers the cyclonic or anticyclonic tendency over a large area of the central North Atlantic between 30°N and 60°N, and shows that only during the 1930s to 1960s was the large-scale Atlantic windfield dominated by a major cyclonic centre in mid-ocean, with easterlies sweeping around its northern rim across the Irminger Sea.

The conclusion that the West Greenland stock was maintained through the spread of warmth and larvae from Iceland bears the implication that its abrupt decline as well as its rapid rise was due primarily to large-scale climate change, not fishing pressure. It also poses the question as to whether and under what circumstances there might have been a similar interchange further downstream between the cod stocks of West Greenland and the Labrador coast of Canada, even though it is clear from the outset that the possibilities of such an exchange must be limited to the three or four decades in this century when the West Greenland stock was sufficiently strong to act as a source of larvae.

Reviewing the available evidence – none of it conclusive – we note with Hovgård that a proportion of the West Greenland larvae was spread west into the Davis Strait in eight out of ten years (1955–1964), but we believe that in only one of these years (1957) was there evidence for an actual, long-range, inter-stock exchange. In that year, not only were the spawning-stock biomass and year-class strength of cod at West Greenland close to their absolute maximum (Hovgård and Buch, 1990; their Figs. 3.4 and 3.5), but the anomalous airflow off West Greenland in May–July 1957 was such as to divert the bulk of this large larval production offshore into the Davis Strait, so that at any rate in its initial stages, the "conveyor" was at its most productive and its most direct.

Whether these larvae reached the Labrador Shelf is conjectural. We can document the arrival on the northern shelf of juvenile *Sebastes mentella* of the same year class and apparently from much the same spawning grounds off southwest Greenland, because they were encountered there as 1-groups by Templeman (1961) in the summer of 1959. However, the evidence that an effective transport of cod larvae to Labrador might have taken place in that year is a reduction in the mean vertebral count, and a sequence of high mortality esti-

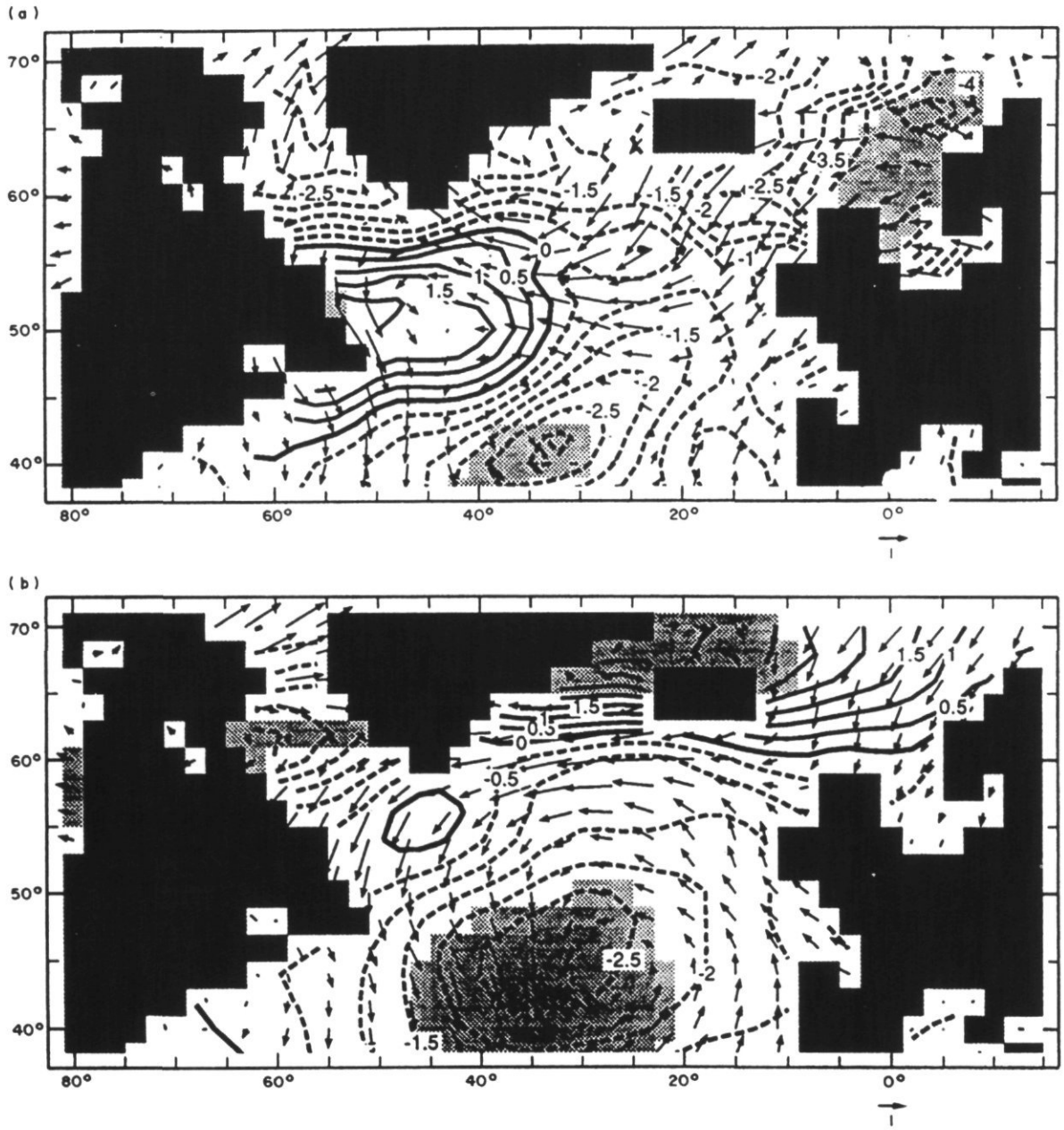


Figure 2. Change in winter mean sea level pressure and winds associated with the change from cold to warm conditions in the northern North Atlantic (a) from 1900–1914 (cold) to 1925–1939 (warm) and (b) from 1970–1984 (cold) to the antecedent warm period, 1950–1964. Adapted from Kushnir (1994). These periods are indicated by horizontal bars in Figure 1(a).

mates (F) in the 1957 year class of the northern cod at ages (6+) when the adults of any larval emigration would be returning to Greenland.

To some extent, to attempt to refine this conclusion by piecing together other evidence from other data sets is to risk missing the point. The main point is already made: that the chain of circumstances required to promote effective exchange between the cod stocks of West Greenland and Labrador is sufficiently tenuous that successful intermixture is a rare event.

Thus the close correlation between the cod catches at West Greenland and Labrador in recent decades is not

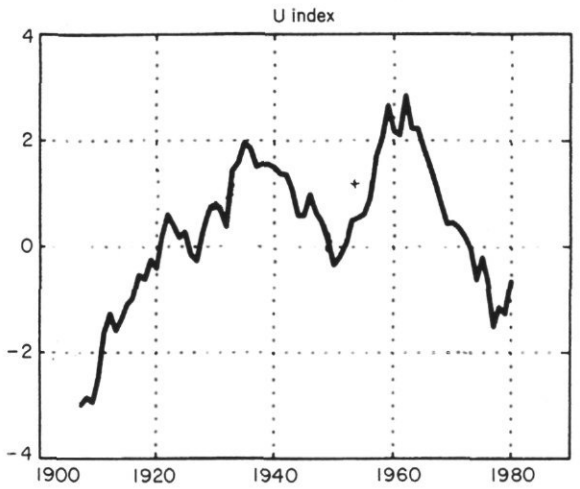


Figure 3. Fifteen-year running means of the difference between the wintertime zonal wind component at (30–40°N, 20–40°W), and (50–60°N, 20–40°W). A positive (negative) index value indicates that a cyclonic (anticyclonic) circulation dominated the central North Atlantic (from Kushnir, 1994).

evidence of any dynamical interplay between the two stocks, and although Jakobsson (1992) leaves open the question of whether climatic conditions might have contributed to this "short-term outburst of cod in this area" during the 1960s (the first since 1850), the evidence is that it will only very rarely have concerned the climatic stimulation of larval exchange from Greenland – either in years such as 1957 when the normal current system might have been short-circuited, or in years of extreme cold when larval development might have been sufficiently prolonged to allow the young fish to reach Labrador by the normal route.

Throughout the century-long change in the cyclonicity/anticylonicity index in the central North Atlantic (Fig. 3), a further key index – the waxing and waning of high pressure at Greenland – was undergoing a parallel slow evolution (Fig. 4). As the Greenland Ridge reached its 20th-century maximum in the mid to late 1960s, it triggered four separate impacts in three Atlantic cod stocks.

First, it directed an intense and refrigerating northerly airflow across the Norwegian–Greenland Sea, especially during winter, ushering in the first post-World War II period of prolonged cooling in the marine environment of the Barents Sea (Fig. 5) with adverse effects on the year-class strength of the Arcto-Norwegian cod.

Second, the southward transport of cold fresh, Polar Water in a swollen East Greenland Current, and its preservation through convective capping and ice formation north of Iceland (Malmberg, 1969, 1973; Dickson *et al.*, 1988), provided the initiating conditions for the Great Salinity Anomaly, which then entered the circulation of the Northern Gyre via the Denmark Strait. The reversal of Kushnir's cyclonicity index (Fig. 3) had already, from the early 1960s, begun the process of climatic deterioration on the West Greenland Banks, progressively withdrawing the basis for the easterlies which had spread warmth to these waters via the Irminger–West Greenland current system. Now, after a short advective time-lag, the arrival of the chill fresh conditions of the GSA in the last years of the 1960s accelerated the deterioration of the marine climate there, and continued the reduction/retraction of the West Greenland cod stock (Blindheim and Skjoldal, 1993).

One decade later, during the last years of the 1970s, the slowly propagating signal of the GSA arrived in the Barents Sea (Dickson and Blindheim, 1984; Dickson *et al.*, 1988). Throughout most of its long drift, off north Iceland, West Greenland, Labrador, and the Norwegian coast, the GSA signal had been accompanied by a minimum in surface and subsurface temperatures also, and the near-record cooling which spread across the Barents Sea shelf in the late 1970s/early 1980s (the second post-war cold episode at Kola in Fig. 5) can therefore fairly be described as a third *deferred* effect of 1960s pressure changes at Greenland. Its effects on the Northeast Arctic cod stock are now known to be only one part of a complex of changes which affected the Barents Sea ecosystem at this time (Sundby and Godø,

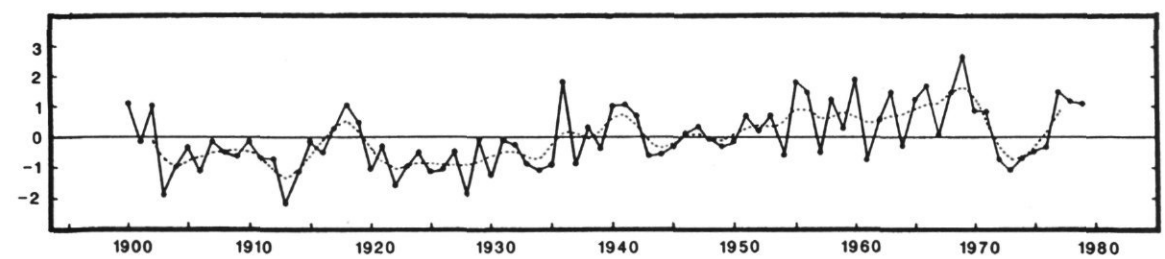


Figure 4. Normalized winter mean pressure anomaly for the region 60–70°N 30–65°W, 1900–1979 (from Rogers, 1984).

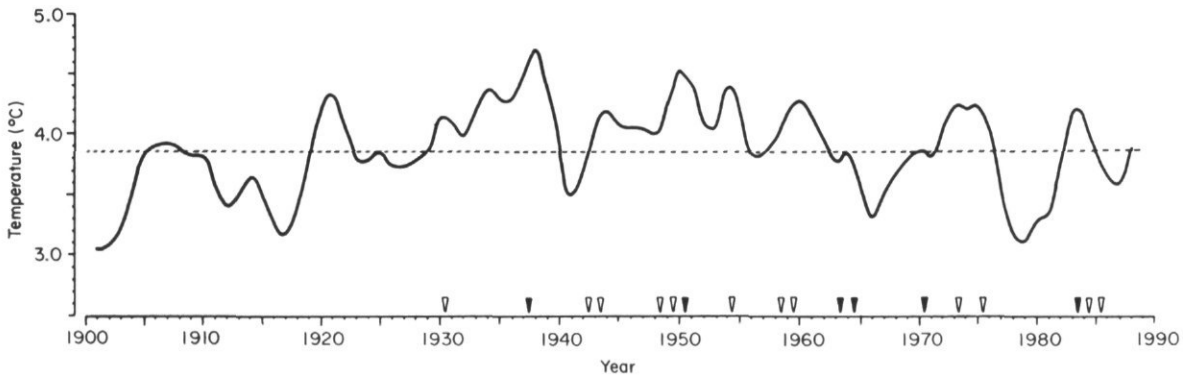


Figure 5. Three-year running averages of yearly temperature along the Kola Section of the Barents Sea, 1900–1990 (from Loeng, 1991) with indications of good (▼) and moderate (▽) year classes of the Northeast Arctic cod since 1930 superimposed (from Loeng, 1989).

1994), but with much the same net effect as during the earlier direct-cooling episode of the 1960s, i.e., low growth and a succession of poor year classes.

The fourth separate effect of the 1960s pressure anomaly at Greenland is found in a comparison of Figures 4 and 3 with Figure 6. As the winter pressure at Greenland (Fig. 4) and the cyclonicity over the central North Atlantic (Fig. 3) reached their 20th-century maximum intensity, the North Atlantic Oscillation (essentially a measure of their pressure difference) dropped to its long-term minimum (Fig. 6), indicating a minimum in the strength of the mid-latitude westerly circulation.

At the "event scale" of windiness, Holt (1991) reports that the prevalence of specified classes of strong wind events in the Northeast Atlantic showed something of a parallel evolution, decreasing gradually but steadily

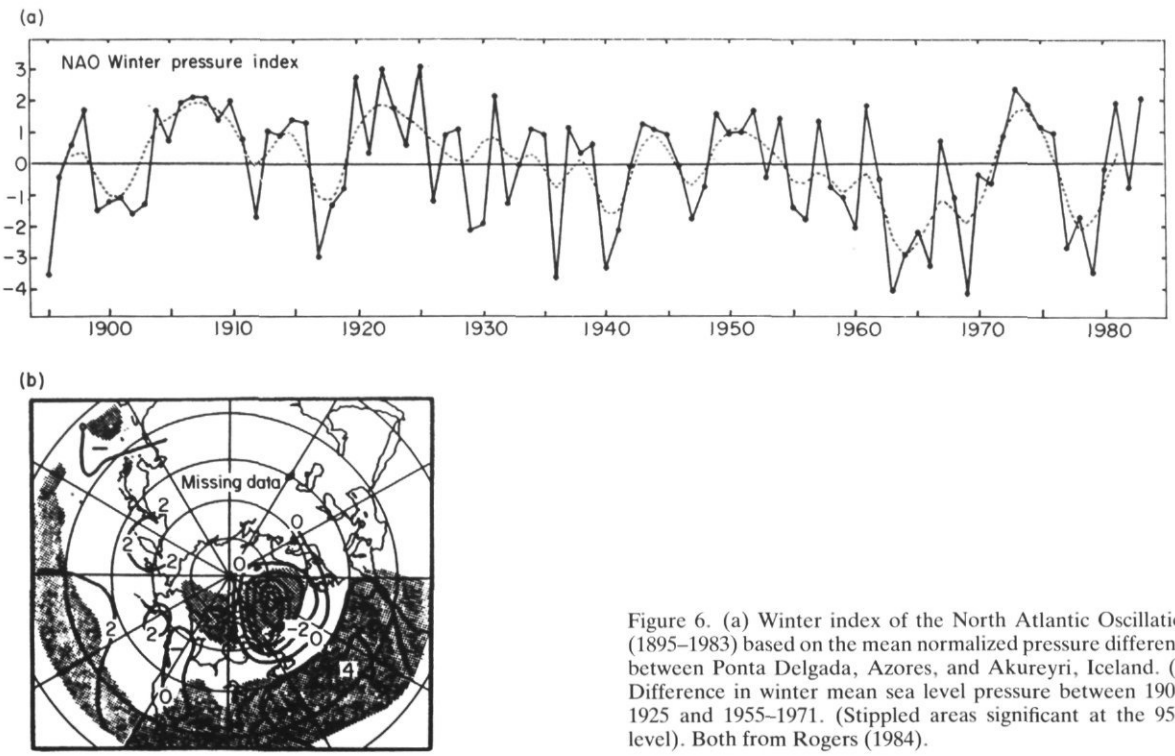


Figure 6. (a) Winter index of the North Atlantic Oscillation (1895–1983) based on the mean normalized pressure difference between Ponta Delgada, Azores, and Akureyri, Iceland. (b) Difference in winter mean sea level pressure between 1904–1925 and 1955–1971. (Stippled areas significant at the 95% level). Both from Rogers (1984).

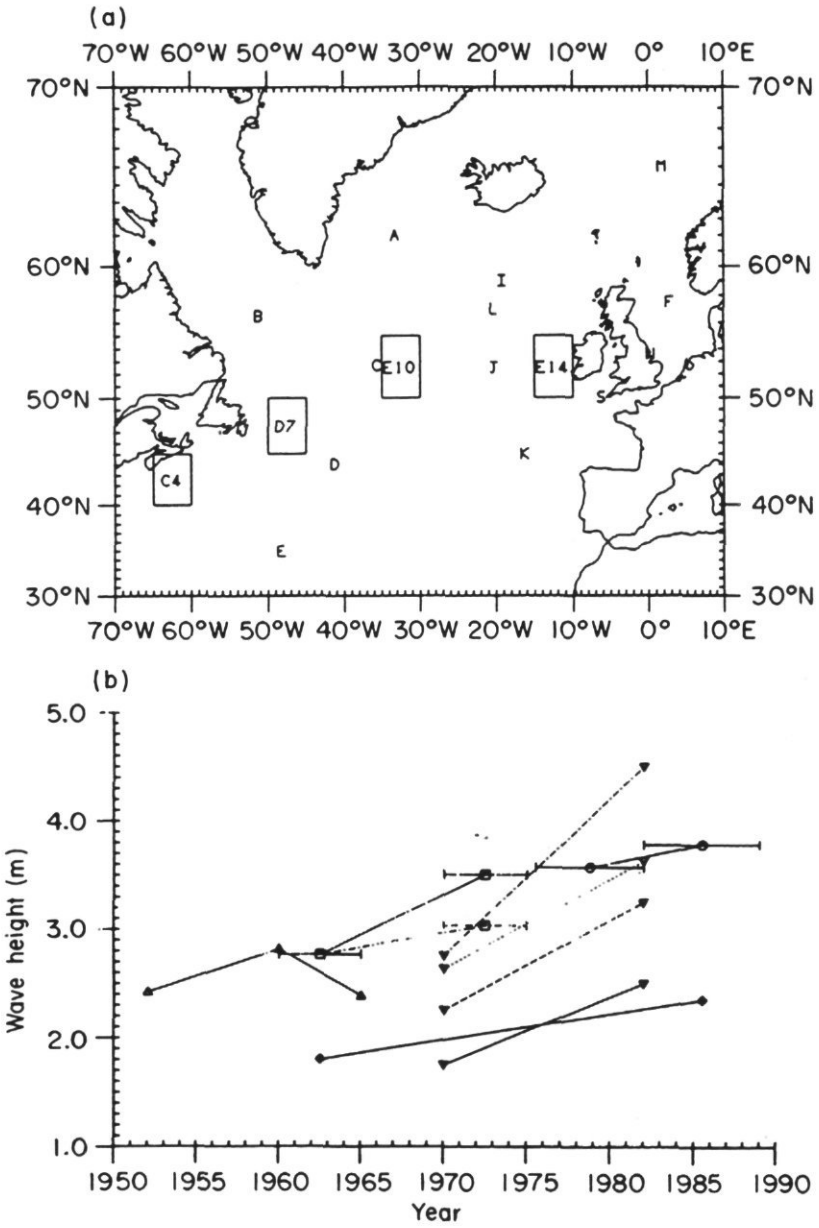


Figure 7. (a) Location and (b) trend in mean wave height data from a range of sites in the North Atlantic and from the early 1950s to 1989. From Bacon and Carter (1991). In 7(a), Ocean Weather Ship positions are shown by A, B, C, D, E, I, J, K, L, M; Dowsing Lightvessel as W, Seven Stones Lightvessel as S, the North Sea Rescue ship FAMITA by F, and four of the 5° × 5° boxes analysed by Neu (1984) are labelled C_4, D_7, E_{10} and E_{14}. For the key to Figure 7(b), see Bacon and Carter (1991).

over 60 years to the 1950s or early 1960s. Since then, the North Atlantic Oscillation index and westerlies have increased again only fitfully (short-term upturns in the 1970s and 1980s; Figs. 6 and 8), but there has been a steadier increase in gale frequency, and – apparently in confirmation – a steadily increasing trend in mean wave heights across a broad swathe of the mid-latitude North Atlantic (Fig. 7). It is not known whether the large scale and the short space/time-scales of windiness are dynamically linked, but Bacon and Carter (1993) have recently demonstrated a connection between mean wave height trends and a large-scale atmospheric pressure gradient which drives the Atlantic westerlies.

The response to these long-term shifts in windiness at

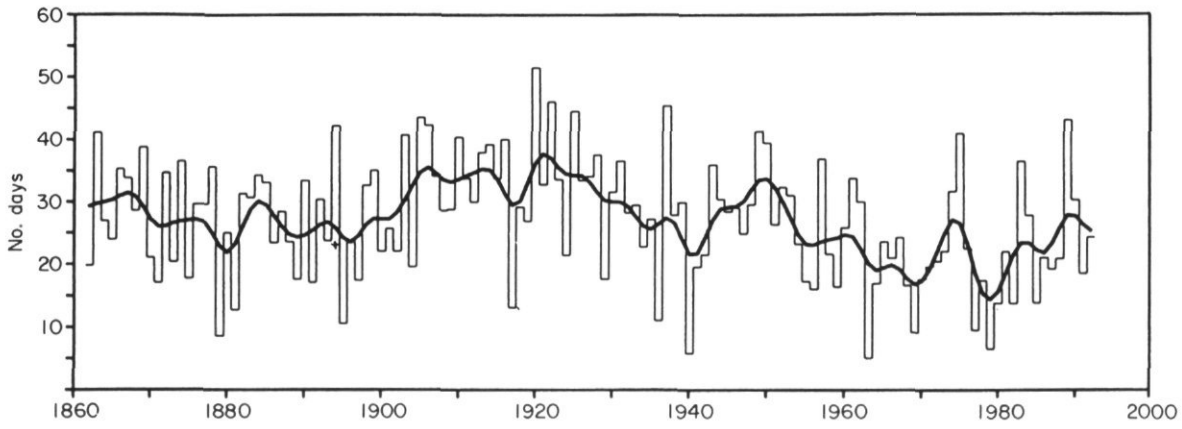


Figure 8. Number of days of the westerly weather type over the British Isles in winters 1860–1993. (From Briffa *et al.* (1990), updated by Briffa (CRU/UEA, pers. comm., 1993)). Smoothed lines are decadal filtered values.

both the large scale and the storm scale seems to be reflected most clearly in the gadoids of the Faroe Plateau, where Hansen *et al.* (1990) find a similarly evolving trend in the ratio of haddock to cod in catches over almost 100 years. (No long records of year-class strength are available for either species).

That this change is a real response to environmental conditions rather than mere coincidence is suggested by the growing evidence from the Faroes and elsewhere that juvenile haddock exhibit such a markedly greater preference for stratified conditions as to render themselves the more vulnerable to changes in windiness as a result. A long-term increase then decrease in the haddock:cod catch ratio at Faroe is therefore the expected result of a long-term decrease then increase in non-directional windiness. While this case study hinges much more on the response of the haddock than on that of the cod to environmental change, this in itself is not irrelevant to the present review, since it highlights by contrast the conditions which promote stability in at least one of the cod stocks under review. At Faroe the factors which seem to buffer the cod against change seem to include a small stock size, a relatively well-mixed environment as juveniles and a retentive horizontal circulation. None of these is immutable, however (Gaard *et al.*, 1993).

The case of the Baltic cod provides a final example of the way in which a stock may respond to wind-induced changes in its physical environment. In this specialized case, there seems little room for doubt as to the proximate cause of change. If conditions at the depth and location of spawning are so fresh as to cause eggs to sink and so anoxic as to prevent their development, it becomes obvious that, as with so much else, the success of this major stock is linked to the inflow/stagnation cycle of the Baltic Deeps. The cause of *that* is much more conjectural and is bound to be complex, yet there seems to be a growing consensus, now validated by models, that *prolonged periods of westerly wind, above a certain strength, during winter* are an essential pre-condition of major inflows. The 130-year winter index of westerly weather for the British Isles (Fig. 8) does not exactly capture these requirements, but must be a reasonable proxy for them, and there is a sufficient correspondence between the short-term peaks in that index and the known chronology of major Baltic inflows to encourage that conclusion. If so, it is the only example in this review of a major stock responding to short-period changes in the regional windfield, even though these short-term events are then rectified into longer-term environmental change by the stagnation processes of the Baltic Deeps.

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Cod and climate: the spatial and temporal context[1]

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This article attempts to establish a spatial and temporal context for present cod and climate studies, with special reference to the West Greenland stock. After establishing the chronology of the three main cod periods of record on the West Greenland Banks, we investigate whether stock size during the cod periods of the 19th century were controlled by similar mechanisms to those which appear to have acted during the third great cod period of the mid-20th century; we further investigate whether the key environmental changes were the product of local, regional or global climate change.

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Introduction

It will be evident from many of the papers presented to this Symposium that the cod stocks of the North Atlantic sector have all responded to the shifts of regional climate in one way or another (e.g., Dickson and Brander, 1993, 1994); in certain cases, such as that of the West Greenland stock, the climatic control appears the dominant one, regulating the supply of warmth and larvae on which the stock depends.

Such case studies beg three questions, however: first, are the relevant environmental changes the product of regional or global climate change? Second, did similar climatic mechanisms control stock size in earlier years? Third, is our knowledge of climatic trends adequate to predict whether any key element of environmental change is likely to increase or decrease with time? All three are questions of spatial and temporal *context*. Here we attempt to answer them with special reference to the case of the West Greenland cod stock.

The cod periods at West Greenland in the 19th century

Any attempt to assess whether the major climatic controls on a cod stock are likely to have changed with time is bound to be a myopic process, since the quality or even the existence of both fishery and climatic statistics degrades rapidly with age. This attempt concentrates on the West Greenland stock, since its story is not so much one of changing abundance as of presence or absence, with equally stark accompanying changes in environmental temperature. The hope is, in other words, that the operation of the supposed control – a wind-induced change in the spread of warmth and larvae (Dickson and Brander, 1993, 1994) – will be evident even in a gappy and inconsistent 19th-century record.

The 19th-century abundance of cod at West Greenland is known in semi-quantitative terms from reports by Rink (1857) and others; these historical records have been conveniently summarized by Jensen (1925) and Jensen and Hansen (1931). According to what was reported to Rink, the *first cod period* occurred during the 1820s, when cod were present "in enormous quantities" in the Julienhåb District and reached as far north as Disko Bay. Thereafter, cod appear to be absent until ca. 1845–1850 when a *second cod period* occurred on both the offshore banks and inshore waters. In these years, the banks fishery was sufficiently abundant to attract vessels from Britain, with boats from Lerwick, Berwick and Hull taking part. The brig "Banchory" and the schooner "Jenny Hay" began the British involvement in 1845, the latter making a paying catch of 30 000 fish on the banks, the other not. This British presence increased to 10 ships annually at the time of the best fishing in 1848, when the largest catch was 44 000 fish for a 26-man crew from June to the end of September, but with all the other vessels catching 15 000–30 000 fish in the same year. By 1851 the fishery had declined once again; in that year only two boats from Lerwick and one from Berwick took part, and Rink records (p. 225) that the Berwick boat with a 21-man crew and fishing a

[1]See R. R. Dickson and K. M. Brander: "Effects of a changing windfield on cod stocks of the North Atlantic (Extended abstract)" in this volume.

"great-line" with 3000–4000 hooks got only 4036 cod. The years of this second cod period are also confirmed in the records of the local fishery. In 1845 a cod fishery was successfully undertaken at Holsteinsborg, initially on behalf of the Greenland Board of Commerce, later managed by a merchant named Thomsen. By 1850, however, the fishery went into rapid decline and by 1851 it was finished. In 1850 Thomsen had found very few cod at Fiskenaeset, only a single cod on the Bank off Godthåb, and only moderate catches off Sukkertoppen, but 1851 yielded practically nothing and the fishery was abandoned.

"Thus during the period 1845–1849 there was an abundance of cod in the southernmost district, Julienhåb, and the shoals extended up to Disco Bay; here during the autumn months the Greenlanders caught such enormous quantities of cod that they even learnt to dry and preserve them for winter supplies; but after this, in 1850, the cod were practically non-existent" (Jensen and Hansen, 1931 p. 5).

For the rest of the 19th century and into the early years of the 20th century, there were no reports of abundant cod either in inshore waters or out on the Banks. Thirty-one fishing voyages from Gloucester, Massachusetts, to the Davis Strait in 1866–1881 found "insufficient numbers to warrant their being salted" (Scudder, 1883). In 1901, V. Thorsen of the Greenland Administration and the brig "Lucinde" found no cod on Fylla Bank; in 1906, two Faroese cutters under Napoleon Andreasen of Thorshavn found not a single cod on the Banks from Holsteinsborg to Godthåb. ("I have never at any place searched longer and more keenly after fish than here at the coast of Greenland to be rewarded with such a poor result"); in 1908 and 1909, despite an extensive search along the Greenland Coast from the fjords to the offshore banks, Ad. S. Jensen and the brig "Tjalfe" found not a single fish on the Banks or along their seaward margins. In 1913, V. Thorsen fished the banks again on the steamer "Hans Egede" but in vain. Only in 1922–1924 did the Danish inspection vessels "Fylla" and "Islands Falk" find quantities of cod on Fylla Bank, and this experience was repeated by Johan Hjort in 1924 and 1925 aboard "Michael Sars" and "Dana". In 1925 the cod were found spawning for the first time (from Fiskenaes Bank to Store Hellefiske Bank; Jensen, 1926), while in 1928–1929 the cod had spread right up to Holsteinsborg and Disko Bay, signifying that hydrobiological change had once again swung full circle in these waters and that the *third great cod period of record* at West Greenland was well under way. Jensen and Hansen (p. 39) note that the spread of cod to Holsteinsborg since 1924 was accompanied by a scattering of coalfish (*Gadus virens* L.) "which had not been noticed at Greenland since far back in the previous century". The fact that the earlier coalfish occurrences referred to were caught off Frederikshåb in 1831 (Jensen, 1939) is perhaps an indication that the first Greenland cod period extended beyond the 1820s into the early 1830s.

Jensen (1939) is correct (p. 13) to be cautious when he states that "we have no certain information regarding good cod periods" from the mid-19th to the early 20th centuries, so that one or more may have happened unnoticed, but the evidence that does exist points to three cod periods at West Greenland – the first in the 1820s and extending possibly into the early 1830s, the second from the mid-1840s to 1850 and the third from the 1920s to be 1960s. And Dansgaard *et al.* (1975) are therefore also correct when they point out (p. 27) that "on the face of it, the recent warm peak was an unusual event".

Local change: the association of cod periods with climatic amelioration at West Greenland

Lacking direct observations, we have only tenuous and indirect evidence that the marine climate off West Greenland was as warm during the two brief cod periods of the early 19th century as it was during the third, more extended cod period of the mid-20th century. In his study of the state of the West Greenland Current up to 1944, Dunbar (1946) suggested that the decades of the 1820s and 1840s were "already well known to have been warm", citing Jensen's (1939) review; however, Jensen's conclusion appears to have been based on the presence of cod shoals northwards to Disko Bay, so that although we would agree the *likelihood* of the link with warming, its actual demonstration is not advanced.

Equally, we have little direct meteorological evidence with which to link the 19th-century cod periods to changes in the regional windfield. As Jones *et al.* (1987) show in their reconstruction of historic mean monthly pressure distributions for the European and North American sectors, no local pressure data are available until the beginning of the Stykkisholmur (Iceland) record in 1846, while Jones and Bradley (1992) cite 1866 as the start of meteorological records at Godthåb.

We do have a proxy record, however, which spans all three cod periods at West Greenland. From 1820 to 1930, Speerschneider (1931) has provided a semi-quantitative annual assessment of the state of ice ("Storis") in the Davis Strait based on the position of the ice-edge in summer reported in the daily logs of trading vessels. Since the Storis rounds Cape Farewell from the east, its presence and extent in the Davis Strait are not in any way a reflection of local ice formation, but a complex proxy for changes in the large-regional windfield and for the changing balance between the cold East Greenland and warm Irminger currents that might result

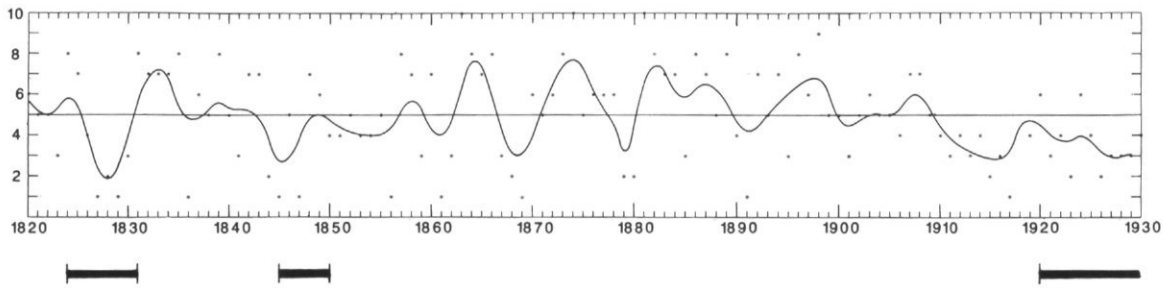


Figure 1. The state of the ice in the Davis Strait, 1820 to 1930, from Speerschneider (1931). Bars indicate the timing of the first two cod periods of record at West Greenland and the beginning of the third cod period.

(see Kelly *et al.*, 1987). Here we do not investigate the link between "Storis" extent and the windfield in any greater detail than Speerschneider himself did. We merely point out from Figure 1 that if such a link exists, then a similar change in the regional windfield is likely to have prevailed during each of the West Greenland cod periods, since all three were accompanied by long-term minima in the extent of "Storis".

Regional change: increased spatial coherence at longer time scales

Figure 2, from Briffa and Jones (1993), presents annual time series of mean air temperatures for a global scatter of 14 individual regions and for each hemisphere over the period 1901–1990. For details of method, see Jones and Briffa (1992) and Briffa and Jones (1993).

With a record length of only 90 years, these authors are principally concerned with describing the spatial coherence of air temperature variations in the particular band of time scales (years to decades) that is most accessible in their data. For these scales they show clearly that correlation decay lengths reach their hemispheric minimum values (<1500 km) at mid to high latitudes of the Northern Hemisphere, with absolute minima over Greenland and its adjacent seas in the annual, winter (DJF), and spring (MAM) analyses. They also remind us that at this particular (multi-year) time scale, the air temperature fluctuations at Greenland (GNLD) and Northern Fennoscandia (NFS) tend to be of opposite sign, part of the well-known Greenland–Northern European seesaw reviewed by van Loon and Rogers (1978).

However, the regional time series of Figure 2 also provides a glimpse of the much longer decade-to-century time scale in air temperature, and for this it is apparent that a very much larger coherence scale would be appropriate. On this multi-decadal time scale, Greenland, Iceland and Northern Fennoscandia all show a *common* wave of warming during the middle years of this century, and in Dickson and Brander's (1993) account this "Warming in the North" was also clearly present in sea-temperature records from Greenland, the Faroes and the Barents Sea.

The same conclusion regarding the greater spatial coherence of the longer-period fluctuations is also drawn by Dansgaard *et al.* (1975, p. 26) in describing the 1420 year variation of the δ function which describes the changing concentration of the heavy oxygen isotope (^{18}O) in ice-cores from Central Greenland: "The significant correlation [with central England temperatures in this case] suggests that the δ curve is representative of temperatures far beyond the Greenland area. But this applies only to the climatic changes of medium frequencies (60 to 200 year periods) that strongly dominate the records through the recent centuries (for short periods the δ curve is barely representative for the whole of Greenland)."

While the temperature changes at this scale are thus *internally* consistent in the northern North Atlantic, Figure 2 also suggests, however, that this limited sector of the northern hemisphere was the principal site in either hemisphere in which the recent global warming signal (Jones and Briffa, 1992) was relatively suppressed or non-existent. Though the winter and summer time series (not shown) are less regular in their evolution than the annual series shown in Figure 2, they show an essentially similar result (Briffa and Jones 1993, their Figs. 4 and 5).

Whether or not the cause is correctly understood, this recent regional suppression of warming or even cooling in parts of the northern North Atlantic is now reflected in the results of a range of general circulation models (GCMs). The assumption is that this regional anomaly is due to the presence in this sector of a globally important site of deep and intermediate water formation; that convection and sinking cause a convective heat flux from the deep ocean to the upper ocean; and that if the surface layer is stabilized by warming or freshening,

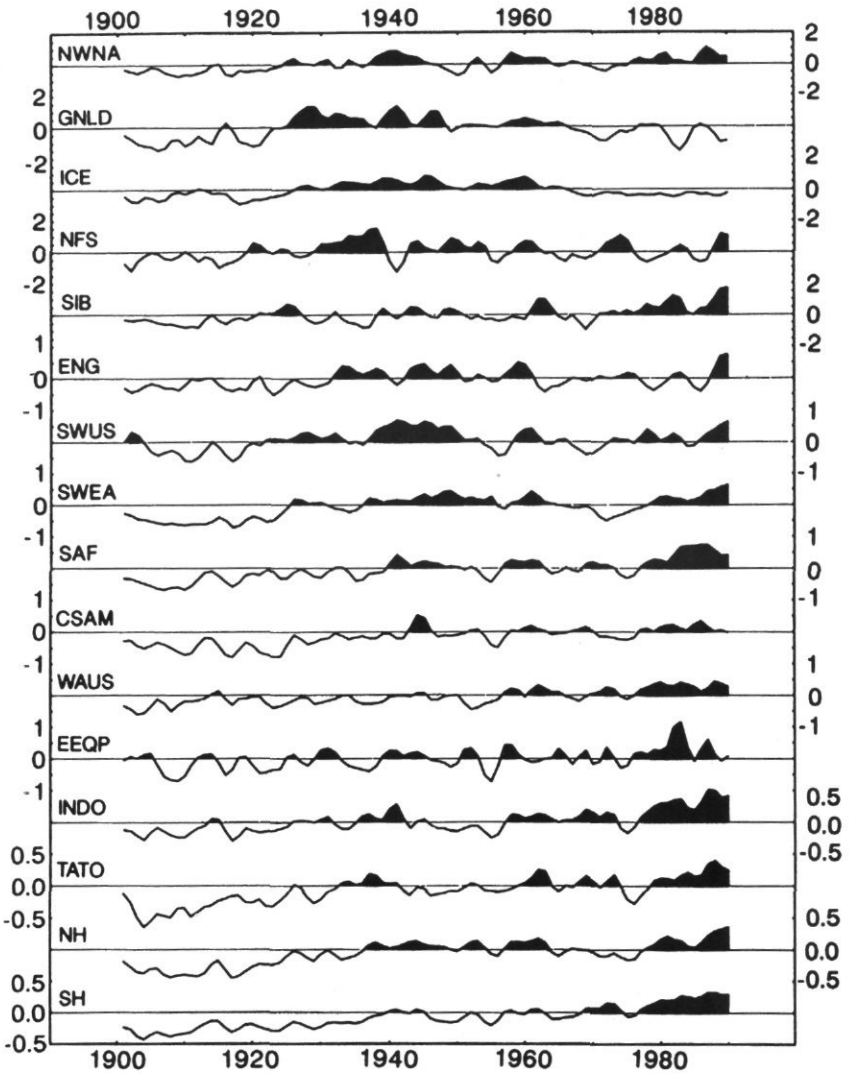


Figure 2. Annual time series of mean air temperatures for a global scatter of 14 individual regions and for each hemisphere 1901–1990 (from Briffa and Jones, 1993). Key: NWNA = Northwest North Atlantic, GNLD = Greenland, ICE = Iceland, NFS = Northern Fennoscandia, SIB = Siberia, ENG = England, SWUS = Southwest USA, SWEA = Southwest Europe, North Africa, SAF = South Africa, CSAM = Central South America, WAUS = West Australia, EEQP = Eastern Equatorial Pacific, INDO = Indian Ocean, TATO = Tropical Atlantic Ocean, NH = Northern Hemisphere, SH = Southern Hemisphere.

convection is suppressed, the heat fluxes are reduced and the upper ocean cools. Thus the response to "global warming" is cooling in this sector.

Using coupled ocean-atmosphere GCMs (but with a very coarse-resolution ocean model) Stouffer *et al.* (1989) found cooling in the northern North Atlantic in response to a gradual increase in atmospheric CO_2, while Washington and Meehl (1989) found reduced warming there. Using a coupled model but with no annual cycle, Manabe *et al.* (1990) found reduced warming around the Antarctic but not in the North Atlantic, perhaps because North Atlantic Deep Water production was already unrealistically weak in their model. Mikolajewicz *et al.* (1990) used an ocean-only model forced by a pattern of air temperatures consistent with some global warming experiments and found a local SST cooling in the Irminger Sea with reduced warming elsewhere in the northern North Atlantic. These results were essentially supported in the fully coupled ocean atmosphere model of Cubasch *et al.*, 1992.

If the models and their conclusions are valid, then the anomalous evolution of environmental temperature (air and sea) over recent decades in the northern North Atlantic may not be a regional peculiarity, locally driven, but the different regional response to a common global change.

Global change: detecting the onset and impact of global warming

It is of some importance to the present argument that climatic fluctuations of a few decades and longer, e.g. the wave of warming in the mid-20th century appear to be spatially coherent throughout the northern North Atlantic since it permits us to draw certain *regional* inferences from the ultra-long but more *localized* time series that have been constructed within this sector.

Figure 3 provides a reconstruction of northern Fennoscandian summer temperature anomalies (relative to 1951–1970) over the past 1400 years based on tree-ring width and density data from near the northern treeline of Scandinavia (Briffa *et al.*, 1990, 1992). The dominant long-term fluctuations revealed are not only paralleled in the instrumental record over the last 100 years or so (smooth curve, Fig. 3) but are also shown in the 600-year record of summer melting on the Svalbard ice cap nearby, as revealed in ice-core analyses by Tarussov (1992). The large-scale comparability of these proxies is further demonstrated and extended by Bradley and Jones (in press).

The 1400-year series of Figure 3 establishes the context of cod-and-climate in two main ways. First, it demonstrates that waves of warming similar in scale to that which pervaded the European Arctic and subarctic during the middle decades of this century have occurred before, for example in the 8th, 12th, 15th, 16th, 18th, and 19th centuries, well before any significant climatic forcing by anthropogenic greenhouse gases.

Conversely we also point out above (section (iv)) that the most recent thermal history of the northern North Atlantic, including the suppression of warming that was

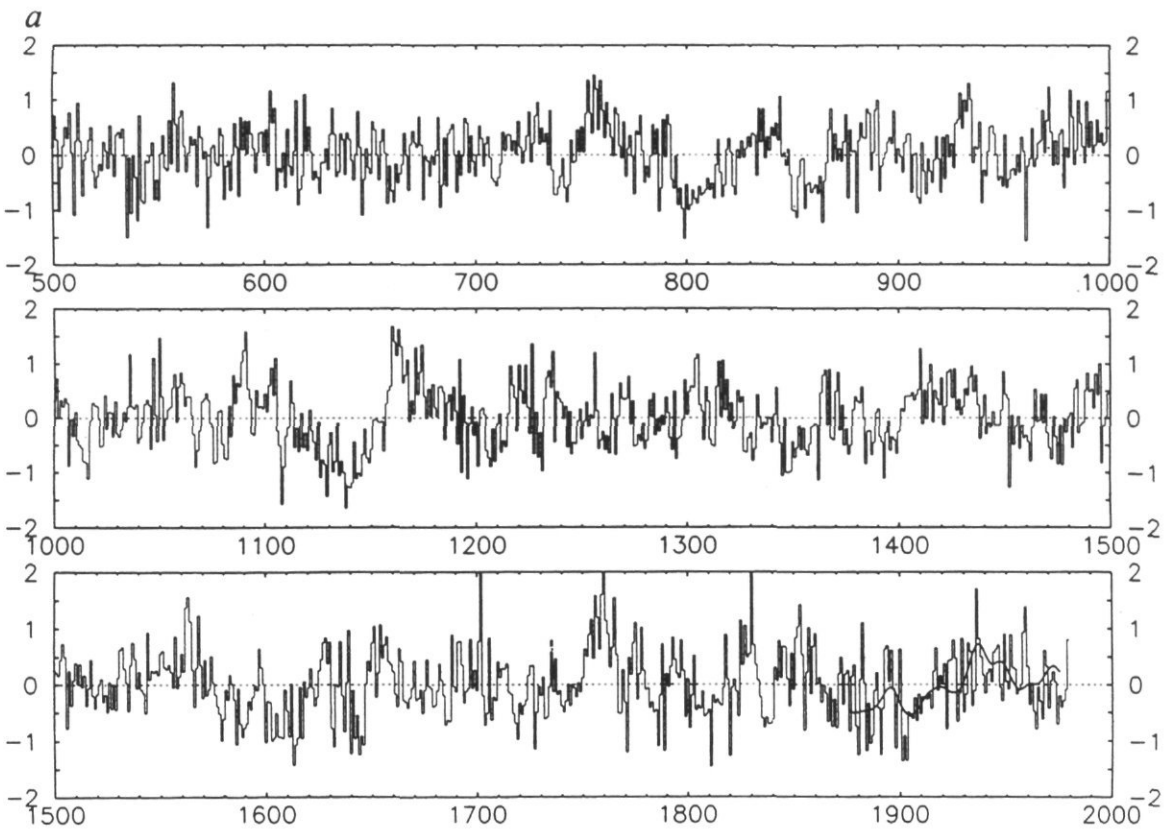


Figure 3. Northern Fennoscandian temperature anomalies in summer [°C; April–August means; normal period 1951–1970] reconstructed from tree-ring densities from the northern treeline of Scandinavia (from Briffa *et al.*, 1990). The instrumental record, smoothed with a 10-year low-pass filter, is superimposed after 1876 (smooth curve).

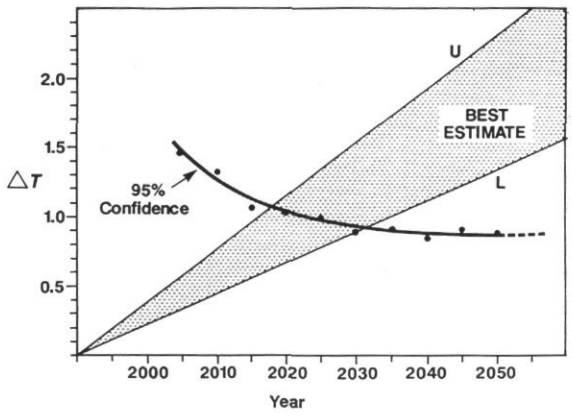


Figure 4. Upper and lower best estimates of northern Fennoscandian summer temperature increase expected to result from increases in greenhouse gases (straight lines through origin) together with the curve which describes the "detection threshold" for the greenhouse warming signal. For the latter, the full 1481 year reconstructed temperature record has been used to estimate the temperature trend over the 15, 20 . . . 60-year periods which followed each occasion on which temperatures were equal to those of today, and each point plotted is the upper-95-percentile point for a given length of trend. For example, the point plotted at 2030 (40 years after 1990) is derived from the distribution of 40-year trends in the reconstruction (from Briffa *et al.*, 1990).

observed and simulated in this sector in recent decades might yet include a partial response to greenhouse warming. The second use of the ultra-long time series of Figure 3 is to provide a basis for resolving this point or at least for predicting when the point is likely to be resolved. The logic is explained graphically in Figure 4 from Briffa *et al.* (1990). The upper and lower trend lines and the stippled area they enclose represent the best-guess range of northern Fennoscandian summer temperature increase expected to result from increased atmospheric loadings of greenhouse gases. The expectation is that northern Fennoscandian summer temperatures (April–August) will rise by between 0.9° and 1.5°C over the 40-year period from 1990 to 2030. Briffa *et al.* (1990) then used the full 1481-year proxy temperature record to identify each past occasion in which Fennoscandian summer temperatures were near to those of today and from each such occasion they then calculated the subsequent change of temperature over the ensuing 15, 20, 25 . . . 60 year period. Plotting the upper-95-percentile point from each such group of points (dots and curved line in Figure 4), Briffa *et al.* (1990) show that we are unlikely to be able to discriminate the cause (natural or anthropogenic) of any long-term change in Fennoscandian summer temperatures with much confidence until some time between 2020 and 2030.

Conclusions

1. In the period of record (essentially the 19th and 20th centuries) we can identify three major cod periods at West Greenland: in the 1820s (-1831?), in 1845–1850 and in the 1920s to 1960s. In terms of both frequency and duration, the most recent cod period was a most unusual event.
2. From what we know or suspect of the coupled physical and biological mechanisms which sustained the third great cod period in the 20th century it would seem unlikely that the two earlier periods could have been generated without some wind-induced increase in the spread of warmth and larvae from Iceland via a strengthened Irminger–West Greenland Current System. We lack direct observational evidence for such a change in the windfield or for warming along the West Greenland Banks during the cod periods of the 19th century, but the northerly extension of cod shoals to Disko Bay at such times, and long-term minima in sea-ice extent in the Davis Strait (itself a proxy for the windfield in the early part of the year) are partial evidence that similar hydrobiological processes were involved.
3. Although short-term climatic fluctuations at periods from years to decades exhibit small spatial coherence, the longer period fluctuations from decades to centuries appear to be more widely representative. Within the period of the instrumental record, the "warming in the north" and subsequent cooling are observed throughout the northern north Atlantic in the middle to late decades of this century. These common regional trends differ from the calculated global trends in air temperature, exhibiting suppressed warming or even cooling compared with the progressive warming trend elsewhere.
4. This different climatic behaviour may reflect the lack of greenhouse-gas warming in our sector or it may merely be the result of a different regional response to it. Analysis of the past 1400 year proxy record of Fennoscandian summer temperatures suggests that we will not be able to determine which with any confidence until the years 2020–2030, when present projections of global warming in this region are expected to exceed the normal range of past climatic behaviour.

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Cyclonic gyres in the North Atlantic

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Jónsson, 1994. Cyclonic gyres in the North Atlantic. – ICES mar. Sci. Symp., 198: 287–291.

The Subarctic gyres in the North Atlantic are the circulation cells between the Polar and Subarctic fronts. There are several of these gyres, they are all cyclonic, and their boundaries are determined mainly by topography. In the Nordic seas there is the Greenland Sea gyre and the Iceland Sea gyre, and there are separate gyral circulations in the Irminger and Labrador seas. The prevailing weather system in this part of the world is the Icelandic Low and the maximum windstress curl along its path runs through the cyclonic gyres. The climatological mean wind system imposes a large positive vorticity on the ocean below it. It is shown that the climatological mean transport in the gyres is of the same order of magnitude as predicted by the flat-bottom Sverdrup transport. The Icelandic Low shows wide-ranging seasonal variations, being extremely strong during winter. The transport variations caused by this, using the flat-bottom Sverdrup relation, are much larger than the observations indicate. This can probably be accounted for by the inclusion of topography, which reduces the transport variations significantly. The Icelandic Low also displays considerable interannual variations, which are shown to affect the conditions in the gyres; these effects are discussed for the gyres of the Greenland, Iceland, and Irminger seas. It is shown that a strong Icelandic Low creates favourable conditions for deepwater and bottom water formation in the gyres by decreasing the stratification in their central parts. A strong Icelandic Low probably also speeds up the circulation in the gyres, increasing the area covered by Atlantic water and displacing the Polar Front to the west.

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Introduction

In order fully to understand climate changes in the ocean it is necessary to understand how the ocean responds to the forces that impinge on it. One of the primary forces acting on the ocean is the wind system and most of this paper is devoted to study of the effect that this has on the cyclonic gyres in the North Atlantic. The atmosphere is of course also influenced greatly by the ocean beneath, and the two are strongly interrelated.

The circulation of the ocean at high latitudes is characterized by a number of large-scale cyclonic gyres (Fig. 1). In the North Atlantic there is such a gyre in the Greenland Sea, the Iceland Sea, the Irminger Sea, and the Labrador Sea. In the North Pacific there is the Alaskan gyre in the Gulf of Alaska. In the southern hemisphere there is the Weddell Sea gyre and the Ross Sea gyre. In many respects, this has a bearing on, for example, deep and bottom water formation in the world oceans. These gyres are situated in areas where low-pressure systems dominate, and it is therefore appropriate to discover what kind of influence the wind has on these gyres and especially whether the wind systems control the interannual variability that is observed, and what effect the wind has on the current structure in them.

Since many of the cod stocks in the North Atlantic live on the shelves marking the edges of the cyclonic gyres, it is of primary interest to study the circulation of the gyres and their influence on the conditions over the shelves. The gyres contain much more water than the surrounding shelves and thus have a much greater effect on the large-scale climate than the shelf waters. Many of the habitats of the cod lie close to the Polar Front such that one might expect the cod to be vulnerable to changes in the position of the Front.

Wind system

Since it is the curl of the windstress ($\nabla \times \vec{\tau}$) that appears as the dominant term in the quasi-geostrophic potential vorticity equation, the windfield is discussed in terms of

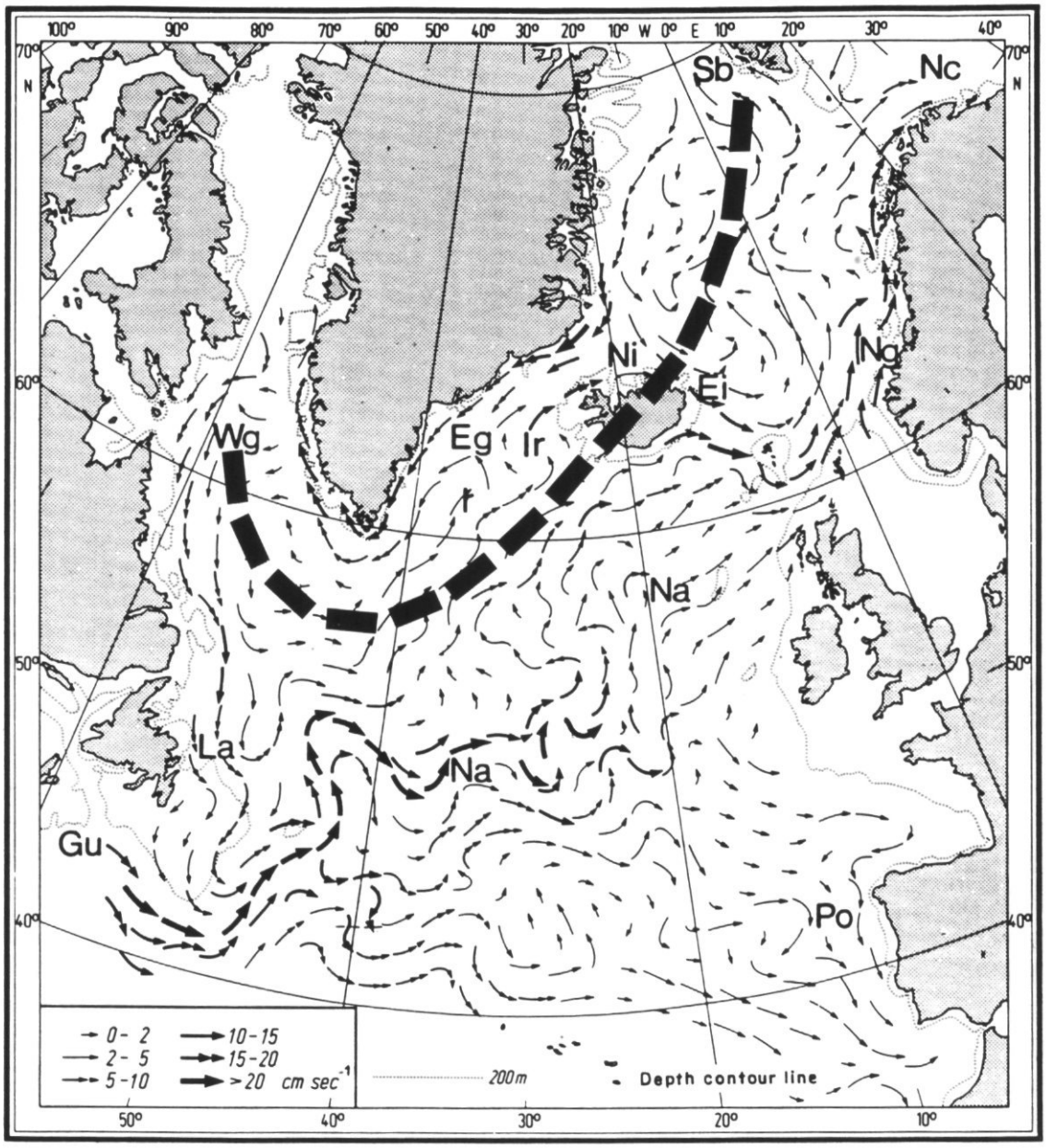


Figure 1. The circulation in the North Atlantic (from Dietrich *et al.*, 1975). Also, the position of the local maximum of windstress curl over the North Atlantic as calculated by Hellerman and Rosenstein (1983) and Jónsson (1991) (drawn as a thick dashed line).

this parameter. The wind system governing the area over the Subarctic gyres in the North Atlantic is the Icelandic Low. The surface winds blow cyclonically around the centre of the low pressure system, thus imposing a positive vorticity on the ocean below. The windstress curl is a measure of this vorticity. Hellerman and Rosenstein (1983) studied the global distribution of windstress curl and found that it was extremely large during winter in the areas dominated by the Icelandic Low, with the maximum over the Irminger Sea. They had limited data coverage of the area, however, and the error estimates were of the same order as the windstress curl itself. Using a more extensive data set, Jónsson (1991) studied the windstress curl over the Nordic seas

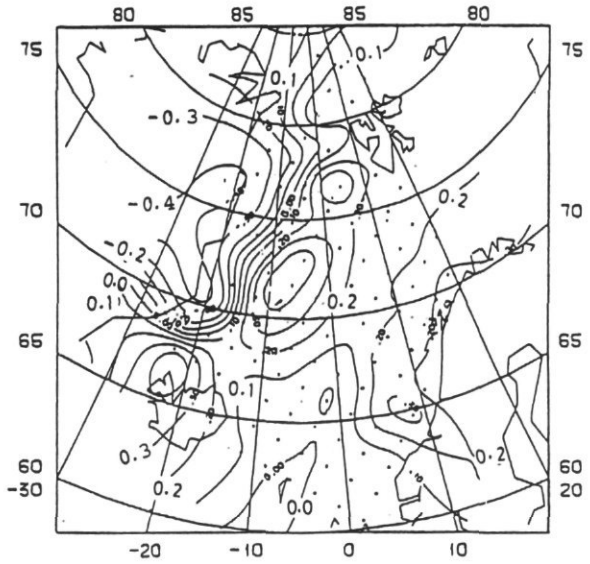


Figure 2. Mean windstress curl over the Nordic seas for the period 1955–1987. The unit is Pa/1000 km and the contour interval is 0.1 Pa/1000 km (from Jónsson, 1991).

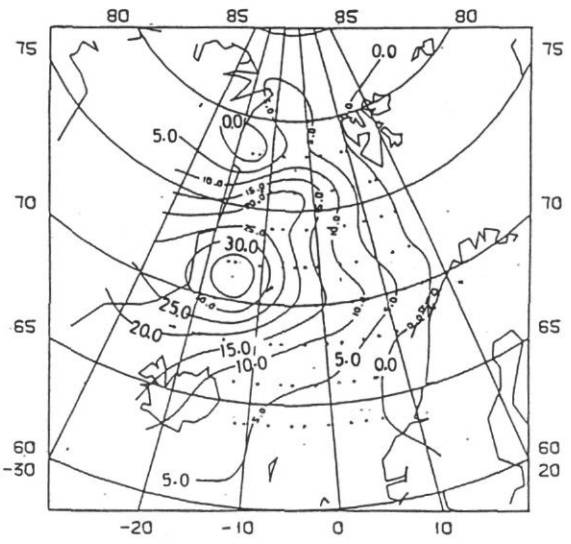


Figure 3. The flat-bottom Sverdrup balance corresponding to the mean windstress curl in Figure 2. The unit is Sv and the contour interval is 5 Sv (from Jónsson, 1991).

and found that the local maximum curl was observed on a track ranging from Northeast Iceland towards Spitsbergen (Fig. 2). Using these two sources, the local maximum in windstress curl has been drawn in Figure 1, together with the circulation pattern in the North Atlantic as determined by Wegner (1973). The local maximum of windstress curl along the path of the Icelandic Low is seen to coincide with the central parts of the Subarctic gyres.

Sverdrup transports

The windstress curl can be used to calculate the flat-bottom Sverdrup transport, which is the integral along a latitude of the windstress curl divided by the north–south derivative of the Coriolis parameter f. Aagaard (1970) calculated this quantity for the Nordic seas and found the maximum transport to be 35 Sv. The same result was attained by Jónsson (1991) using a more extensive data set (Fig. 3). Both these studies showed a single gyre circulation in the area. The topography splits the circulation into two gyres, one in the Greenland Sea and one in the Iceland Sea. The transport of 35 Sv in the western boundary current is very high, but unfortunately very few estimates of the transport based on current measurements are available. Meincke (1989) has estimated transport of the gyre over the Greenland Basin to be 18 Sv. This was based on one-year-long direct current measurements from a section across the East Greenland Current at about 75°N, and a linear decay towards the centre of the gyre was assumed. No estimates based on direct current measurements are available for the Iceland Sea gyre, but if it is similar in size to the Greenland gyre this can account for the 35 Sv of Figure 3.

Malmberg and Kristmannsson (1992) calculated the windstress curl over the Irminger Sea at 63°N, 30°W, and using their values for the average from 1974–1988 to calculate the flat-bottom Sverdrup transport this comes to 25 Sv. The flat-bottom Sverdrup transport into the Labrador Sea past Cape Farewell was estimated by Leetmaa and Bunker (1978) to be about 40 Sv. Clarke (1984) estimated the flow past Cape Farewell, based on geostrophy and moored current meters, to be 33.5 Sv, which is of the same order as the flow estimated by the flat-bottom Sverdrup balance. It was pointed out by Thompson *et al.* (1986) that the flat-bottom Sverdrup relation for the mean transport into the Labrador Sea past Cape Farewell is of the same order as the transport calculated in various models. In the Pacific Ocean, the annual mean transport of the Alaskan gyre was found by Musgrave *et al.* (1992) to be close to values estimated by the flat-bottom Sverdrup relation. All this evidence points towards the windstress curl being one of the main forces driving the mean circulation.

Aagaard (1970), Thompson *et al.* (1986), and Musgrave *et al.* (1992) all found that seasonal variations in the transport calculated using the flat-bottom Sverdrup relations were much greater than observations indicated. An example of such seasonal variation is shown in

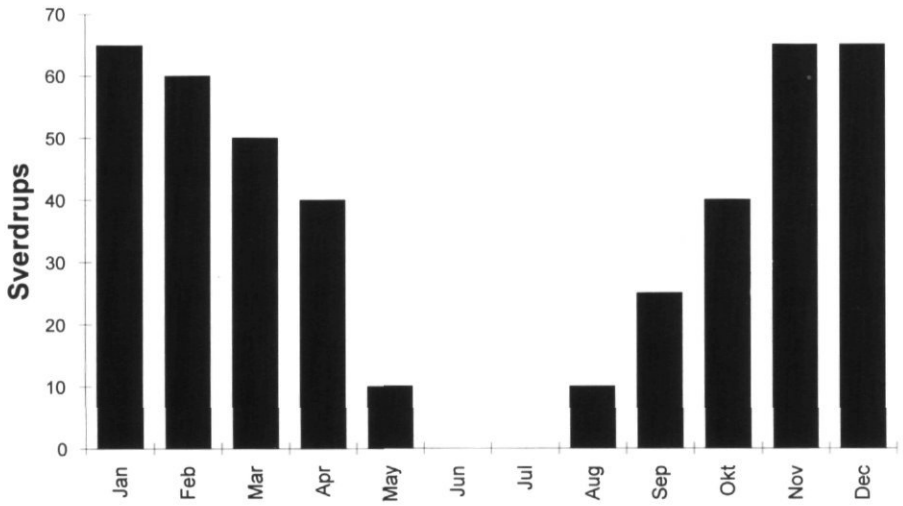


Figure 4. The seasonal variations in the flat-bottom Sverdrup transport in the Nordic seas.

Figure 4 for the Nordic seas. This is the average of the flat-bottom Sverdrup transport in the Nordic seas over the years 1955–1987 for each month based on data from the Hindcast database developed by the Norwegian Meteorological Institute (Jónsson, 1991). The transport is insignificant during the summer months, but rises to 65 Sv during November through January. Such enormous changes of transports are not consistent with observations. This problem was studied by Anderson and Corry (1985) using numerical models, where they examined the seasonal variation in the flow through the Florida Straits using observed seasonally varying windfield. They found that the response away from the western boundary was essentially barotropic and in the form of a topographic Sverdrup balance. A topographic Sverdrup balance means that the integration is not along a latitude but along a contour of f/H, where H is the bottom depth. The equation describing the topographic Sverdrup balance is:

$$\vec{u} \cdot \nabla \left(\frac{f}{H} \right) = \frac{\nabla \times \vec{\tau}}{\rho H^2}.$$

Anderson and Corry (1985) showed that the inclusion of topography reduced the amplitude of the annual cycle of the transport by a factor of two relative to the flat-bottom case. Thus, even though they could account for the long-term mean transport of the Gulf Stream using the flat-bottom Sverdrup balance, the magnitude of the seasonal transport variation was much less than predicted by this balance, and more in accordance with the topographic Sverdrup balance. Similarly, Thompson *et al.* (1986) found that the seasonal variation of the Sverdrup transport in the Labrador Current was reduced from 53 Sv to only 6 Sv when adding the topography. Thus the presence of topography seems to have the effect of reducing the variability of the circulation, relative to the flat-bottom case, thus rendering the system more stable to variations in the wind forcing. This does not mean that the wind system does not affect the variability of the gyres, just that the effect is not as drastic as predicted by the flat-bottom Sverdrup balance.

It has proven very difficult to provide direct evidence for the existence of wind-driven currents in the deep ocean. Thompson *et al.* (1986) were able to reduce the residual variance of sea level at the Labrador coast by a statistically significant amount by including the topographic Sverdrup balance, thus providing indirect (although not conclusive) evidence for it. In trying to identify the topographic Sverdrup balance in the North Pacific, Koblinsky *et al.* (1989) found some correlation between the local windstress curl and the deep currents. They estimated the amplitude of the locally forced topographic Sverdrup balance, i.e. the flow induced perpendicular to lines of constant f/H, to be about 0.1 cm s^{-1} and for the non-local topographic Sverdrup balance, i.e. the flow along lines of constant f/H, to be about 1 cm s^{-1}. It is therefore no wonder that it is very difficult to establish direct evidence for the topographic Sverdrup balance, since it is much weaker than the eddy kinetic energy signal. This was also confirmed in a study by Jónsson *et al.* (1992) in Fram Strait, between Spitsbergen and Greenland, where no systematic correlation pattern was found between the windstress curl over the Nordic seas and the current in the strait.

Interannual variability

Even if the drastic seasonal variations in windstress curl do not cause such large changes in the transports as predicted by the flat-bottom Sverdrup relation it can affect both the short-term circulation and the interannual variability of the circulation. It is mainly the interannual variability that is of interest here, some examples of which are discussed below. The wind affects the surface layer directly and because of the rotation of the earth it transports the surface layer to the right of the wind direction in the Northern hemisphere. This means that a low-pressure system will push the surface water out from the centre, i.e. there will be a divergence at the surface leading to an upwelling of deeper lying water. Another result of this will be a strengthening of the cyclonic circulation, i.e. a speeding up of the gyre circulation. Examples of this have been shown by Jónsson (1992) and Meincke *et al.* (1992) for the Iceland Sea and Greenland Sea gyres, respectively. For the Irminger Sea gyre some evidence exists for the circulation being speeded up there during the winter and that this causes an increase in the amount of Atlantic water that enters the North Icelandic Shelf (Malmberg and Kristmannsson, 1992). They also found that the amount of Polar water on the North Icelandic Shelf was less when the windstress curl was large over the Irminger Sea and the Iceland Sea, or simply when the Icelandic Low was strong. The implication of all these occurrences is that a strong Icelandic Low has the effect of increasing the flow of Atlantic water and increasing the area over which it spreads. It also has the effect of sharpening the Polar Front and displacing it westwards.

Conclusion

The effect of the windstress curl on the currents in the Subarctic gyres in the North Atlantic has been discussed. The flat-bottom Sverdrup transport estimated from the climatological mean windstress curl is of the same order as the observed transport in the gyres. The observations are scarce, however, and more work needs to be done if more precise estimates based on direct measurements of the transports are to be achieved. The seasonal time scale is too short for the flat-bottom Sverdrup balance to build up and the response to the wind is described by the topographic Sverdrup balance where the topography is important and renders the circulation more stable than predicted by the flat-bottom Sverdrup relation. It has proved to be very difficult to provide observational evidence for the topographic Sverdrup balance.

A strong Icelandic Low creates favourable conditions for deep and bottom water formation in the gyres by decreasing the stratification in their central parts. It probably also speeds up the circulation in the gyres, increasing the area covered by Atlantic water and displacing the Polar Front to the west.

Acknowledgments

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Changes in oceanic circulation of the North Atlantic as a result of an increase in atmospheric greenhouse gas concentrations

Uwe Mikolajewicz, Ulrich Cubasch, Gabriele Hegerl, Heinke Höck, Ernst Maier-Reimer, Benjamin D. Santer, and Stephan Schultz

Mikolajewicz, U., Cubasch, U., Hegerl, G., Höck, H., Maier-Reimer, E., Santer, B. D., and Schultz, S. 1994. Changes in oceanic circulation of the North Atlantic as a result of an increase in atmospheric greenhouse gas concentrations. – ICES mar. Sci. Symp., 198: 292–296.

The coupled ocean–atmosphere general circulation model developed at the Max-Planck-Institut für Meteorologie is forced with slowly increasing concentrations of atmospheric CO_2, corresponding to the International Panel on Climate Change "business as usual" scenario. As a consequence of this forcing the global mean surface air temperature increases by 2.9 K after 100 years of simulation. In the northern North Atlantic the warming is much less. This is connected with a continuous reduction in the formation rate of North Atlantic Deep Water. The thermohaline circulation of the Atlantic slows down and the structure of sea-surface salinity changes develops with negative values at 50°N and positive values at low latitudes.

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Introduction

During the last decade the problem of climate change as a consequence of the continuous increase in atmospheric greenhouse gas concentrations due to anthropogenic emissions has attracted an increasing interest from the public. Early three-dimensional modelling studies with atmospheric general circulation models (AGCM) coupled to a 50-m mixed layer ocean (e.g., Hansen *et al.*, 1984; Wetherald and Manabe, 1986; Wilson and Mitchell, 1987; Schlesinger and Zhao, 1989) focused public interest on global warming. More recent simulations with AGCMs coupled to three-dimensional ocean general circulation models (OGCMs) have shown the importance of a more realistic treatment of the thermohaline circulation of the ocean for a reliable estimate of future climate changes (e.g., Stouffer *et al.*, 1989; Cubasch *et al.*, 1992, 1993). The large heat capacity of the ocean makes the adaptation of the climate system to a change in the radiative forcing a much slower process than was estimated from the early modelling studies with AGCM plus slab ocean.

Model

In this paper we discuss results from simulations with the coupled ocean–atmosphere general circulation model (COAGCM) developed at the Max-Planck-Institut für Meteorologie in Hamburg. The atmospheric component of the model is the ECHAM1 AGCM (Roeckner *et al.*, 1989). This spectral model has a T21 resolution and 19 levels in the vertical. The oceanic component is the Large-Scale-Geostrophic OGCM (Maier-Reimer *et al.*, 1993). The horizontal resolution which has been adapted to match that of the AGCM, is $5.6° \times 5.6°$, and the model has 11 layers in the vertical. A sea-ice model with simplified treatment of stresses is included. Details of this coupled model, as well as of the coupling technique applied, have been described in Cubasch *et al.* (1992).

Results and discussion

With this model, two simulations have been carried out. In the first simulation the atmospheric concentrations of

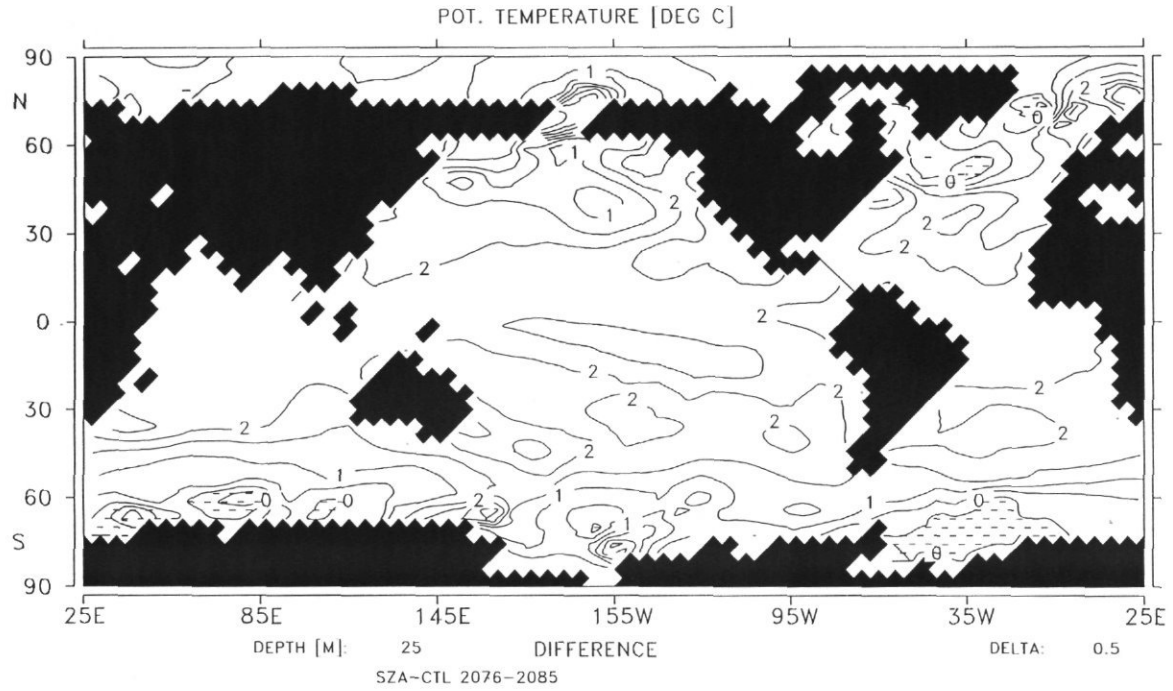


Figure 1. Annual mean difference in sea-surface temperature of the last decade between the greenhouse experiment and the control run.

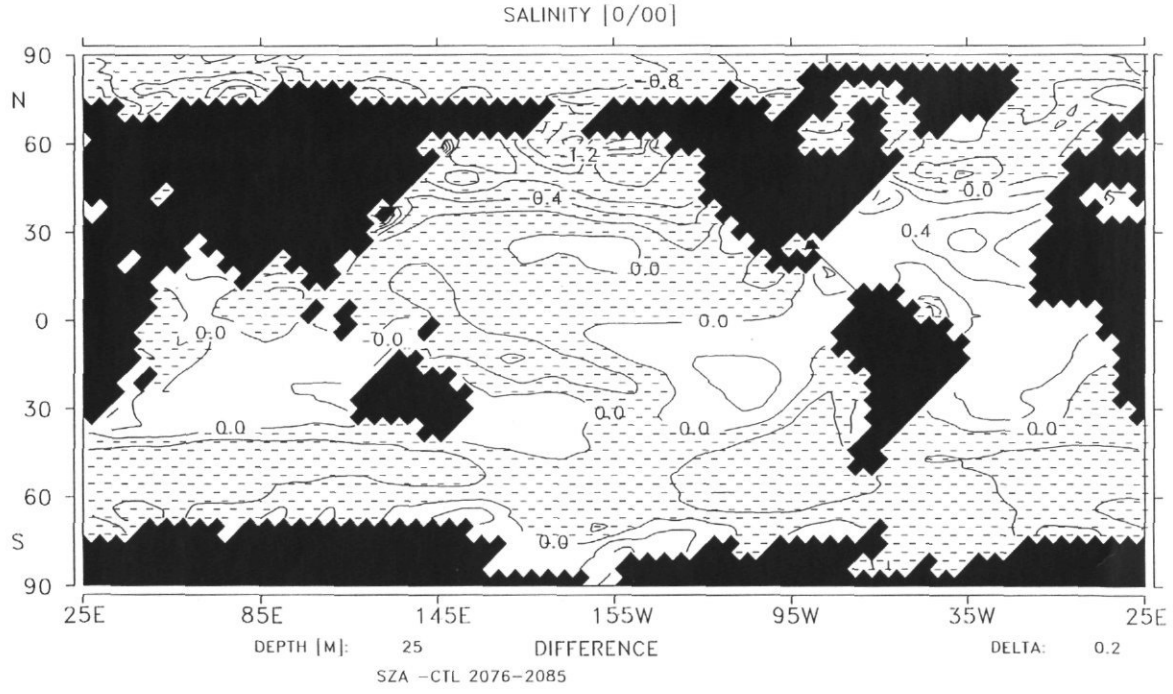


Figure 2. Annual mean difference in surface salinity between the greenhouse experiment and the control run averaged over the last decade.

greenhouse gases varied in accordance with the IPCC "business as usual" scenario (Houghton *et al.*, 1990). This simulation started with a forcing corresponding to 1986 conditions and was run for 100 years. In a second integration, termed the control run, the forcing was kept constant at conditions corresponding to 1985.

The most important consequence of the inclusion of ocean circulation in these coupled model runs is the modification of the pattern of climate change in the near-surface air temperature and sea-surface temperature. At the end of the greenhouse simulation the global mean average near-surface air temperature is 2.9°C warmer than the average over the corresponding decade of the control run. Compared to the first decade of the control run, the warming is only 2.6°C (Cubasch *et al.*, 1992). Because of the much bigger heat capacity of the ocean, land warms faster than the ocean. The global mean change in SST is only 1.9°C at the end of the integration. The pattern shifts from almost zonal, with highest warming in high latitudes, especially in the winter season, to regionally strongly variable, with minima in the northern North Atlantic, in the North Pacific, and in the Southern Ocean (see Fig. 1). In small regions of the northern North Atlantic even a cooling is predicted. This cooling is a consequence of the reduction in the formation rate of North Atlantic Deep Water (NADW). At the surface a freshwater lens develops. Winter cooling is not strong enough to overcome the stable stratifi-

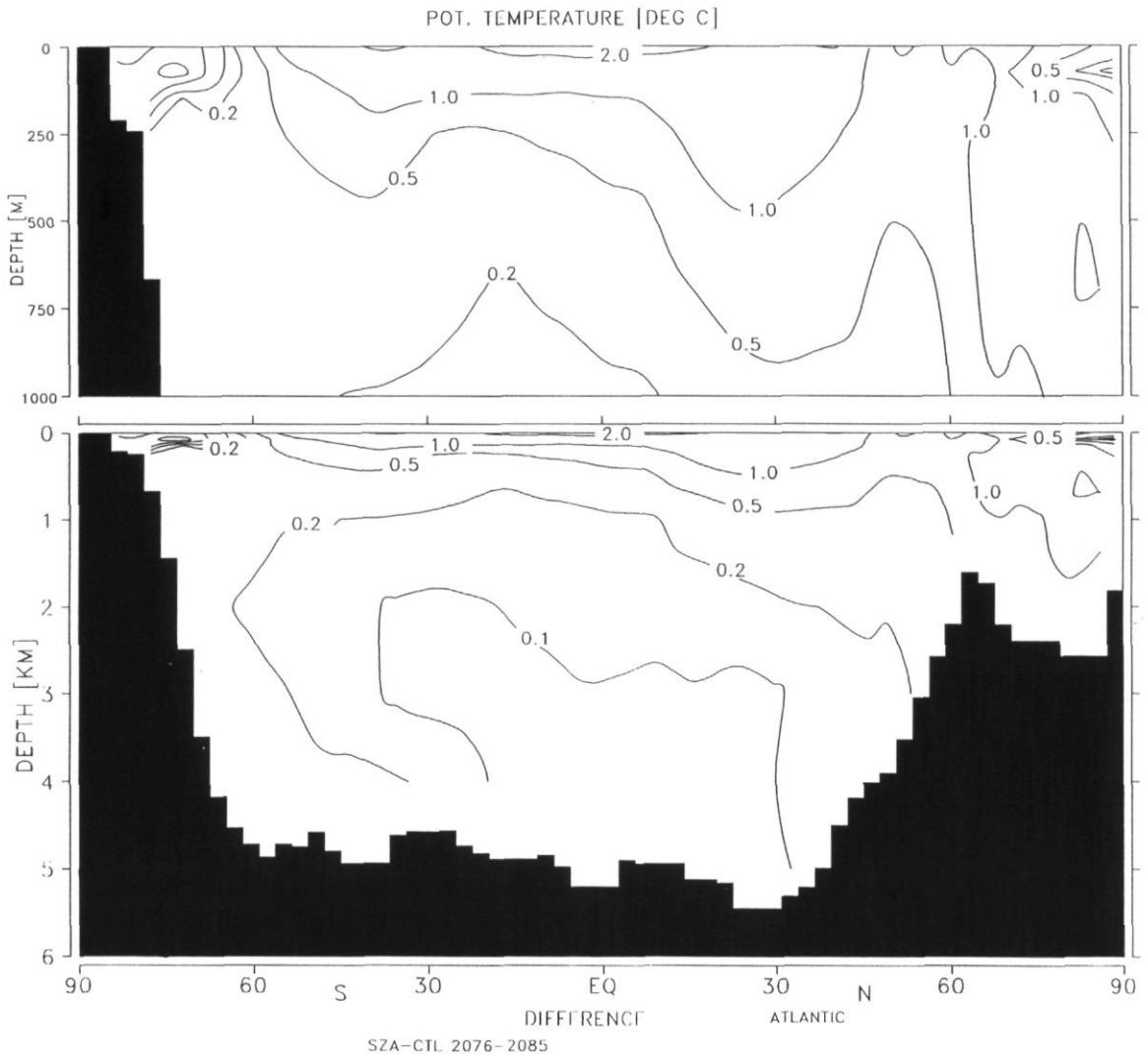


Figure 3. Difference in vertical temperature distribution between the greenhouse experiment and the control run in the Atlantic. The picture shows the zonally averaged response. Note the variable contour interval.

cation between the relatively fresh surface water and the warm and haline Atlantic water underneath. The effect is an intensification of the freshening at the surface. As a consequence, the formation of NADW is reduced and the thermohaline circulation of the Atlantic is slowed down by about 25% at the end of the integration. In the last decade of the greenhouse experiment the meridional overturning of the Atlantic has a maximum of 24 Sv compared with 33 Sv in the control simulation. The resulting enhanced residence time of a water particle at the surface leads to a stronger uptake of precipitation and thus to a further freshening. This mechanism provides a positive feedback for the negative salinity anomaly. In the subtropical gyre, a positive salinity anomaly develops at the surface as a consequence of the longer exposure to the net evaporation in the subtropics. Here the anomaly reaches values of more than 0.6 psu in the eastern subtropical North Atlantic. In the subpolar gyre the anomaly is weaker, but still with a strength of typically 0.2 psu. The resulting anomaly of near-surface salinity is shown in Figure 2. As a consequence, the stability in the near-surface layers is increased and the ventilation of intermediate and deep water is reduced.

An effect apparently not a unique feature of our model, as similar greenhouse integration with other COAGCMs show a similar region of strongly reduced warming or cooling in the northern Atlantic (for a review see Gates *et al.*, 1992). Although a simple sea-ice model is included, this has only a negligible effect on the formation rate of NADW in the model (as was shown by Maier-Reimer (1993), but rather influences Antarctic bottom water formation.

The warming is not restricted to the surface layers of the ocean, but penetrates into greater depths. The deepest penetration occurs in regions where the stratification is weak, i.e., in the northern North Atlantic and in the Southern Ocean. The change in the vertical temperature structure of the Atlantic resulting at the end of the greenhouse experiment is shown in Figure 3.

Whereas the model seems to give a reliable estimate of variations on large spatial scales and of the changes in integral properties of the ocean circulation, a direct estimate of local effects from these simulations remains of course limited because of the coarse resolution of the model. For example, the model does not resolve Iceland and thus the question of how the local hydrographic properties around Iceland might change as a result of the greenhouse effect cannot be answered directly from these simulations. Currently, a model with twice the resolution is under development at our Institute. Further refinement would be achieved by embedding a regional model of the North Atlantic in the global ocean model.

Another possible method would be to relate local properties of the hydrography around Iceland and their variation to large-scale patterns of the ocean and atmosphere (e.g., wind forcing) which the model can simulate. Estimates of the changes in local conditions could then be derived from the changes in the large-scale conditions. The relation between the large-scale properties and the local variations, however, should be estimated from observations. Storch *et al.* (1993) have recently applied this technique to Iberian rainfall.

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Climate, cod, and capelin in northern waters

Svend-Aage Malmberg and Johan Blindheim

Malmberg, S.-A., and Blindheim, J. 1994. Climate, cod, and capelin in northern waters. – ICES mar. Sci. Symp., 198: 297–310.

The hydrographic conditions in the Iceland Sea reveal three different regimes on the North Icelandic Shelf: Atlantic, Arctic, and Polar. Thus, time series of temperature and salinity in the shelf waters show that Atlantic Water from the warm Irminger Current dominated during a long period prior to the mid-1960s. During the latter half of the 1960s, however, there was a dramatic change to lower temperatures, as Polar surface waters from the East Greenland Current were carried into the area. As a result, the northern and partly also the eastern coasts of Iceland were frequently blocked by drift ice in the late winter and spring of these years. Oceanographic effects of this extremely cold period, the so-called "Great Salinity Anomaly", were observed during the following years over wide areas in the northern North Atlantic. Since this event, conditions in North Icelandic waters have been alternating between cold and warm periods, but stable and warm conditions similar to those before 1965 have not returned. There have not always been Polar surface waters on the North Icelandic Shelf during later cold periods, sometimes Arctic Water from the Iceland Sea has occupied the area. These shifts in hydrographic conditions in the Iceland Sea have important ecological impacts, because the North Icelandic Shelf is a nursery area for the Icelandic cod and capelin populations. Thus the variable flow of Atlantic Water into the North Icelandic waters may influence the drift of larvae from the spawning areas on the South Icelandic Shelf to the nursery grounds. In the nursery area the changing oceanographic conditions further bring about varying living conditions for the larvae and juvenile fish. The data show that survival rate of cod has been highest in periods with warm water from the Irminger Current on the North Icelandic Shelf. The Atlantic, Polar, and Arctic conditions in North Icelandic waters also seem to influence the size of the Icelandic capelin stock, which was at its lowest during Arctic conditions. As the "Great Salinity Anomaly" could be traced as it advected around the Subpolar Gyre in the Northern North Atlantic, the ecological impacts of this event on several cod stocks can be compared, i.e. the stocks off Iceland, West Greenland, Newfoundland, and Norway. On these fishing grounds the catches of cod declined from 1960 to 1990 by about 50%, recruitment by about 67% and spawning stocks by about 75%. This indicates an increasing fishing load from 1960 to 1990. Furthermore, improving hydrographic conditions in Icelandic waters after 1990 did not result in a new strong year class of cod. It is questioned whether this failure in recruitment was due to a critically small spawning stock.

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Introduction

The distribution of cod (*Gadus morhua*) in the northern North Atlantic is confined to shelf areas (as shown in Fig. 1). The spawning areas of the stocks are reached by relatively warm and saline water of the North Atlantic Drift, while stock distribution in some regions may extend into Arctic waters (see Fig. 1 in Jónsson 1994, pp. 287–291). Capelin (*Mallotus villosus*), however, is a cold-water pelagic species which spawns in shallow waters along the northern boundaries of the warm-water drift, but feeds and grows up farther north in Arctic waters, occasionally even beyond the Polar Front. Capelin is an important food item for cod when the distribution of the two species overlaps during certain life stages. This is also the case for the Icelandic cod and

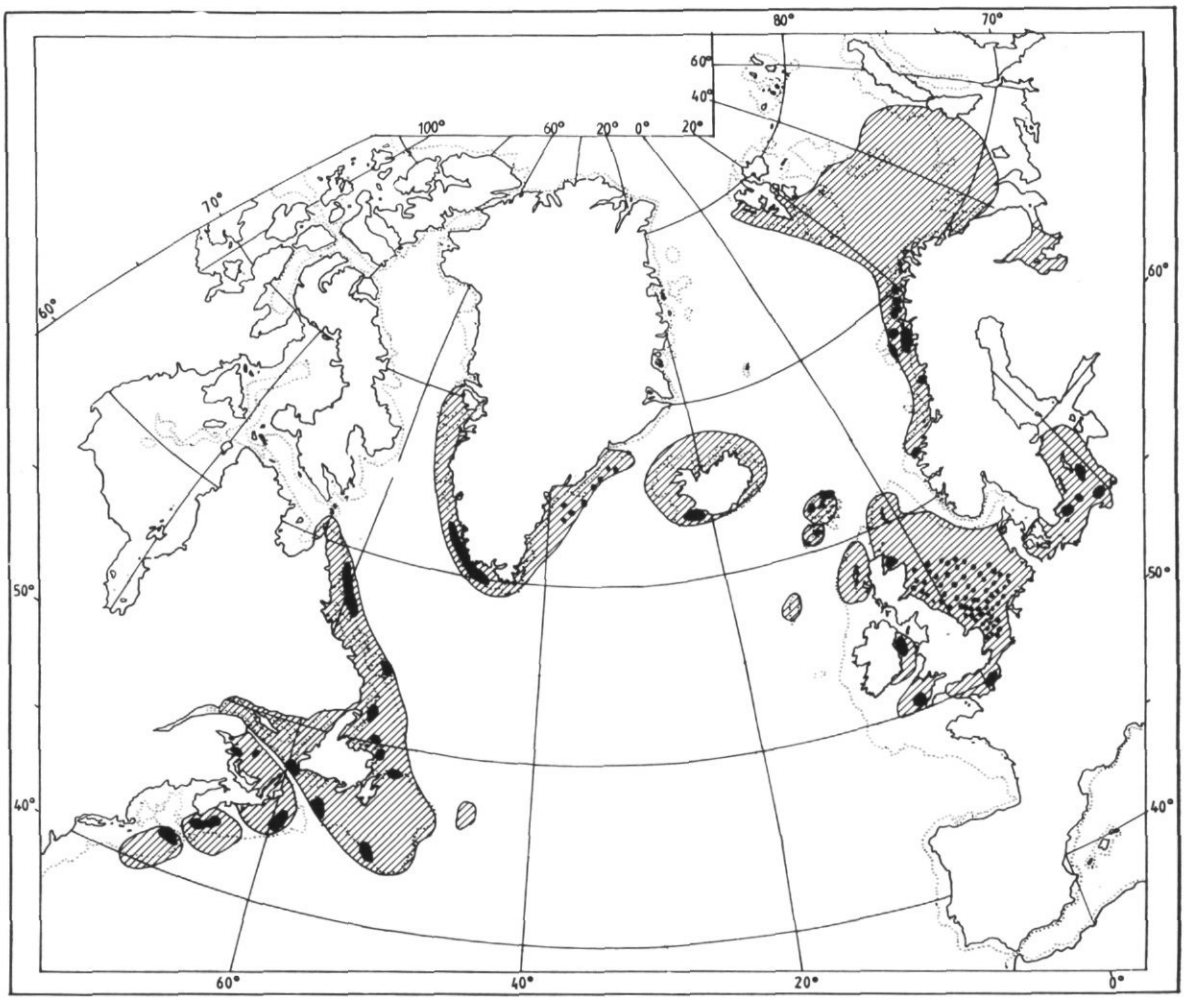


Figure 1. Spawning areas of the different cod stocks in the northern North Atlantic and adjacent seas (ICES, 1991).

capelin populations that will be discussed here. Spawning of both cod and capelin takes place off the south coast of Iceland in relatively temperate waters, while the spawning products drift with the current to nursery areas on the North Icelandic Shelf.

Primary production in this area is mainly concentrated in a spring bloom based on nutrients brought up to the photic zone by winter convection, although there is a moderate blooming throughout summer. The intensity and development of primary production depends on how stratification in the water column develops when the surface layer is warmed during spring and summer. This will further be reflected in the distribution and abundance of zooplankton and, hence, in feeding conditions for plankton consumers like capelin and postlarvae cod. As the strength of year classes in the cod stock depends on survival rate during larval and postlarval life stages, variability in the oceanographic structure may largely influence recruitment to the cod stock.

The present paper deals mainly with relationships between variability in the hydrographic conditions and the state of the Icelandic cod and capelin populations, particularly growth and reproduction. Emphasis is put on the North Icelandic Shelf waters, which is the nursery area for these species. Oceanographic structure and variability in this area depend on fluctuations in transports and properties in the major current systems in the region, i.e. the supply of warm water masses from the Irminger Current and cold waters from the East Greenland Current (Fig. 2).

Some thoughts are also given to parallel relationships in some of the other cod stocks in the northern North Atlantic, mainly those off Labrador and Newfoundland, West Greenland, and in the Barents Sea.

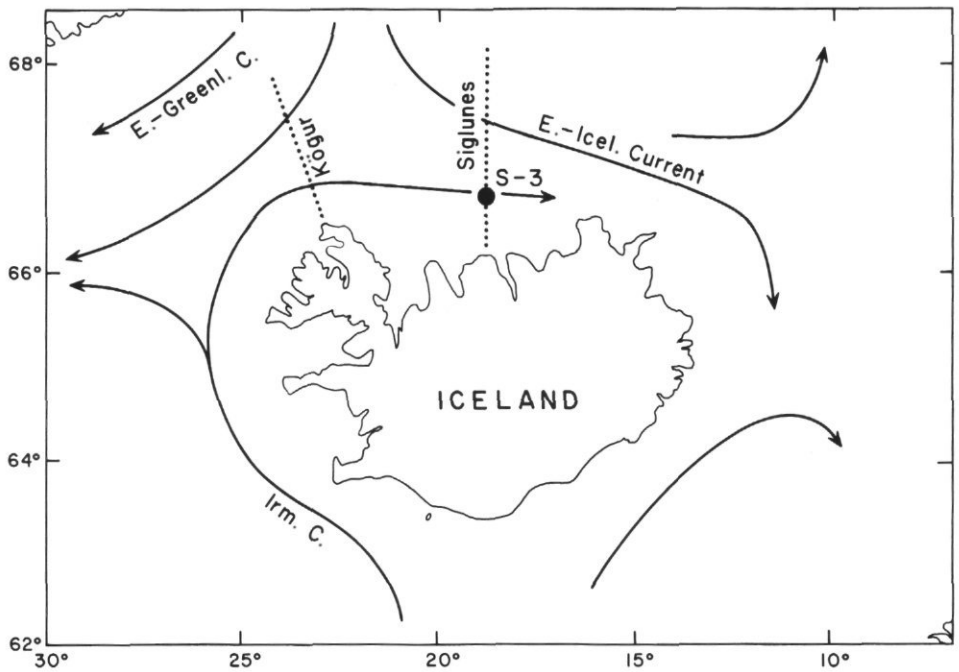


Figure 2. Main ocean currents in Icelandic waters and location of sections and stations studied.

Data

The hydrographic data used in this paper are mainly time series collected in Icelandic waters by the Marine Research Institute, Reykjavík. Hydrography and plankton have been observed in standard sections since 1924. Since 1950, data have been collected annually in spring; prior to 1950 sampling frequency was more irregular. Since 1970 a grid of standard sections around Iceland has been observed four times a year. The present study is based mainly on a standard section carried out in spring northwards from Siglunes on the North Icelandic coast (Fig. 2), and time series from Station S3 from the coast in this section are chosen as representing the conditions in North Icelandic shelf waters. This section and station reflect the overall conditions in North Icelandic waters throughout the year (Malmberg and Kristmannsson, 1992).

Annual assessments of the cod and capelin stocks are taken from annual status reports from the Marine Research Institute (e.g. Anon., 1993). The time series used in the present paper for the cod stock cover the period back to 1950, while there are data on the capelin stock since 1978.

The Iceland Sea

General circulation

Iceland is situated in the junction between two large submerged ridges, the Mid-Atlantic Ridge and the Greenland–Scotland Ridge. This major bathymetric feature is decisive for the hydrography in the region. The Iceland Sea, which covers the area between Iceland, Greenland, and the island of Jan Mayen, consists of mainly cold waters from the north (Stefánsson, 1962; Swift, 1980; Swift and Aagaard, 1981), while the area south of Iceland is characterized by the North Atlantic Drift with relatively warm waters of southern origin. Thus, the circulation is dominated by two major current systems (Fig. 2). To the south, the Irminger Current carries warm waters from the North Atlantic Drift to the area south of Iceland and with a transport of approximately 3 Sv it continues northward along the west coast of Iceland. It splits into two branches in the Denmark Strait. One turns southwestwards to flow along the East Greenland Shelf and slope, where it gradually becomes a warm intermediate component of the East Greenland Current. The other branch follows the Icelandic slope and with varying transport of 1–2 Sv (Kristmannsson *et*

al., 1989) it flows eastwards into North Icelandic shelf waters where it ultimately disperses off the eastern coast (Stefánsson, 1962).

The East Greenland Current carries cold and fresh waters southward along the east coast of Greenland with an offshoot into the Greenland Sea – the Jan Mayen Current – and a larger one – the East Icelandic Current – into the Iceland Sea. The major portion of its transport, however, flows out of the Iceland Sea through western Denmark Strait to continue southwards along the East Greenland shelf. The Polar Water is separated from the basin water masses in the Greenland and Iceland Seas by a zone with increased horizontal gradients, particularly in salinity. This is the Polar Front, which is normally located along the shelf break, except where Polar Water to a varying extent spreads into the Jan Mayen and East Icelandic Currents (Malmberg, 1984, 1985).

Water masses

Important water masses with their sources outside Icelandic waters are brought into the area by this circulation system (Stefánsson, 1962): Atlantic Water, carried into Icelandic waters by the North Atlantic Drift and the Irminger Current, is the warmest water mass in the area, with temperatures ranging from 3 to 8°C and salinities of about 35. On entering the Iceland Sea it is typically at temperatures of 3–6°C and salinity 34.9–35.1. Polar Water occupies upper layers in the East Greenland Current. It originates mainly from the Arctic Ocean, but in summer in particular it also contains some runoff from Greenland. It is generally colder than 0°C, while its salinity is below 34.5.

Arctic Intermediate Water occurs in several modifications and from various sources. An Arctic intermediate component of the East Greenland Current flows below the Polar Water. It has circulated from the West Spitsbergen Current into the northern Greenland Sea southward and along the East Greenland Shelf. The relatively high temperatures, between 0 and 2°C, indicate its Atlantic origin, but for the same reason its salinity is also high, about 34.95. It is therefore heavier than the Polar Water.

The Iceland Sea Deep Water, with temperatures close to −1°C and salinities of 34.90–34.92, occurs at depths greater than approximately 600 m in the Iceland Sea proper. It has partly been transported southward along the East Greenland slope with a major source in the Arctic Ocean (Aagaard and Carmack, 1989; Malmberg *et al.*, 1990; Rudels and Quadfasel, 1991; Buch *et al.*, 1992), and partly it arrives from the Norwegian Sea south of the Jan Mayen platform.

Some water masses are also formed within the Icelandic waters: Coastal water on the shelf around Iceland, with temperatures varying seasonally between wide limits, is diluted by runoff to salinities below 34.0. Arctic Intermediate water types formed during winter, partly in the Greenland Sea and partly in the northern and central Iceland Sea, are defined by Swift (1980) and Swift and Aagaard (1981). In the Iceland Sea these water types are characterized by temperatures around 0°C and salinities of between 34.7 and 34.9.

North Icelandic Winter Water, with temperatures of 2–3°C and salinities from 34.8 to 34.9, is defined by Stefánsson (1962) to be formed on the North Icelandic shelf during winter by convective mixing of cold and warm water masses.

Arctic waters in the upper few hundred metres of the southern Iceland Sea may be relatively pure forms of intermediate water either from the East Greenland Current or from the Iceland Sea, or they may be mixtures between these and the other water types in the area. It is hardly necessary in the present discussion to distinguish between these varieties, the term Arctic Water being used for all water types of temperature 0–3°C and salinity 34.5–34.95.

These Arctic water masses are found above the Bottom Water in the Iceland Sea. South of Jan Mayen, some water of Atlantic origin penetrates from the Norwegian Sea and goes into a cyclonic circulation in the eastern Iceland Sea (Stefánsson, 1962). The southern side of this circulation joins with the East Icelandic Current which brings Arctic waters through the southern Iceland Sea and, to some extent, into the southwestern Norwegian Sea. The border between the Arctic waters of the East Icelandic Current and Atlantic waters forms the Arctic Front. In Icelandic waters the location of this front may vary with fluctuations in volume transport in the North Icelandic branch of the Irminger Current as well as in the East Icelandic Current. In some years the front may be found off the shelf break north of Iceland. This was the situation for example in 1980 (shown in Fig. 3). In other periods, the shelf area too may be occupied by Arctic or Polar waters. During such periods there is no Arctic or Polar front north of Iceland. Instead it may "hit" land at about Kögur and "leave" land somewhere on the northeast or east coast, as demonstrated by the situation from 1979 in Figure 3.

Polar Water is normally distributed over the East Greenland shelf and not far into the East Icelandic Current. Periodically, however, it spreads far into the Iceland Sea and, during the period from 1965 to 1971, in particular, Polar Water was carried into the North Icelandic Shelf. As a consequence, conditions were of a polar character during winter and spring, as drift ice frequently blocked the north and east coasts and even ice formed in North Icelandic waters (Malmberg, 1969, 1984).

Hence, Atlantic, Arctic, and Polar regimes on the North Icelandic Shelf may be defined according to the dominating water masses: During an Atlantic regime, as

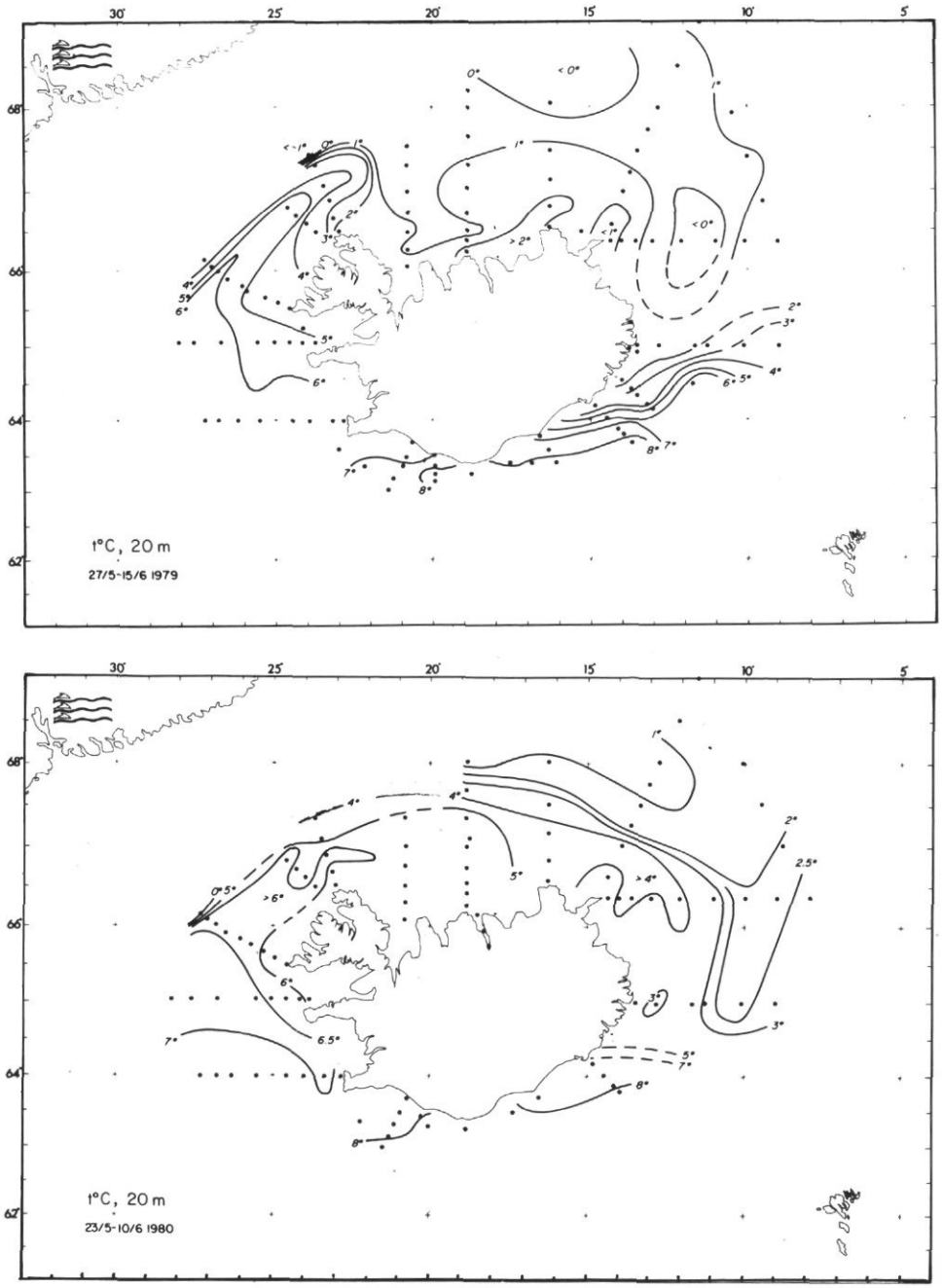


Figure 3. Temperature at 20 m in Icelandic waters in May/June 1979 and 1980 (Malmberg, 1983).

exemplified by the section from 1980 in Figure 4, there is Atlantic Water on the shelf and the front toward the Arctic waters to the north is found off the shelf break. In spring (May), the temperatures are above 3°C and salinities above 34.9 in the upper 200 m of the water column; surface layer temperatures may be 5–6°C.

An Arctic regime, as shown by the section from 1981 in Figure 4, is characterized by Arctic waters on the shelf; temperatures everywhere are below 3°C and salinities are around 34.8.

During a Polar regime, see the section from 1979 in Figure 4, there is cold, low-salinity Polar Water in the

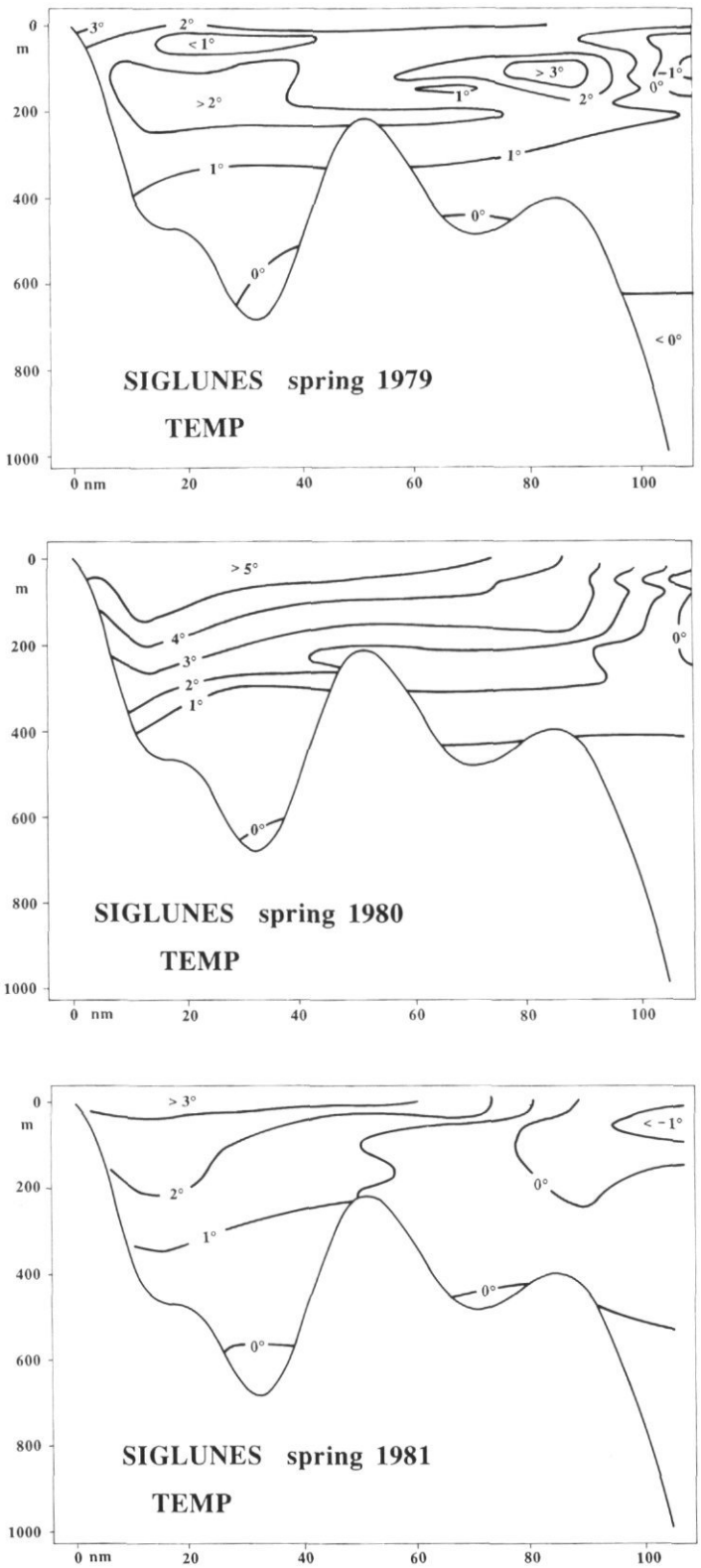


Figure 4. Vertical distribution of temperature and salinity on a section in North Icelandic waters in May/June 1979, 1980 and 1981 (for location, see Fig. 2).

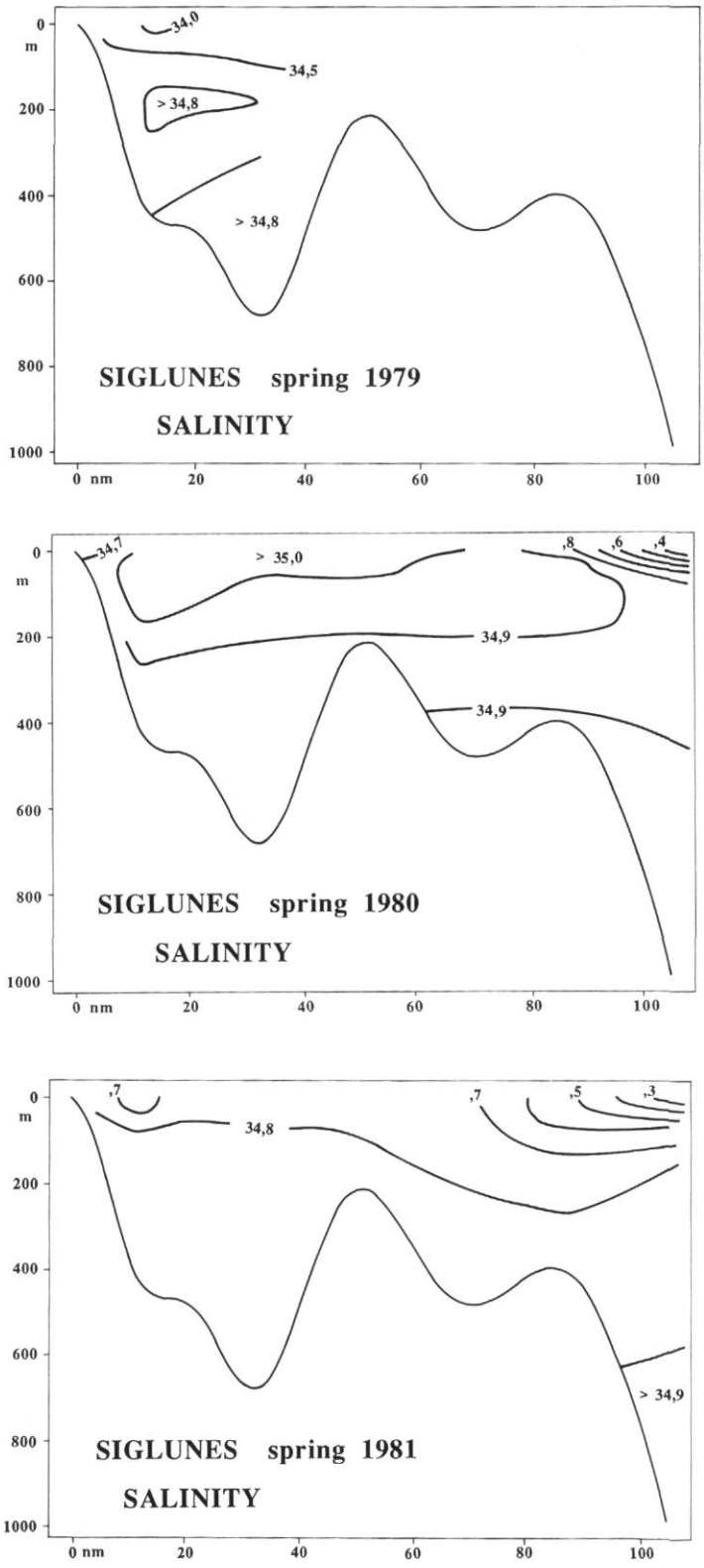


Figure 4. Continued.

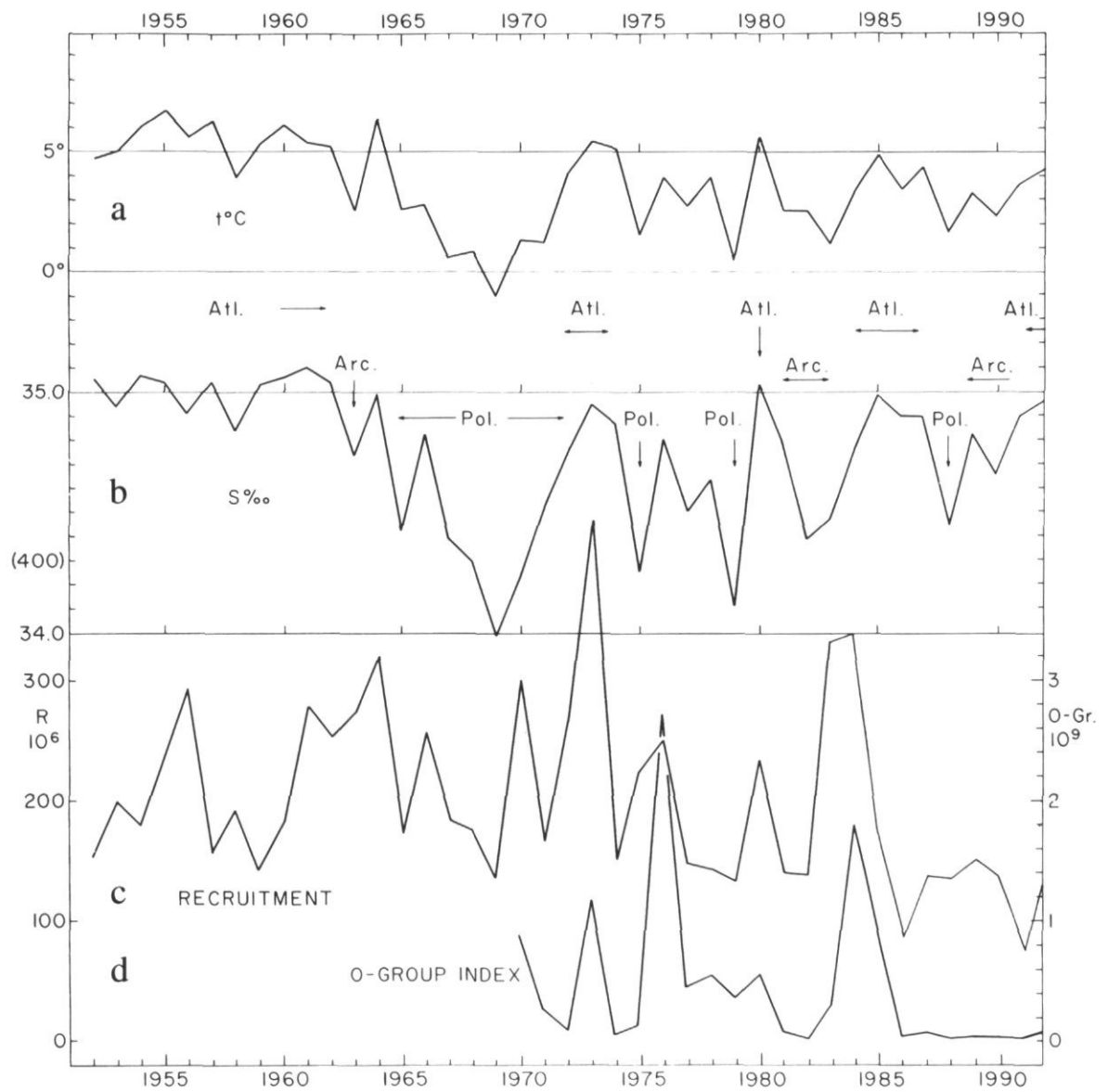


Figure 5. a, b. Temperature and salinity at 50 m depth at Station S3 in North Icelandic waters in May/June 1952–1992 (for location, see Fig. 2). c. Recruitment of 3-year-old cod (year classes) in Icelandic waters in 1952–1992. d. 0-group indices of cod in Icelandic waters 1970–1992.

surface layer with increased density gradients toward the deeper water mass, which may be Arctic or even Atlantic in character. The shelf waters may be covered by ice during winter and spring.

Time series

The time series of temperature and salinity observed at 50 m depth at Station S3 (Fig. 2), covering the period since 1952, are shown in Figure 5. Observations earlier than 1924 are not shown in the figure. All observations during the period 1924–1964 indicated that temperatures varied between 4 and 6°C and salinities between about 34.9 and 35.1. Although the observational frequency was irregular before 1950, there are several indications that there was a continuous Atlantic regime during this period. Hence, there have been no winters with drift ice on the coast during this period since 1918

(Sigtryggsson, 1972). Furthermore, on the island of Grimsey, on the North Icelandic shelf, sea-surface temperatures have been observed since 1871; there were no indications of Polar or Arctic water in the surface layer during the actual period as temperatures were generally above 3°C during winter and spring (Stefánsson, 1969). It is therefore unlikely that Polar or Arctic regimes occurred in years in which there were no observations. After this long and stable period with an Atlantic regime, conditions changed in the mid-1960s with a drastic cooling and freshening of the upper water column to the lowest values on record in 1969 with temperature close to −1°C and a salinity near 34 at Station S3. As a result, the north, east, and even southeast coast of Iceland experienced the worst ice years since early in this century.

Since this cold period, which lasted through the rest of the 1960s, conditions have been more changing. There have been four short periods with an Atlantic regime, around 1973, 1980, 1985, and 1992, but temperatures have usually been below 5°C and salinities have hardly exceeded 35. Polar regimes occurred in four years, 1975, 1977, 1979, and 1988, while Arctic regimes occurred during 1981–1983 and 1989–1990. On average, the period from 1964 to the present has been considerably colder and fresher than the 40 years between 1924 and 1964. The Arctic regimes in 1981–1983 and in 1989–1990 were both related to low salinities in the Arctic Intermediate Water returned from the West Spitsbergen Current (Malmberg *et al.*, 1990; Malmberg and Kristmannsson, 1992). In 1981–1983 the low salinities were due to the return of the "Great Salinity Anomaly" (Dooley *et al.*, 1984; Dickson and Blindheim, 1984; Dickson *et al.*, 1988).

Current measurements in the core of the eastern branch of the Irminger Current off Kögur during the years 1985–1990 reveal stronger currents during the Atlantic period from 1985 to 1987 than during the Polar and Arctic regimes in the following three years. This indicates that the change from an Arctic to an Atlantic regime is not only due to changes in properties of the inflowing water masses, but also to larger volume transport in Atlantic inflow to the shelf north of Iceland (Kristmannsson, 1991).

In general, the influence of warm Atlantic Water has decreased in the northern North Atlantic since its most extensive distribution during the period from about 1930 to 1960 (Smed, 1975; Rodewald, 1967, 1972). There has thus been a general cooling trend since the 1950s from West Greenland and Newfoundland waters in the west to the Barents Sea in the east (Malmberg and Svansson, 1982). In North Icelandic waters this has brought about more variable and, in general, weaker Atlantic inflow. Instead, periods with cold and fresh Arctic and Polar Water have been more prevailing, even with drift ice as in the late 1960s. The forcing of this changed oceanic circulation is not well understood, although the increased outflow of Polar Water from the Arctic Ocean during the mid-1970s anomaly (Great Salinity Anomaly) was linked to variations in the Greenland High and the Iceland Low (Rodewald, 1967, 1972; Dickson *et al.*, 1975; Aagaard, 1972; Jónsson, 1991). The increased outflow of fresh Polar Water from the Arctic Ocean may also weaken the deep water formation in the Greenland Sea (Meincke *et al.*, 1992), which again has an impact on the Atlantic inflow to the Nordic Seas.

Cod and hydrography

Icelandic cod matures to first spawning at an age of around 7 years (Schopka, 1994; Jónsson, 1982). Spawning takes place in warm water to the south and southwest of Iceland during the period March to May. Hatching occurs after 2 to 3 weeks, while eggs and larvae drift northward along the west coast. By August most of the spawning products occur as 0-group cod on the North Icelandic Shelf and, often, a smaller portion drift toward East Greenland in the western branch of the Irminger Current. Young cod is distributed on the Icelandic shelf, mainly off the northwest, north, and east coasts. Adult year classes feed largely in the same areas, but have spawning migrations back to the warm waters.

Estimates of the recruitment to the Icelandic cod stock since 1952 are shown in Figure 5 given as assessments of year-class strength at the age of 3 years. The values, however, are entered in the years when the year classes were spawned. Indices on 0-group estimates of cod in August 1970–1992 in Icelandic waters are also shown in Figure 5, but are not discussed further in this paper (see Astthorsson *et al.*, 1994).

The figure shows interannual variations in year-class strength throughout the period, but since 1970 there has been a decreasing trend in the weaker year classes. All strong year classes after 1966 were recruited either within Atlantic periods on the North Icelandic Shelf, or in years with increasing temperature prior to such periods. Hence, when conditions started to improve after the Polar period in the late 1960s, a strong year class was recruited in 1970, and the 1973 year class, which is the strongest in the time series, was produced in the warmest year of the Atlantic period from 1972 to 1974. Strong year classes were also recruited in 1983 and 1984 at the beginning of the Atlantic period from 1984 to 1987 (Malmberg and Kristmannsson, 1992). The fluctuations in year classes during the long Atlantic period before 1965 show that a warm environment is not the only prerequisite for the production of strong year classes. However, there does seem to be a closer relationship between Polar and Arctic periods and weak

year classes as recruitment was generally low in the periods with such conditions after 1965, although there were exceptions in 1966 and 1975 when relatively strong year classes were recruited simultaneously with Polar regimes in North Icelandic waters.

Standing alone, the relationship in the present, relatively short time series may not be absolutely convincing, but it is in agreement with similar relations in other cod stocks. In this context the most obvious relationship is observed in the West Greenland cod stock, which lives near the lower limit of the temperature range for the species. This population was reduced almost to depletion when temperatures decreased during the 1960s and 1970s (Blindheim, 1974; Hovgaard and Buch, 1990). In Northeast Arctic cod in the Barents Sea, Sætersdal and Loeng (1987) found similar relationships with most year classes of strong or medium abundance occurring in the early part of a warm period or shortly prior to a shift to a warmer regime. It therefore seems reasonably likely that the present time series indicates similar relationships in North Icelandic waters.

The mechanism behind the survival rate of larval and early juvenile stages may lie in the feeding conditions in the nursery area. Ellertsen *et al.* (1989) suggested a temperature-induced timing of the first-feeding prey, the nauplii of *Calanus finmarchicus*, as a possible link between temperature and recruitment success for Northeast Arctic cod, which has its main spawning area in Lofoten. In this cod stock, spawning is fixed at the same time from year to year, while low temperatures may delay the spawning of *C. finmarchicus*, with a difference of up to 6 weeks between warm and cold years. As the survival of cod during its early larval stage depends on the presence of suitable concentrations of food items, e.g. nauplii, such time shifts in plankton spawning may result in serious mass starvation owing to lack of prey at the most critical life stage. Although conditions for the Icelandic cod stock are not identical to those of Northeast Arctic cod, the two stocks have several conditions in common. Both stocks live in outer branches of the North Atlantic Current system. Northeast Arctic cod depends on the Norwegian Atlantic Current and its branching into the Barents Sea, while Icelandic cod depends on the Irminger Current and its branch into North Icelandic waters. *C. finmarchicus* dominates the zooplankton population in both regions (e.g. Astthorsson *et al.*, 1983; Blindheim and Skjoldal, 1993). It therefore seems likely that simultaneous production of cod larvae and *Calanus* nauplii is an important factor for the survival success of Icelandic cod too. An ideal situation would probably be one in which the planktonic spawning products and the fish larvae are advected in the same volume of water, where the cod larvae and their prey have a parallel growth.

During Atlantic periods in North Icelandic waters, surface temperatures are relatively high and decrease gradually with depth. The mixed layer will deepen relatively slowly and supply nutrients to the productive layer over a relatively long period. The primary production will have a relatively high and long-lasting spring bloom with a more moderate production later in the season (Thórdardóttir, 1977, 1986; Stefánsson and Ólafsson, 1992). This will be reflected in the secondary production of zooplankton (Astthorsson *et al.*, 1983).

During an Arctic regime temperatures are generally below 3°C and there is not much stratification in the water column during winter. Because of this the formation of a stratified surface layer by warming in spring may be somewhat slower than in an Atlantic regime, but still, development of blooming during spring and summer may not be much different from that in an Atlantic regime, although species composition may be different. Observations show that primary production may be large (Malmberg, 1986, 1988), but abundance of zooplankton is generally much lower than in Atlantic regimes. Furthermore, the zooplankton population will have a considerably larger component of Arctic species than in Atlantic periods (Astthorsson *et al.* 1983) and the spawning of *C. finmarchicus* will be delayed and early juvenile cod may not find suitable food items on the North Icelandic Shelf.

In a Polar regime, conditions for plankton production will be different. Here there is a surface layer with low density and relatively strong density gradients before the warming in spring starts. The warming will therefore result in a shallow surface layer with a short and intense spring bloom (Thórdardóttir, 1977; Stefánsson and Ólafsson 1992). The nutrients will be quickly depleted and deepening of the layer will be modest because of the sharp pycnocline below the mixed layer. Blooming later in the summer will therefore be almost negligible. The plankton fauna will have a relatively large component of Polar and Arctic species which may be less suitable food items for juvenile cod. In North Icelandic waters the decrease in abundance of zooplankton is considerable (Astthorsson *et al.*, 1983). Also low temperatures as such may be an important factor. Cod as a species belongs in temperate and boreal regions and adult cod avoids low temperatures and seldom occurs in abundance in temperatures near 0°C. Although it is claimed that cod larvae and juveniles adapt better to low temperatures than adult fish (Goddard *et al.*, 1992), there are also reports of increased mortality of 1- and 2-group cod during extremely cold winter temperatures (Ponomarenko, 1984). The overall effect of low temperatures, directly and indirectly, may be concluded to have an adverse impact on the recruitment.

Capelin and hydrography

The Icelandic capelin spawns at the age of 3–4 years in late winter in the coastal waters south of Iceland (Vilhjálmsson, 1983, 1994). From there the larvae drift westwards and northwards into the nursery grounds in the Denmark Strait and in North Icelandic waters. During the following years the capelin feeds mainly in the area between the Polar and Arctic fronts in the Iceland Sea, until it migrates southwards again, mainly along the shelf break north and east of Iceland, to the spawning areas. Capelin suffers mass mortality after spawning.

Hydrographic fluctuations in North Icelandic waters also affect the living conditions of capelin. Assessments of capelin stock abundance are available for the period since 1978 and entered in Figure 6. Maximum salinity in the upper 300 m of the water column at Station S3 (for location, see Fig. 2) is also entered in the figure. Here salinities above 34.9 indicate Atlantic periods, while lower salinities represent Arctic Water. The salinity trends are similar to the salinity curve from 50 m, which is shown in Figure 5, but the low surface salinities in a Polar period do not appear to the same extent as at 50 m depth. The interrelationship between abundance of capelin and salinity is reasonably good, although not perfect, and a very low abundance of capelin during the Arctic periods 1981–1983 and 1989–1990 is clear. In 1981–1983 in particular the abundance was at such a low level that fisheries were stopped in 1982. In these years the decline in abundance may have begun before the Arctic period, i.e. in the Polar years 1979 and 1988, as there are indications of low survival rate and reduced growth of 0-group capelin during Polar conditions (Vilhjálmsson, 1983, 1994; Malmberg, 1986, 1988).

Furthermore, the abundance of capelin is reflected in the growth of cod, which feeds on capelin (Pálsson, 1983). The weight of five-year-old cod is also entered in Figure 6 and the relationship with the abundance of capelin is fairly good. Although the temperature fluctuations will have a similar trend (Fig. 5), with a similar physiological effect on growth, it is unlikely that this alone will result in the differences shown in Figure 6. The most likely reason for the low abundance of capelin and, indirectly, the low growth of cod, is the reduced zooplankton biomass during Arctic periods (Astthorsson *et al.*, 1983; Malmberg, 1986, 1988). Similar effects are also observed in the Iceland Sea, where adult capelin feeds during summer. Abundance and distribution of plankton are therefore probably important links between environment and abundance and growth of capelin (Jakobsson, 1992). Growth of cod, however, seems not to be very dependent on hydrographic conditions, but more on abundance of capelin (Malmberg, 1986; Steinarsson and Stefánsson, 1991).

Effects of fishing in relation to environment

There are indications that the widespread cooling since about 1960 has entailed adverse effects on cod stocks in the Northern North Atlantic as a whole. While this is most recorded for the West Greenland cod stock (Blindheim, 1974; Hovgaard and Buch, 1990), there have been decreases in the abundance also in other North Atlantic

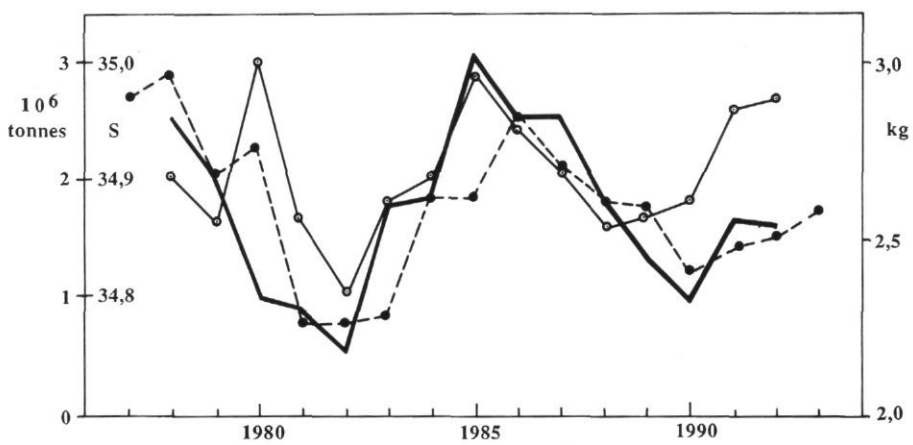


Figure 6. a. Maximum salinity observed in the upper 300 m at Station S3 in North Icelandic waters in May/June 1978–1992 (solid thin line). b. The abundance of Icelandic capelin stock (t) in 1978–1992 (solid thick line; Vilhjálmsson 1994). c. Weight of 5-year-old cod (kg) in Icelandic waters in 1977–1993 (broken line; Anon., 1993).

Table 1. Catches, recruitment, and spawning-stock biomass of cod in Northern Waters around 1960 and 1990 (Iceland, West Greenland, Newfoundland, and NE Arctic; from Jakobsson 1992).

	Catch 10^3 t		Recruitment 10^6 n		Spawning stock 10^3 t	
	1960	1990	1960	1990	1960	1990
Iceland	450	300	300	100	700	200
West Greenland	400	100	400	100	1 000	100
Newfoundland	600	300	1 000	150/500	1 000	300
Northeast Arctic	1 000	200/500	1 500	300	600	250
Sum	2 450	1 200	3 200	1 000	3 300	850

cod stocks over recent decades. This seems to be important especially for stocks which live near the lower limit of the temperature range for cod, e.g. off Labrador/Newfoundland, West Greenland, and even North Icelandic waters. In these areas it seems that the environmental conditions again must improve before stocks and catches can be expected to be of the same strength as before the mid or late 1960s. Here it is pertinent to ask to what extent the decrease in the cod stocks is due to the deteriorating ocean climate or overfishing. Some indication of this is given in the relation between the decline in catches and the decreases in recruitment and spawning stock in these cod stocks (see Table).

Summed up, for all these fishing grounds in the northern North Atlantic there has been a decline, from 1960 to 1990, in catches of about 50%, in recruitment of about 67%, and in spawning stocks of about 75%. The smaller decrease in catch than in recruitment and spawning stock, in particular, indicates an increasing fishing load from 1960 to 1990.

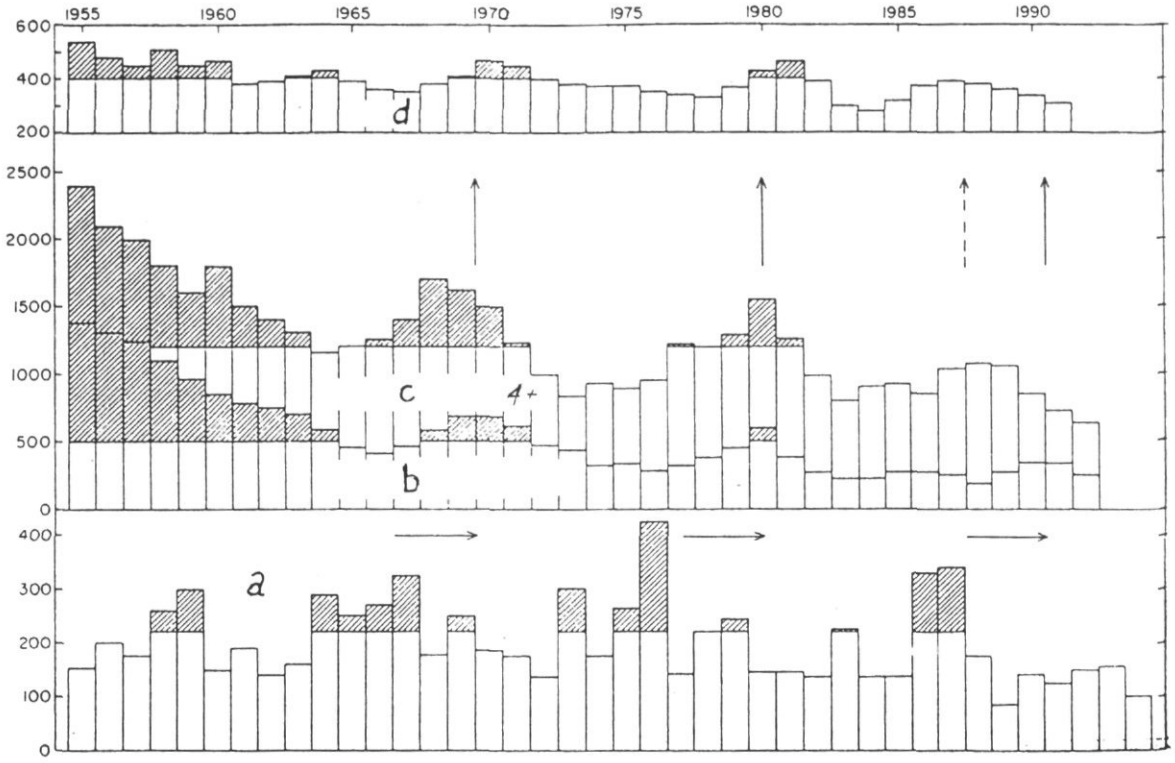


Figure 7. Conditions of the Icelandic cod stock 1955–1991/92. a. Three-year recruits in millions by number. b. Spawning-stock biomass in thousand tonnes. c. Fishing-stock biomass (4-year-old and older fish) in thousand tonnes. d. Catches in thousand tonnes (from Anon., 1993). Shaded columns indicate periodic maxima observed and the arrows the time lack from 3–4-year-old recruits up to the year of maximum in fishing and spawning stocks as well as catches a few years later.

For Icelandic cod a similar indication appears from Figure 7, which shows recruitment by 3-year-old fish, spawning biomass, fishing stock biomass and catches since 1955. Before 1980 the recruitment of strong year classes was reflected in increased fishing-stock biomass and, but to a lesser extent, increased spawning stock. It is, however, noteworthy that strong 3-year-old recruiters in 1986 and 1987 (year classes 1983 and 1984) did not result in an increased spawning stock or catch a few years later despite Atlantic conditions in North Icelandic waters, but contributed in catch already in 1986–1988. Consequently, a good part of these year classes were not allowed to develop to maturity.

It is difficult to say which of the factors, fishery or environment, is the more decisive in relation to the decline in the cod stocks. The crucial difference between them is that while we are unable to do anything about environmental fluctuations, we should be able to manage the fishery. Careful regulation is particularly important when a fish stock is weak as a result of unfavourable environmental conditions. At worst, an efficient trawling fishery could easily exploit a spawning stock below a critical level of abundance, from which point it may take many years for the stock to be restored.

Concluding remarks

Time series of oceanographic observations reveal variability in processes such as stratification and advection over regional and large ocean areas in connection with air–sea interaction. They contribute to a better understanding of the processes underlying the oceanic and biological variability. The authors believe that a major factor concerning the variation in size and behaviour of fish stocks, at least along the Arctic and Polar fronts, is the maritime climate, which influences the living conditions including spawning, feeding, recruitment, and maturation. The mechanisms behind this may not be well understood. Temperature may have a direct effect on fish stocks or be associated with variable current activities such as climatic events and turbulence and other physical parameters, which again affect the multiple living conditions. The overall results of this paper may be summarized as follows:

There has been a dramatic decline of cod stocks in the northern North Atlantic during recent decades. In parallel with climatic changes in the northern North Atlantic during the same period, the spawning, feeding, and fishing grounds of cod in these waters seem to have declined since the 1960s.

Capelin stocks reflect great interannual variance in abundance and growth, depending on environment and feeding conditions.

Growth of adult cod is dependent more on food supply, such as abundance of capelin, than on hydrographic conditions.

Cold years in North Icelandic waters as well as in the waters off Labrador, West Greenland, and in the Barents Sea, seem generally to give weak year classes of cod.

The critically small spawning stock in Icelandic waters during recent years has given weak year classes during both cold and warm years.

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Climatic changes and environmental conditions in the Northwest Atlantic, 1970–1993

E. Colbourne, S. Narayanan, and S. Prinsenberg

Colbourne, E., Narayanan, S., and Prinsenberg, S. 1994. Climatic changes and environmental conditions in the Northwest Atlantic, 1970–1993. – ICES mar. Sci. Symp., 198: 311–322.

Oceanographic, meteorological, and ice data were examined to establish the average conditions that prevailed on the Newfoundland and Labrador continental shelves during recent decades, and to describe the variability on seasonal and interannual scales. The results indicate that the below-normal air temperatures established in 1989 persisted over much of eastern Canada, resulting in increased ice growth and reduced ice melt during the early 1990s. Since 1990, ice conditions have been more severe and have lasted longer, with 1991 being the worst in 30 years. The net effect of these conditions was a delayed and reduced heat input into the ocean, which resulted in a thinner and fresher mixed layer and a lower heat content in the water column. Conditions during similar anomalous periods of the early 1970s and mid-1980s were also examined. In general, the large negative temperature and salinity (fresher than normal) anomalies of the early 1990s were found to be similar to events of the early 1970s and to a lesser extent of the mid-1980s and were associated with colder than normal winter air temperature and heavier than normal ice conditions in the coastal region of the Northwest Atlantic.

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Introduction

In contrast to forecasted global warming trends worldwide, the Northwest Atlantic has experienced three anomalously cold periods since the early 1970s, particularly in Atlantic Canada's Newfoundland and Labrador areas. The latest cold period, which began in early 1989 (Findlay and Deptuch-Staphf, 1991) continued into the summer of 1993. These lower temperatures are associated with more persistent and stronger winds from the northwest. Anomalous meteorological conditions have given rise to increased ice growth and ice transport from northern latitudes, increased extent of ice cover in more southern areas and delayed ice melt during the spring and summer months (Narayanan *et al.*, 1994). For example, 1991 has been identified as the worst ice year on record in terms of both ice-cover extent and duration. As a result, more of the atmospheric heat flux is required to melt the ice, leaving less to heat the oceanic surface layer.

The net effect of these anomalous atmospheric and ice conditions was to create corresponding periods of colder than normal surface layers over large areas, which gradually deepened over the continental shelf through mixing and convection during winter storms and buoyancy flux due to salt rejection from the growing ice cover. In addition, the enhanced ice production during winter and increased ice melt during spring also resulted in a larger than normal amplitude of the annual salinity cycle over most of the shelf.

Coincident with the recent climatic anomalies in the Northwest Atlantic, the stock size and distribution of several fish species, both pelagic and bottom dwelling, have experienced considerable variability. Since the beginning of the most recent cold period very few aggregations of the once-abundant Atlantic cod (*Gadus*

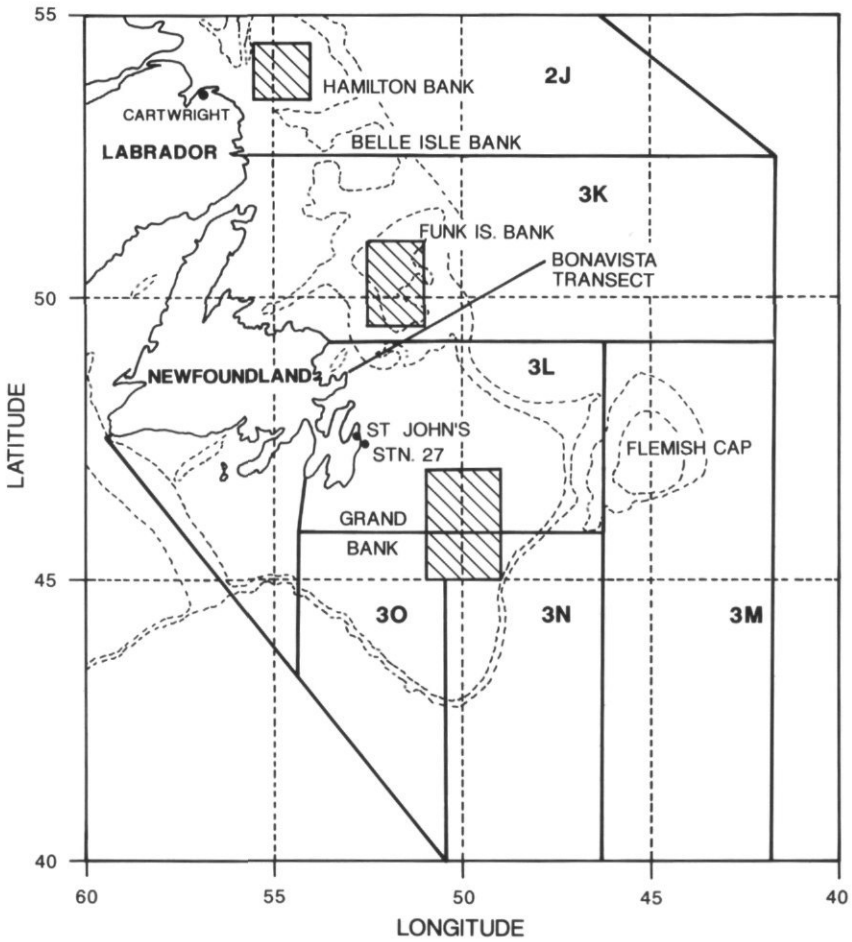


Figure 1. Location map of the study area showing NAFO divisions, the position of the standard Bonavista transect, Station 27, and areas where temperature and salinity anomalies were examined (shaded boxes).

morhua) were found in NAFO Division 2J off the Labrador Shelf (Fig. 1), and in Divisions 3K and 3L the stock size has diminished to such a low level that a moratorium on fishing for northern cod was imposed in July 1992. Pelagic species such as capelin and salmon have also experienced large declines in mean fish sizes, delayed spawning, and overall reductions in stock sizes and distribution.

To assess what environmental factors might have contributed to the variability in the fisheries during the anomalous periods, an evaluation of the climatic conditions, in particular the major differences among the three recent cold periods, is needed. The objective of this paper is to examine how the environmental conditions during recent years compare with the average over the last several decades and with those that existed during other anomalous periods of the early 1970s, mid-1980s, and the early 1990s.

Meteorological and ice conditions

Over the North Atlantic, the winter atmospheric circulation is dominated by a low pressure centred over Iceland (the Icelandic Low) generating northerly to westerly wind patterns in the Northwest Atlantic. In the course of a year, the intensity and position of this system vary, effecting an annual cycle with strong cyclonic wind stress forcing during winter and spring (Thompson and Hazen, 1983).

Following the establishment of the cyclonic circulation over the Northwest Atlantic every year during the fall and winter months, both the air and sea-surface temperatures decrease, the stratification in the water column starts to break down, and ice production begins. The strength, duration, and persistence of wind forcing from the northwest during the winter months determines to a large degree the extent and duration of ice

cover and hence the volume of ice that eventually melts on the Newfoundland and Labrador shelves.

Atmospheric circulation

A convenient index representing the strength of the winter circulation has been termed the North Atlantic Oscillation (NAO) index and is defined as the difference in the winter sea level air pressure between the Azores and Iceland (Rogers, 1984). The periods from 1970 to 1975 and from 1988 to 1992 show strong positive NAO index anomalies (Fig. 2) indicating stronger than normal cyclonic circulation over the Northwest Atlantic during the winter months, bringing more cold Arctic air to the coastal areas of Labrador and Newfoundland. During the mid-1980s, however, the NAO index anomaly amplitude was somewhat lower compared with the other two periods and persisted for a shorter duration.

The geostrophic winds from one location on the Labrador Shelf and another from the Grand Bank, computed by the Atmospheric Environment Service of Canada, were analysed to examine the interannual variability in the frequency of occurrence of northwesterly winds. A time series of occurrence of northwesterly winds for the Labrador and the Grand Banks areas was determined by averaging the percentage occurrence of winds of all speeds between ± 22.5° from northwest over the three winter months (December to February). At both sites there is an increase in the frequency of northwesterly winds during the early to mid-1970s and from 1988 onwards, with values reaching 40% in 1974 compared to values of less than 15% in the late 1970s, consistent with the strong positive anomalies in the NAO index (Fig. 2). However, during the mid-1980s, though there appears to be a slight increase in the percentage occurrence of the northwest wind, the increase is less pronounced and of shorter duration. In addition, the upward trend towards more frequent northwest winds is more apparent at the northerly site off Labrador compared to the Grand Bank.

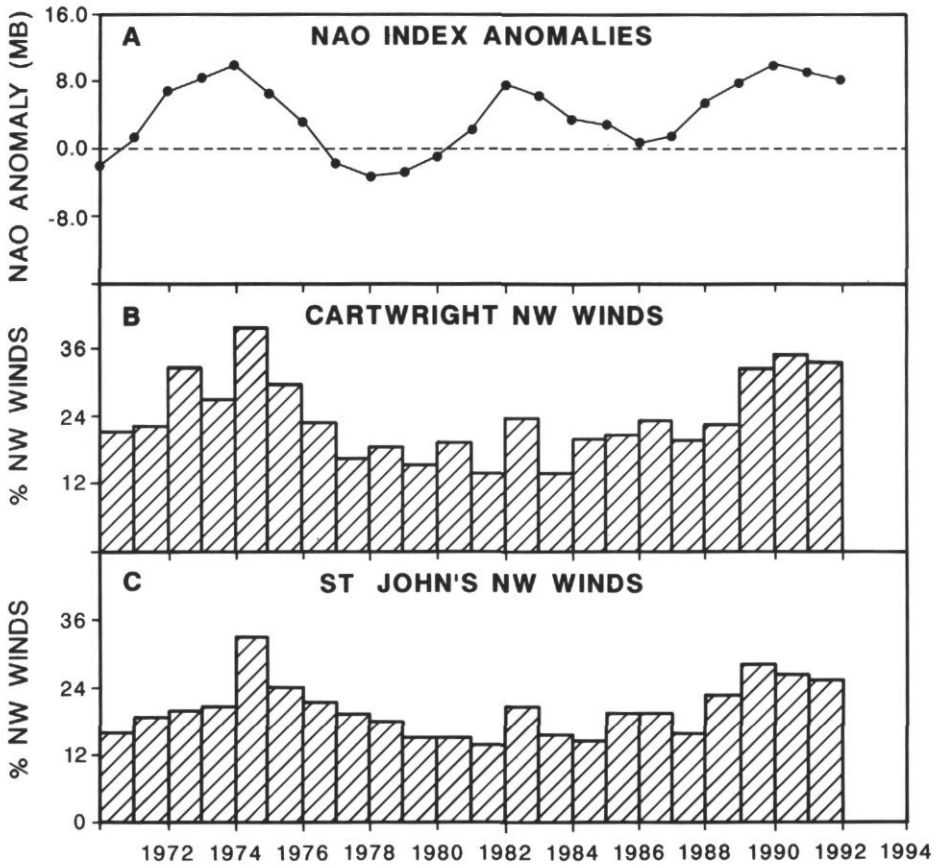


Figure 2. Time series from 1970 to 1992 of (a) the five year averaged NAO index anomaly, (b) frequency of northwesterly winds at Cartwright, Labrador, and (c) at St John's, Newfoundland.

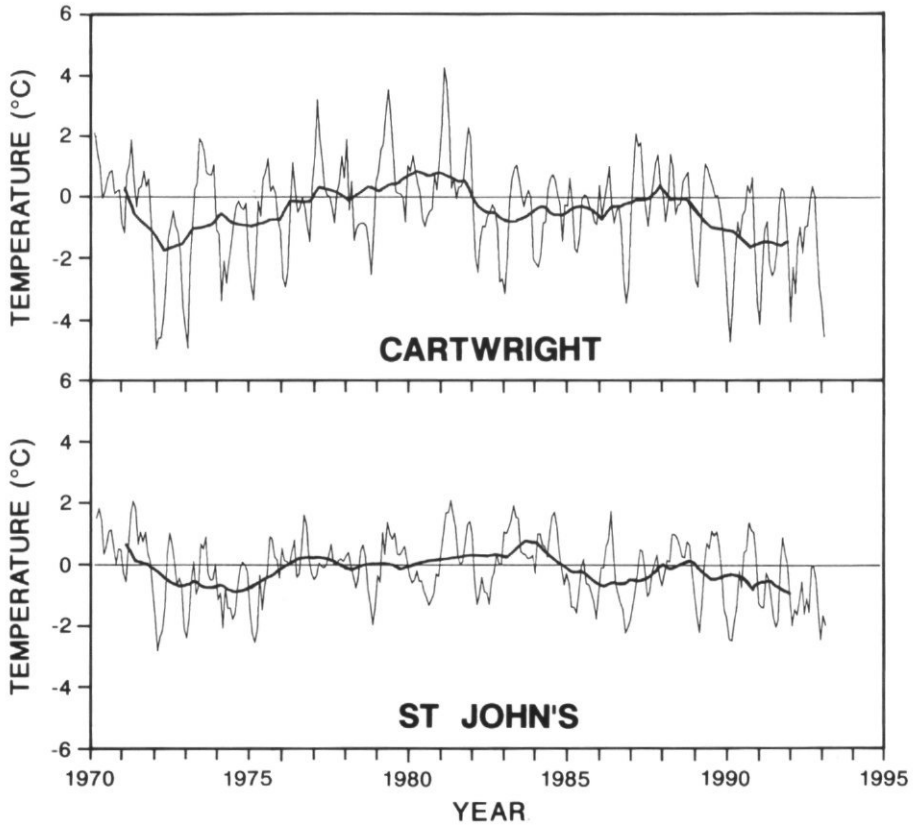


Figure 3. Time series of weekly air temperature anomalies at (a) Cartwright and (b) St John's. The heavy line represents a 25-month running mean.

Air temperatures

Air temperature anomaly data from two meteorological stations, Cartwright on the Labrador coast and St John's, Newfoundland (Fig. 1), are presented in Figure 3. Daily air temperature data from these two locations were averaged to compute a weekly temperature time series, which is then used to compute the annual cycle based on a 25-year period from which the anomalies are calculated. A three-month moving average filter was then applied to the anomalies to highlight the seasonal and interannual scales by suppressing higher frequency components. The superimposed 25-month running mean shows the decadal variations in the anomalies. Interannual variability in the air temperatures is clearly evident at both sites (Fig. 3), even when the weekly data were three-month averaged. The amplitude of the variability is more pronounced at Cartwright, and at more northern latitudes (not shown here). For example, at Godthåb, Greenland, and Iqualuit, N.W.T. Canada, air temperatures during 1983–1984 were 2.5 to 3.5°C below normal (Drinkwater *et al.*, 1992), whereas at Cartwright the temperature was about 1.0°C below normal.

The air temperature anomalies at both sites clearly show three cold periods during the last 20 years. The 1970s started with positive anomalies but changed to extremely cold conditions in 1972 and lasted until 1977. A warming trend was then established at Cartwright until the middle of 1981, whereas at St John's the negative anomalies ended around 1975, after which a warming trend commenced. From 1982 to 1986, Cartwright temperatures were below normal, but not as severe as those in the 1972–1977 period. At St John's, the air temperature anomalies were more or less positive after 1975 until the fall of 1984, when the trend reversed. After a brief period of near normal temperatures during 1987 at Cartwright and 1988 at St John's, extreme cold conditions were once again re-established over the entire region. The intense negative air temperature anomalies established in the late 1980s continued into mid-1993, making this the longest cold period experienced this half of the century. These colder than normal air temperatures are associated with positive NAO index anomalies and more frequent winter northwesterly winds, especially for the 1970 and 1990 cold period.

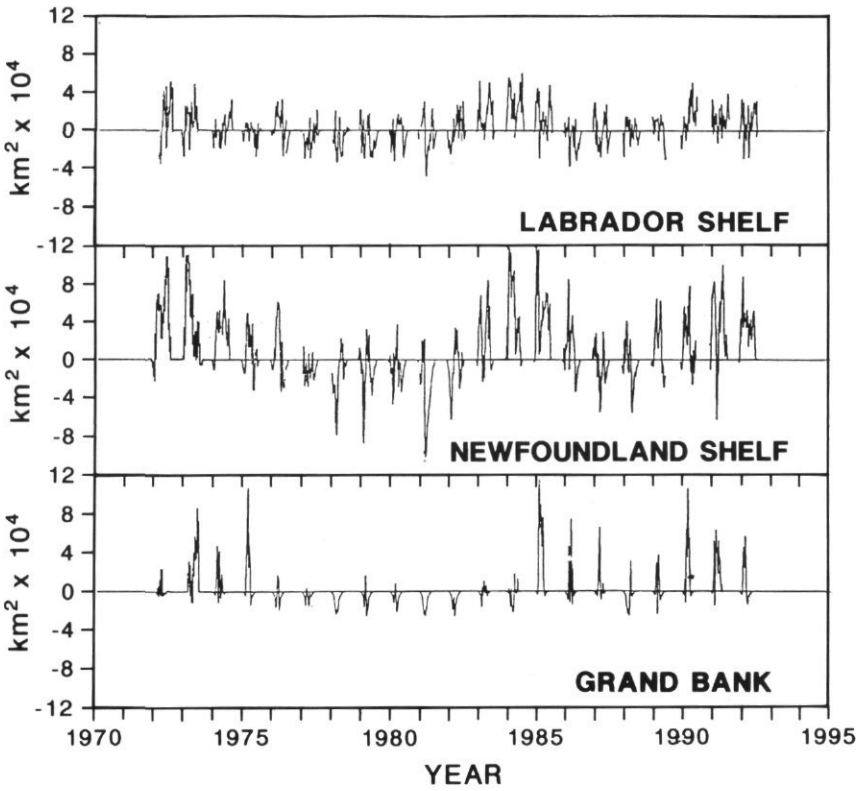


Figure 4. The ice coverage anomalies for the winter and spring months for (a) Labrador Shelf between 53 and 55°N, (b) the Newfoundland Shelf between 49 and 52°N, and (c) the Grand Bank between 45 and 48°N.

For the mid-1980s period, however, it appears that the colder and windier weather pattern did not reach as far south as St John's.

Sea ice

Ikeda *et al.* (1988), using a simple two-layer model of the Labrador Shelf and observed meteorological forcing, were able to reproduce the interannual variability of the annual advance and retreat of the Labrador ice pack for the years 1964 to 1974. These simulations show that although ice production is a function of the air temperatures at northern latitudes, the year-to-year variability in ice cover over the southern Labrador and Newfoundland shelves is largely driven by wind forcing with local temperatures affecting the melt rate.

The ice extent anomalies calculated from a 25-year average of weekly ice cover data for the winter and spring months for the Labrador and Newfoundland shelves and the Grand Bank (Fig. 4) clearly show increased ice cover and longer durations during the three cold periods mentioned above, namely 1972–1974, 1983–1985, and 1990 onwards. In terms of duration 1972, 1974, 1985, and 1991 were among the worst ice years in the 30-year period, with 1991 being particularly unfavourable in the inshore areas due to strong onshore flow during the spring which kept the ice locked into the bays. These heavy ice periods coincided with the large meteorological anomalies discussed above, positive NAO index anomalies, more frequent northwesterly winds, and cold air temperature anomalies during the winter months.

The net result of increased ice cover and extended ice duration is to reduce the amount of solar heat flux into the ocean surface layers, both delaying and reducing the annual warming of the water column on the shelf and along the coast. In addition, the eventual melting of increased volumes of ice generates lower than normal salinity anomalies near the surface which propagate downward through the water column owing to vertical diffusion and vertical mixing when the surface mixed layer deepens in fall and winter.

Oceanographic conditions

The oceanographic conditions along the continental shelf of the Northwest Atlantic are also experiencing a cooling trend that began in the late 1980s and continued into the spring and summer of 1993 (Colbourne, 1993a). These colder and fresher than normal conditions are a direct result of the strong atmospheric and sea-ice anomalies discussed above. The present cold period is the third such event that has occurred since the early 1970s. The cold period of the early 1970s was the subject of a special meeting of ICNAF (ICNAF, 1975), and the more recent cold periods have received extensive reviews (Petrie *et al.*, 1992; Narayanan *et al.*, 1992; Drinkwater, 1993; Colbourne, 1993b). In this section we attempt further to investigate the oceanographic anomalies corresponding to these periods, over wide temporal and spatial scales in NAFO Divisions 2J to 3NO. Water properties, especially those at larger depths, are partly a result of processes that occurred earlier in the year far up north from the actual locations on the Newfoundland Shelf. The seasonal variability at one location is thus a reflection of processes that occurred over a larger area and are not just reflected by local atmospheric and ice-cover conditions.

Temporal anomalies in temperature and salinity

To investigate the spatial variability in the temperature and salinity anomaly fields over time, the historical data set for the region was grouped into three areas in NAFO Divisions 2J, 3K, and 3LNO, indicated by the shaded blocks in Figure 1, together with Station 27 data. The average water depths in these areas ranged from 70 to 80 m in 3LNO, 250 to 300 in 3K, and 150 to 200 in 2J. Station 27 was established as a hydrographic monitoring station in 1946 and is located about 8 km off St John's, Newfoundland; it has a water depth of 176 m. These areas were selected based on the local bathymetry and on the available data.

The data for each area for all years were then sorted by Julian day to determine the annual cycle. Following the general methods of Akenhead (1987), the mean seasonal cycles in the temperature and salinity fields at selected water depths were determined by fitting a least-squares regression to the mean and a sum of four sines and cosines pairs representing four harmonics. Time series of temperature and salinity anomalies for each area were then formed, taking each observation and subtracting the least squares fitted value for the same day of the year. The time series of anomalies were then low-pass filtered to suppress variations shorter than one year.

An in-depth discussion of the annual harmonic was carried out by Petrie *et al.* (1991), and hence not repeated here. However, to provide a background for the discussion on the anomalies and to indicate the temporal structure of, and the scatter from the mean, temperature and salinity values at depths of 0, 20, 50, and 75 m for the 3LNO area are shown in Figure 5. As expected, the largest seasonal cycle in the water temperature occurs in the upper layers, where the strongest coupling to the annual solar flux exists. The amplitude of the seasonal cycle for both temperature and salinity decreases with depth and is not statistically significant at 75 m depth for this location. Maximum temperature at the surface occurred during the summer months with the phase of the maximum increasing with depth at an approximate rate of 1.4 days m^{-1} in the upper water column.

Petrie *et al.* (1991) have shown that although the temperature phase is nearly uniform horizontally, the salinity phase has significant latitudinal and cross-shelf variability. During ice production, near-surface salinities increase because of salt rejection, so that the annual salinity cycle will have a maximum during this period. Similarly, low salinities occur in areas where large volumes of ice melt during the spring and summer months. Thus the heavy ice production, retention, and melt affect both the high and low of the salinity cycle, which propagates to lower latitudes through advection and results in a phase lag with latitude. Furthermore, for any given latitude the salinity phase has more scatter with depth and with longitude compared to the temperature because of the cross-shelf variability in the along-shore current (producing different advection rates) and because of shelf-edge oscillations.

The time series of temperature anomalies at Station 27 at various standard depths (Fig. 6a) are characterized by three major cold periods: in the early 1970s, early to mid-1980s, and the early 1990s. The time series exhibit lower frequency variations in the anomalies in deeper water compared to the shallower depths consistent with the slower response of the deeper water to atmospheric forcing. For all three periods, the negative temperature anomalies at the bottom were established first and appear to last the longest. The cold period beginning in 1972 continued until late 1973 in the upper layers and until 1975 near the bottom at 175 m depth, with anomalies reaching peak values of −2.0°C by early 1973 over the upper water column. From late 1975 to late 1983 the temperature anomalies showed a high degree of variability with fluctuations of ± 2.0°C in the upper water column and a stronger tendency towards positive anomalies near the bottom.

During the second period, by early 1984 in the top 50 m of the water column and early 1983 in the deeper water, intense negative temperature anomalies had returned with peak amplitudes reaching −3.0°C at 30 m depth by late 1984. This cold period lasted until mid-1986 over most depths. By late 1986 near the bottom, by

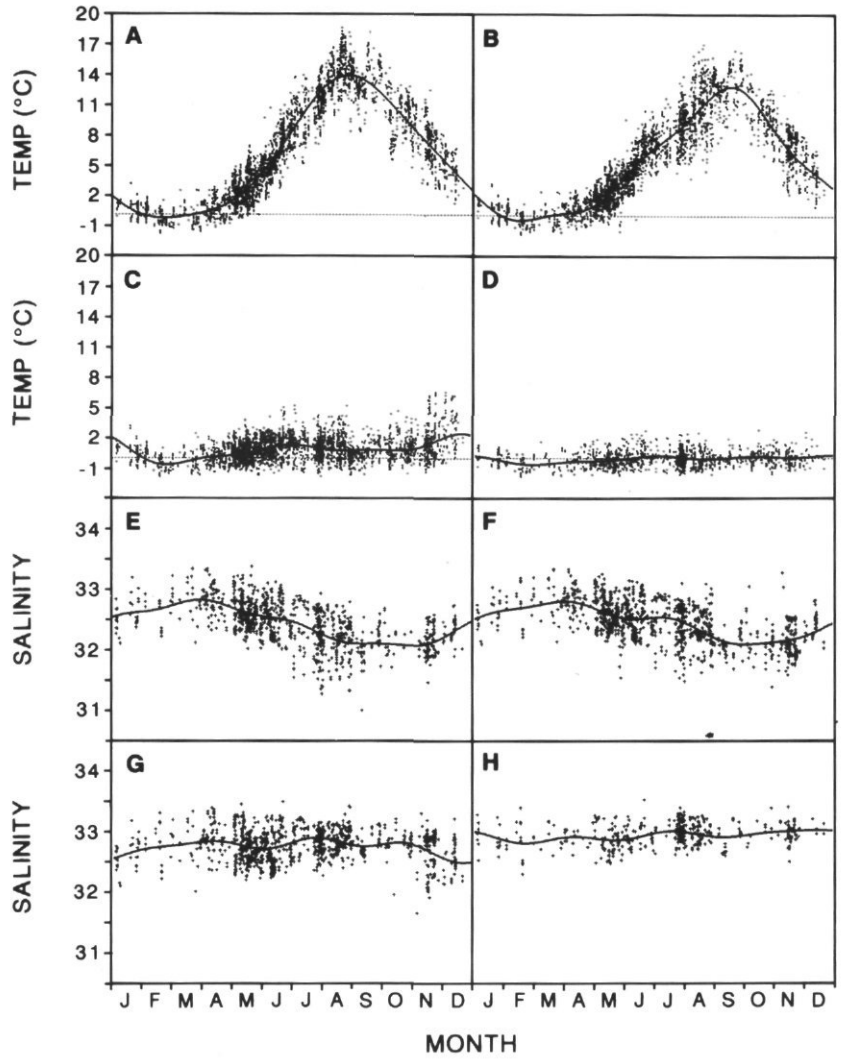


Figure 5. Temperature values for all years at depths of 0, 20, 50, and 75 m (panels A to D, respectively) for the shaded area in NAFO divisions 3LNO (Fig. 1), together with the fitted regression curves, and similarly for salinity (panels E to H).

1990 at mid-depths, and by early 1991 in the surface layers the temperature again fell below normal. In the upper layers the negative temperature anomalies that began in late 1990 and reached a peak of −4.0°C in mid-1991 continued into the summer of 1993; for example, at 30.0 m depth temperature anomalies were about −2.0°C in early June, indicating a delayed warming of the surface water. In general, deepwater temperature anomalies have persisted at Station 27 since 1983, with a few periods of positive anomalies during the mid to late 1980s.

The increased ice production and above normal ice melt have opposing effects on the salinity cycle, such that heavy ice years may result in either positive or negative salinity anomalies depending on the time of year and the location. At Station 27, the time series of salinity anomalies (Fig. 6b) show the large fresher than normal anomaly that began in early 1991 had returned to near normal conditions by the summer of 1992. It continued at near normal levels to the spring of 1993 over all depths except at the surface, where the water was up to 0.25 psu (practical salinity units) lower than normal owing to increased freshwater input from melting ice. Note also the large negative (lower than normal) salinity anomaly beginning in 1983 and lasting to the end of 1984, particularly in the upper water column. The salinity anomaly in the early 1970s preceded the temperature anomaly and was in general weaker compared

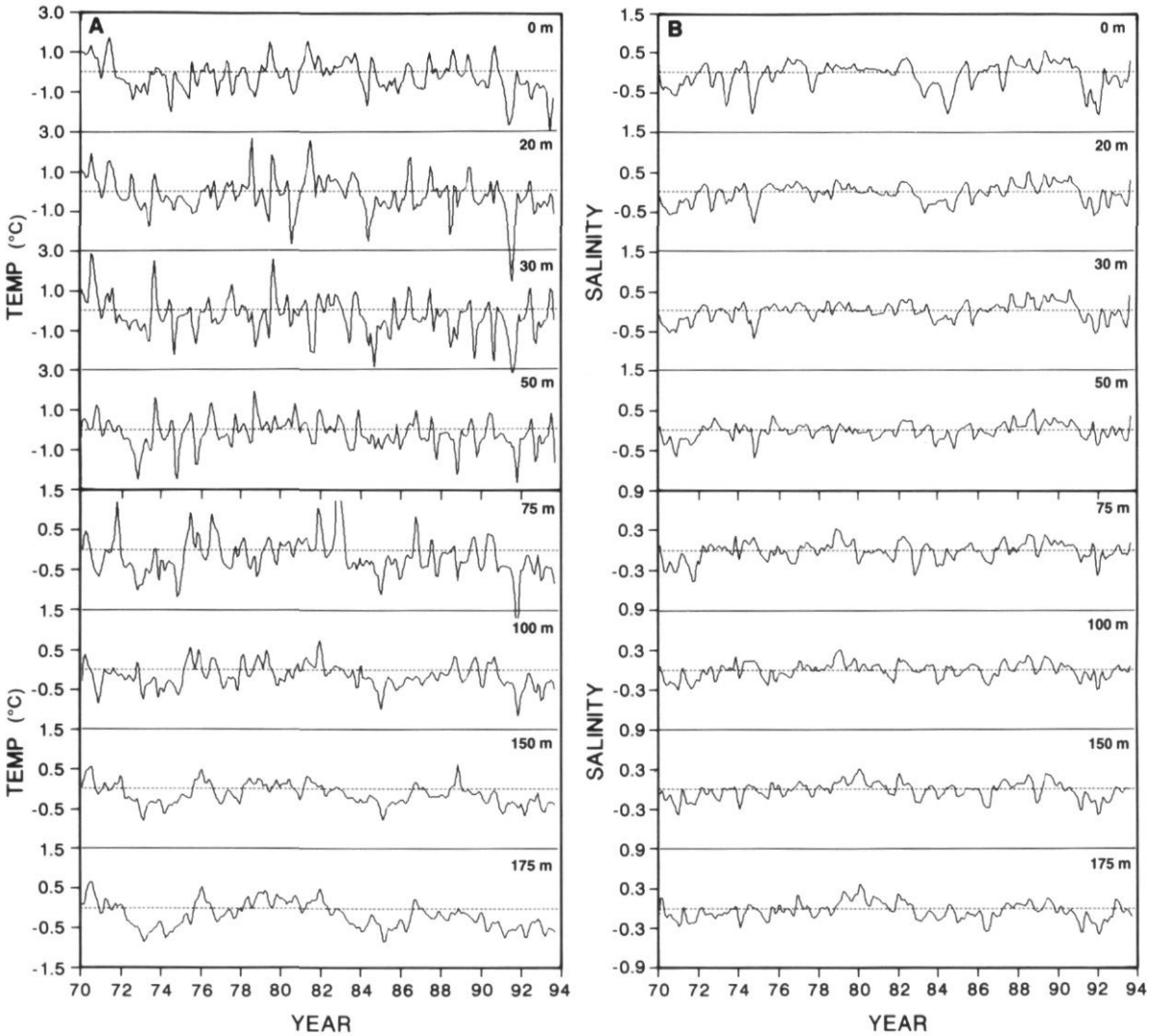


Figure 6. Time series of (a) temperature and (b) salinity anomalies at Station 27 at standard depths from 1970 to 1993.

to the 1990s at all depths, and compared to the 1980s in the upper layers. Like the temperature anomalies the largest negative anomaly amplitude is in the upper mixed layer, where the influence of ice melt is the largest.

Time series of temperature and salinity anomalies for the shaded areas in Figure 1 at standard depths, referenced to a 1950–1992 mean, are shown in Figure 7. Unlike the time series at Station 27, these time series are based on a smaller data set distributed over a wider geographical area; hence the anomalies are subject to larger spatial and temporal biasing.

In Division 2J the time series show large temperature anomalies in the early 1970s, early to mid-1980s, and to a lesser extent in the early 1990s below 20 m depth. The salinity was lower than normal almost throughout the 1970s near the surface (the Great Salinity Anomaly, Dickson *et al.*, 1988) and during the mid-1980s and again around 1989 at mid-depths and 1990 near the bottom (175 m). In Division 3K the time series is again characterized by three colder and fresher than normal periods: the early 1970s, mid-1980s, and early 1990s, throughout the water column. In Divisions 3LNO the cold periods are again clearly evident, the most pronounced occurring in the early to mid-1970s when temperatures fell to 1.5°C below normal at 50 m depth. The cold period of the mid-1980s in Divisions 3LNO was of a shorter duration than in 2J and 3K, particularly in the upper

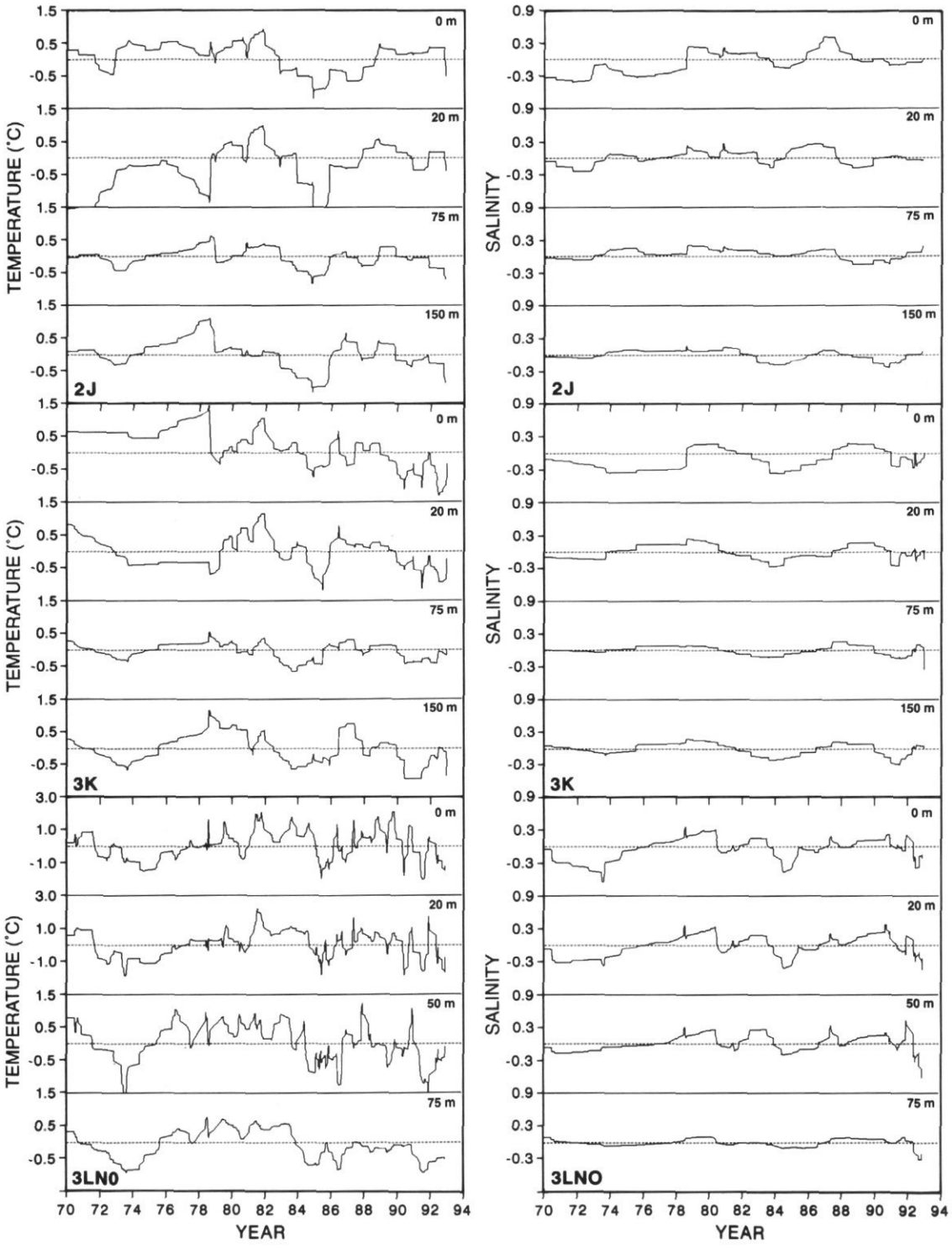


Figure 7. Time series of temperature and salinity anomalies for the shaded areas in Figure 1 at standard depths for NAFO divisions 2J, 3K, and 3LNO, referenced to a 1950–1992 mean.

layers. In addition, the peak of the events occurred up to a year later in Divisions 3LNO compared to 2J, particularly in the mid-1970s and 1980s. By the end of 1992 though, the temperatures remained below normal over all areas throughout the water column, the salinity anomaly had disappeared over most areas except at the surface and in the area of the Grand Bank bordering Divisions 3LNO. In general, these anomalies are very similar to conditions at Station 27, particularly in deep water, and are all associated with severe meteorological and ice conditions experienced over the same time intervals.

Spatial temperature anomalies

A dominant feature of the vertical temperature structure off the east coast of Newfoundland on the continental shelf is the cold intermediate layer (CIL) (Petrie *et al.*, 1988). The layer is formed in winter due at first to fall cooling and later by convective overturning resulting from salt rejection from the growing ice cover. In summer, spring ice melt and seasonal heating increases the stratification in the upper layers to a point where heat transfer to the lower layers is inhibited. The result is a cold layer of water confined to the continental shelf, with temperatures ranging from 0.0 to −1.8°C sandwiched between the warm seasonal upper layer and warmer slope water near the bottom.

In the winter months the surface layer effectively disappears as it cools down to near freezing temperatures and becomes part of the CIL owing to winter cooling and strong surface mixing. By late April and early May the warming of the surface layer commences and the cross-sectional area of colder than 0.0°C water decreases from winter maximum to a fall minimum due to summer heating.

The mean offshore extent of the Cape Bonavista (Fig. 1) CIL is about 220 km with a standard deviation of 44 km, centred at approximately 100 m depth with a mean thickness about 200 m and a standard deviation of 35 m (Fig. 8a). The average cross-sectional area of water less than 0.0°C is 26.4 km^2, with a standard deviation of 8.7 km^2. In 1972 the offshore boundary of the CIL was not defined by the survey extending more than 335 km offshore. In 1984 the CIL reached about 325 km off Cape Bonavista with a cross-sectional area of about 50 km^2, more than 80% above normal. The thickness of the CIL during cold years is also above normal, with 0.0°C water reaching close to the bottom at mid-shelf.

Figure 8b shows the intensity or minimum core temperatures of the CIL for the Bonavista transect for the summer from 1948 to 1992. The time series are characterized by four major cold periods with minimum occurring in the early 1950s, early to mid-1970s, mid-1980s, and early 1990s. Minimum temperatures at the core of the CIL range from −1.84°C in these cold periods (1984 and 1991) to −1.4°C in a warm year (1986). The average core temperature from 1948 to 1992 is −1.64°C centred at about 70 km offshore at approximately 80 to 100 m depth.

The time series of the CIL cross-sectional area anomaly (Fig. 8c) shows a gradual warming trend starting in 1950 and lasting until the mid-1960s. Since the early 1970s the time series is characterized by three major cold periods with peaks in 1972, 1984, and in 1990/91. The area anomaly during these cold periods range from 60% to 88% above average, with 1984 showing the greatest areal extent of sub-zero water. The warmest years were the mid-1960s, mid-1970s, and the late 1980s, when the cross-sectional areas were from 30% to 50% below average.

Summary

Since the early 1970s the oceanography in the Northwest Atlantic has been dominated by three anomalous periods; early 1970s, mid-1980s, and the early 1990s. During these periods, widespread negative water temperature anomalies and lower than normal salinities occurred for several years over the Northwest Atlantic. In general, it was shown that the oceanographic anomalies during the three periods were very similar, especially in deep water, but variations, both spatial and temporal, in the anomalies are significant. The meteorological and ice-cover data also show similar long period trends as the oceanographic conditions.

The results also indicated differences between the mid-1980s and the other two anomalous periods. Both the NAO index and the northwesterly winds were more pronounced in the 1970s and 1990s, whereas the NAO index anomaly was positive during the 1980s, but the frequency of the northwest winds was not much higher than other average years. Furthermore, the air temperature in St John's and water temperature over the southern Grand Bank were near normal during the mid-1980s, whereas both were well below normal during the other two periods. Thus the conditions during the mid-1980s were less severe (in spite of the large July CIL area off Cape Bonavista) over the southern portion of 2J3KL compared to the other two anomalous periods.

The results also indicated that both the meteorological and oceanographic anomalies have moderated only briefly (1986–1987) since the early 1980s. For example, the long-term trends in the Cartwright air temperatures (Fig. 3) and water temperatures at all depths at Station 27 (Fig. 6) have all been below normal since the mid-1980s.

Recent data from the spring and summer of 1993 indicate a continuation of below-normal air tempera-

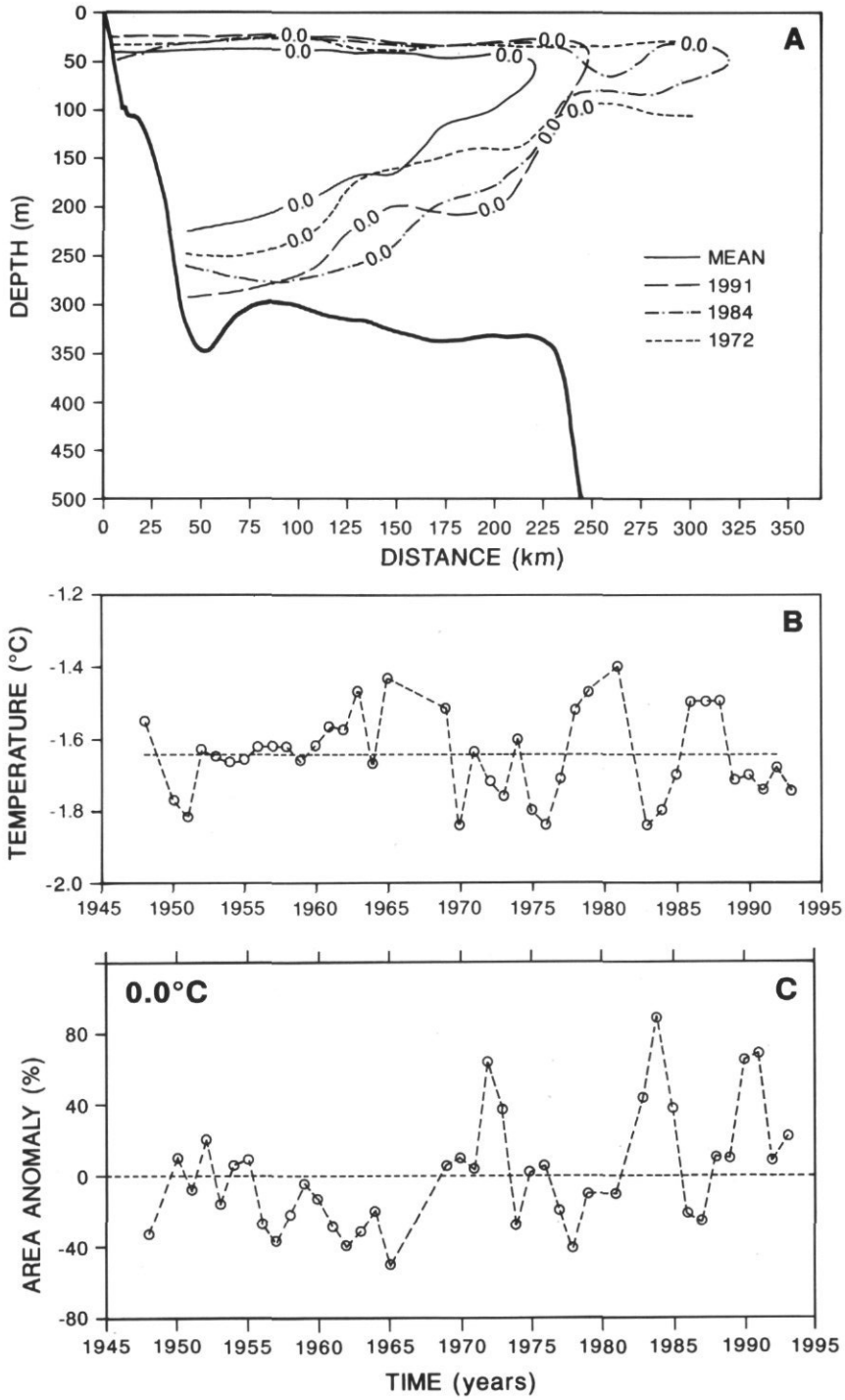


Figure 8. (A) The summer areal extent of the CIL bounded by the 0.0°C isotherm for 1991, 1984, 1972, and the 1948–1992 mean, (B) the minimum core temperatures of the CIL from 1948 to 1993, and (C) time series of the summer CIL cross-sectional area anomaly of water temperature less than 0.0°C from 1948 to 1992.

ture, above-normal ice cover and strong-negative water temperature anomalies over the entire water column in NAFO Divisions 2J to 3NO (Figs. 6 and 8). Salinity anomalies are also continuing a lower than normal trend in the upper layers, particularly in the southern areas (3L to 3NO).

Acknowledgments

We thank K. Drinkwater for providing us with the NAO index anomaly data and the many scientists who have contributed to the national database (MEDS) over the years. We also thank the technical staff of the oceanography section at the Northwest Atlantic Fisheries Center for the professional job done in data collection and processing and for computer software support. We thank D. Foote for data processing and technical assistance in the preparation of the paper.

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Temperature variability during Canadian bottom-trawl summer surveys conducted in NAFO Division 4VWX, 1970–1992

Fred H. Page and Randy J. Losier

Page, F. H., and Losier, R. J. 1994. Temperature variability during Canadian bottom-trawl summer surveys conducted in NAFO Division 4VWX, 1970–1992. – ICES mar. Sci. Symp., 198: 323–331.

The Canadian government has conducted annual research-vessel bottom-trawl surveys in NAFO Division 4VWX since 1970. The interannual variation in the near-bottom water temperatures within the shallow (<90 m) regions of these surveys is described and discussed in relation to regional climatic patterns. The temperatures are weakly coherent throughout the Scotian Shelf region with an indication that the eastern and western portions of the shelf are negatively correlated. The near-bottom temperatures in the eastern Scotian Shelf region (4VW) have decreased during the late 1980s and early 1990s with temperatures being unusually low in 1992.

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Introduction

The Scotian Shelf (Fig. 1) is a large, irregularly shaped, plateau that extends approximately 170 to 250 km from the coast. The shelf is bordered on the east by the Laurentian Channel with depths from 180 to 500^{+} m, on the west by the Fundian Channel with depths greater than 200 m, and on the south by the edge of the continental shelf. The central region of the shelf has several deep basins (depths >180 m) and a deep channel (depth <130 m) connecting the central basins to the deep ocean. Surrounding the central region and sitting along the offshore edges of the shelf are a series of shallow (depths <90 m) banks. Adjacent to the western edge of the shelf is the shallow (depths <100 m) Bay of Fundy.

The shallow areas traditionally have had high abundances of cod and haddock. In recent years the water temperatures in some of these areas have varied by several degrees (F. Page, unpubl.) and these may have significant effects on the distribution, survival and growth of the groundfish (Pinhorn and Halliday, 1985; Smith *et al.*, 1991; Page *et al.*, 1994; Smith *et al.*, 1994).

Interannual variability in water temperatures within the Scotian Shelf and Gulf of Maine area has been described by Colton (1968, 1972), Thompson *et al.* (1988), Petrie and Drinkwater (1993). The analyses indicate the existence of a low frequency trend that is coherent throughout the region at all depths. The trend contains a warming period that began in the 1940s and peaked during 1952–1953. A cooling period persisted, with short interruptions, from 1952–53 to 1967 followed by a rapid warming from 1967 to 1971. From 1971 to 1986 temperatures remained relatively constant and high. A cooling trend existed from 1986 to 1992.

These trends have been determined, for the most part, from long-term records of near-surface water temperatures obtained from across the region (Thompson *et al.*, 1988) and from a few long-term hydrographic monitoring stations that are located in inshore coastal regions (Fig. 1). The horizontal and vertical scale of the trends has been examined from time series of surface and subsurface temperatures at a few of the coastal stations, Prince 5 in the Bay of Fundy, Sydney Bight in Cabot Strait, and at one offshore station, Emerald Basin on the Scotian Shelf (Petrie and Drinkwater, 1993). No comprehensive analysis of the near-bottom temperatures within the shallow offshore regions has been conducted.

The Canadian Department of Fisheries and Oceans has collected hydrographic data in association with its summer groundfish bottom-trawl resource assessment surveys within NAFO unit area 4VWX since 1970. These data provide an opportunity to examine the temporal pattern and spatial scale of interannual variation in the near-bottom summer temperatures over the

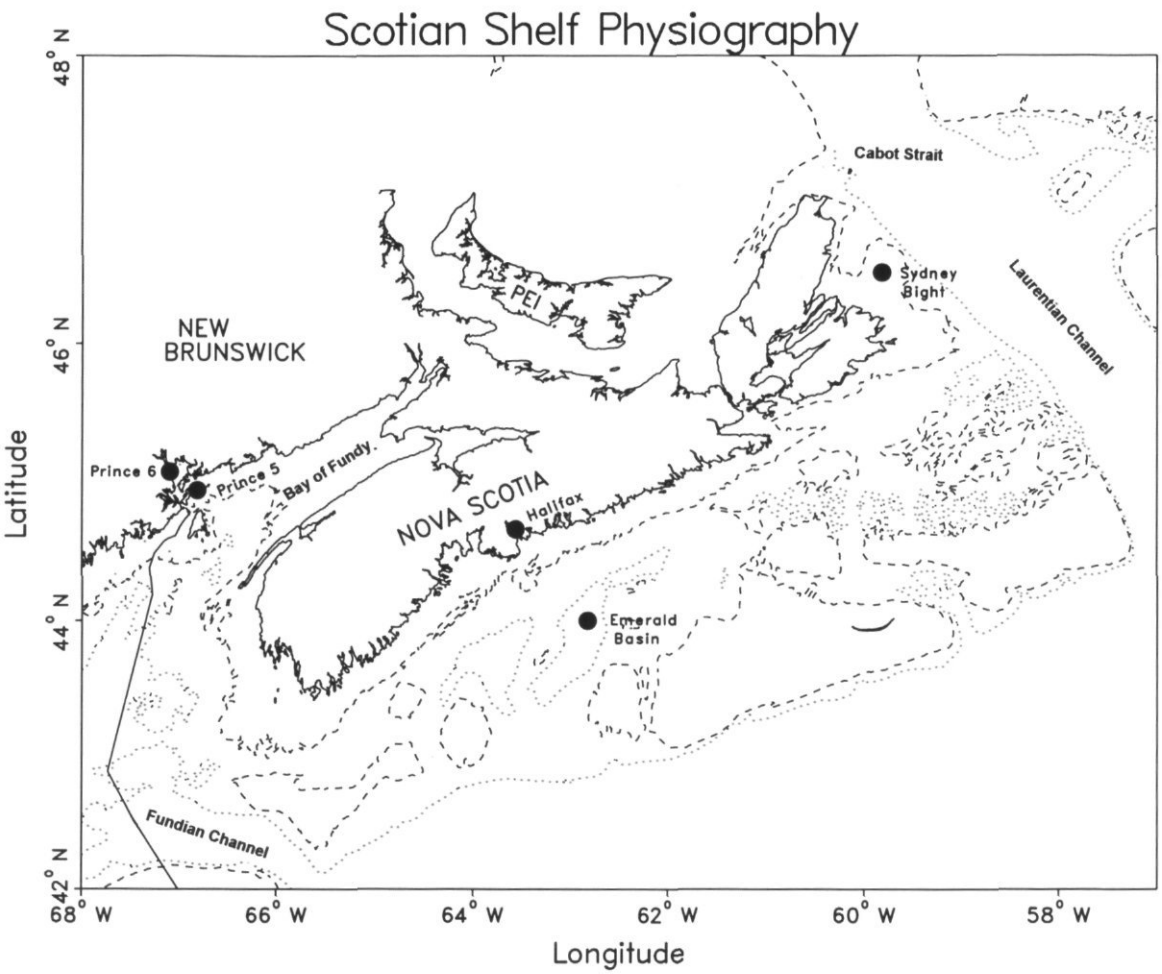


Figure 1. Map of the Scotian Shelf showing the 100 m (dashed line) and 200 m (dotted line) depth contours and the location of long-term temperature monitoring sites (solid circles).

offshore shallow areas; the areas of direct interest to fisheries biologists and fisheries managers. These data are described in section 2. The spatial and temporal patterns of the temperatures are described in section 3 and discussed in section 4.

Materials and methods

Data sources

The temperature data were collected as part of the Canadian Department of Fisheries and Ocean's bottom-trawl research-vessel surveys conducted over the Scotian Shelf (NAFO Divisions 4VWX) as part of the Canadian groundfish stock assessment process. The cruise numbers and types of equipment used are listed in Table 1.

The surveys used a stratified random survey design in which the Scotian Shelf is divided into 48 strata (Fig. 2). The strata boundaries are defined primarily on the basis of depth and secondarily on knowledge of the distribution of the major groundfish species (Doubleday, 1981; Halliday and Koeller, 1981). Each year sampling stations within each strata are chosen at random. Approximately 200 stations are allocated in total. Individual strata receive from 2 to 10 stations with the allocation made on an approximately proportional basis. As a result of this sampling protocol the same sampling stations are not occupied each year. An example of a sampling allocation is shown in Figure 3.

Only the near-bottom temperatures from the shallow strata, strata in which the bottom depth is less than 93 m (51 fathoms) are used in this analysis. Temperatures from other strata are not used because the range of near-

Table 1. The type and intensity of sampling during summer surveys conducted within NAFO Statistical Area 4VWX during 1970 to 1992.

Cruises	Year	Gear used
A175/A176	1970	RT
A188/A189	1971	RT
A200/A201	1972	RT
A212/A213	1973	RT
A225/A226	1974	RT
A236/A237	1975	RT
A250/A251	1976	RT
A265/A266	1977	RT
A279/A280	1978	RT
A292/A293	1979	RT
A306/A307	1980	RT
A321/A322	1981	RT
H80/H81	1982	RT
N12/N13	1983	RT
N31/N32	1984	RT
N48/N49	1985	RT
N65/N66	1986	RT
N85/N86	1987	RT
N105/N106	1988	RT
N123/N124	1989	RT
N139/N140	1990	RT/CTD
N154/H231	1991	RT/CTD
N173/N174	1992	RT/CTD

RT = reversing thermometer; CTD = conductivity, temperature and depth profiler.

bottom depths within these strata is relatively large and the temporal pattern of near-bottom temperatures may be confounded by interannual differences in sampling depths. Furthermore, only temperatures recorded within 20 m of the bottom are analysed. These temperatures are referred to as "near-bottom" temperatures. The composite distribution of sampling stations within the shallow strata for the complete 1970–1992 sampling period is shown in Figure 4.

From 1990–1992, inclusive, near-bottom water temperatures were measured using an internally recording Seabird model 19 or 25 conductivity, temperature and depth (CTD) profiler. These were calibrated with temperatures obtained from reversing thermometers. When the CTD was not available near-bottom temperatures were taken with a reversing thermometer. Before 1990 all near-bottom temperatures were measured with reversing thermometers.

All temperature values were quality controlled and edited using a combination of quantitative and visual despiking and range check routines. Checks for density inversions were also used when full hydrographic profiles were available. The edited data were stored in an ORACLE database.

Data analyses

The spatial coherence between the 1970–1992 time series was estimated using Pearson Product-Moment correlations and Principal Components Analyses of the correlation matrix (Morrison, 1976; Green, 1978; Harris, 1985). The correlations were estimated using the 1970–1992 time series of temperature anomalies. The anomalies for each strata were calculated as the deviation from the 1970–1992 strata means. Correlations were calculated pairwise with missing values not included in the analyses.

Results

Time series

The 1970–1992 mean near-bottom temperatures for each strata are given in Table 2. The mean temperatures range from 1.84 to 9.36°C and increase from east to west. The temperatures east of 62°W are generally less than 6°C. This pattern is consistent with previous findings (e.g. Hachey *et al.*, 1954; McLellan, 1954a, b). The standard deviation of temperatures within each year and strata is in the order of 1°C.

The time series of temperature anomalies for each of the shallow (<51 fathoms) survey strata are shown in Figure 5. The anomalies are typically ±2 degrees, although some larger (4–8°C) anomalies exist. The data suggest the presence of a cooling trend that began in the early 1980s. The anomalies in the recent years, 1990–1992, are weakly negative in most of the time series. In 1992 the anomalies are generally between −1 and −2°C. Auto-correlations of the time series (not shown) indicate, however, no significant serial dependence.

Coherence

The Pearson Product Moment correlations between these time series are given in Table 3. Correlations range

Table 2. Long-term (1970–1992) mean near-bottom temperatures for the shallow strata.

Strata no.	Mean temperature (°C)	Strata no.	Mean temperature (°C)
42	1.84	73	4.12
47	3.18	74	3.56
48	2.62	75	4.38
55	5.59	80	6.63
56	5.21	90	8.02
58	3.85	93	7.58
63	6.61	94	9.36
64	5.51	95	8.73

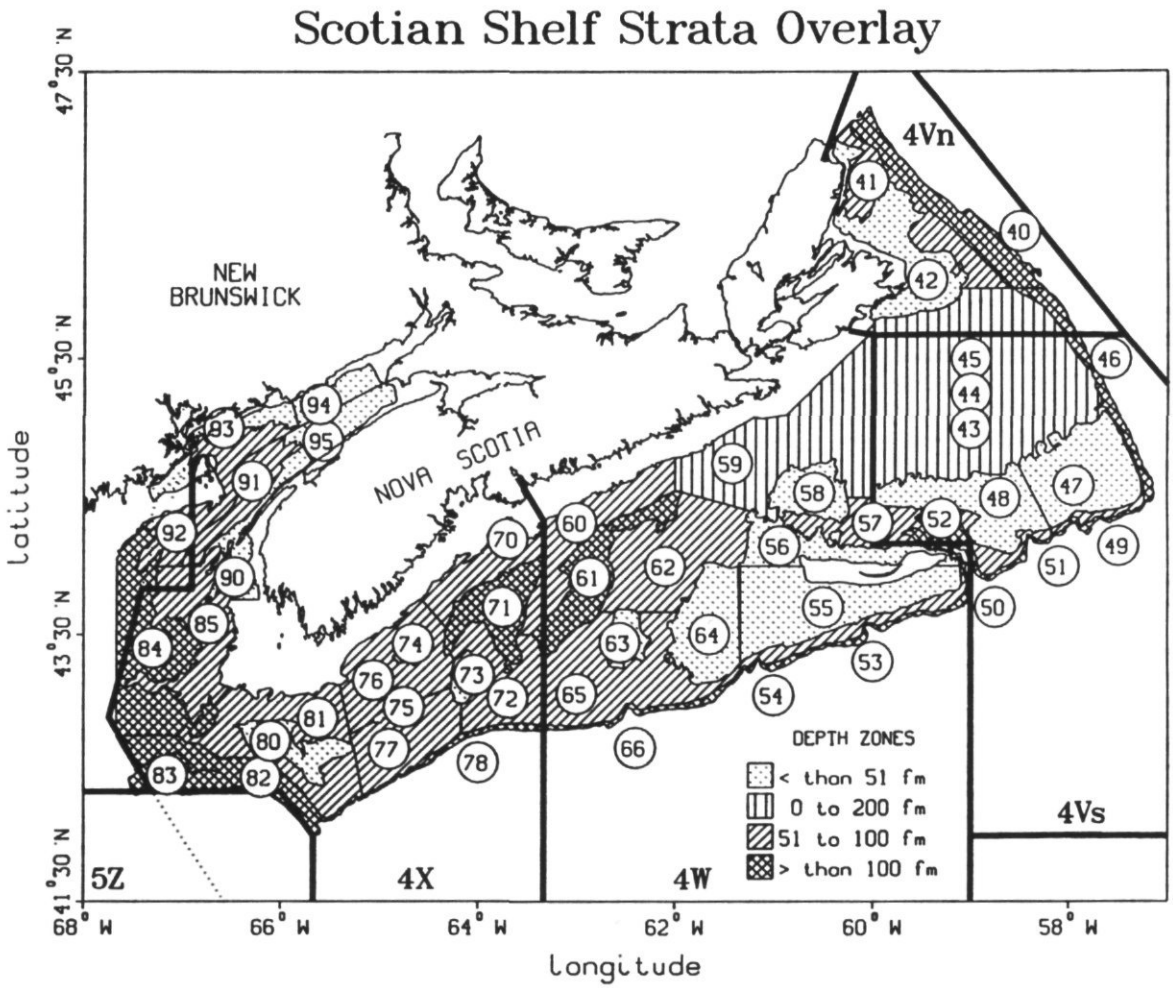


Figure 2. Map of the Scotian Shelf showing the boundaries of Canadian groundfish bottom-trawl summer survey strata. The strata boundaries are indicated by solid lines and the strata domains by shading. The shading patterns indicate the range of bottom depths within each strata. The numbers within open circles indicate the strata number. Only the last two digits of the summer strata designations are shown. Strata 43, 44, and 45 have been combined because of the complexity of the bathymetry and hence boundaries of the individual strata.

from −0.39 to 0.78. Analyses of the correlation matrix indicate that it is not an identity matrix (Barlett's Sphericity test, alpha 0.01) and that it is not consistent with the hypothesis that all off diagonal correlations are equal (Lawley's test alpha 0.01). A PCA analysis of the complete correlation matrix was therefore conducted. The first principal component explained 29% of the variance. Over 48% and 60% of the variance is explained by the first two and three principal components, respectively.

Plots of the principal component weights (Fig. 6) suggest the series can be separated into three strata groupings. One group includes strata numbers 75, 80, 90, 93, 94, and 95. A second group includes strata numbers 47, 58, 63, 64, 73, and 74 and the third group includes strata numbers 42, 48, 55, and 56. For the most part these groupings consist of strata from the western (WS), central (CS), and eastern Scotian Shelf (ES) areas. Strata 47 is the only exception; it is an offshore strata that associates most closely with central shelf strata. The mean correlations between the time series within the western, central, and eastern shelf groupings are 0.62, 0.20, and 0.60, respectively.

The shape of the first and second principal components is shown in Figure 7. The first PC shows a low frequency trend with high temperatures in the early 1970s and low temperatures throughout most of the remaining time. The second PC shows a trend of rela-

Table 3. Pearson product moment correlation matrix between time series of near-bottom strata mean temperatures for the 1970–1992 period. Strata numbers are in the uppermost row and leftmost column.

	42	47	48	55	56	58	63	64	73	74	75	80	90	93	94	95
42	1.0	0.37	0.65	0.38	0.33	0.05	−0.02	0.31	−0.30	−0.20	0.06	−0.13	−0.07	0.19	0.36	−0.07
47	s	1.0	0.36	0.12	−0.37	0.07	0.02	0.15	0.19	0.39	0.27	0.29	0.05	0.23	0.34	0.15
48	s	s	1.0	0.55	0.48	0.37	0.02	0.29	−0.20	0.19	−0.17	−0.25	−0.39	−0.02	0.19	−0.13
55	s	ns	s	1.0	0.58	0.15	0.03	0.33	0.01	−0.07	−0.35	−0.46	−0.28	−0.14	0.05	−0.20
56	s	s	s	s	1.0	−0.02	−0.17	0.24	−0.32	−0.22	−0.37	−0.35	−0.23	−0.19	−0.26	−0.34
58	ns	ns	s	ns	ns	1.0	0.36	0.33	0.14	0.28	0.27	−0.05	0.01	0.08	0.24	0.12
63	ns	ns	ns	ns	ns	s	1.0	0.51	0.05	0.12	0.32	−0.26	0.16	−0.10	0.19	0.33
64	ns	ns	ns	s	ns	s	s	1.0	−0.04	0.07	0.31	0.02	0.26	0.28	0.35	0.21
73	ns	ns	ns	ns	s	ns	ns	ns	1.0	0.18	0.10	0.34	−0.06	−0.15	−0.27	0.05
74	ns	s	ns	ns	ns	ns	ns	ns	ns	1.0	0.44	0.30	0.14	−0.01	−0.04	0.35
75	ns	ns	ns	s	s	ns	s	ns	ns	s	1.0	0.58	0.68	0.53	0.53	0.60
80	ns	ns	ns	s	s	ns	ns	ns	s	ns	s	1.0	0.63	0.61	0.27	0.51
90	ns	ns	s	ns	ns	ns	ns	ns	ns	ns	s	s	1.0	0.61	0.46	0.78
93	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	s	s	s	1.0	0.72	0.61
94	s	s	ns	ns	ns	ns	ns	s	s	ns	ns	ns	s	ns	1.0	0.49
95	ns	ns	ns	ns	s	ns	s	ns	ns	s	s	s	s	s	s	1.0

s indicates univariate significance at the 95% level; ns indicates lack of significance.

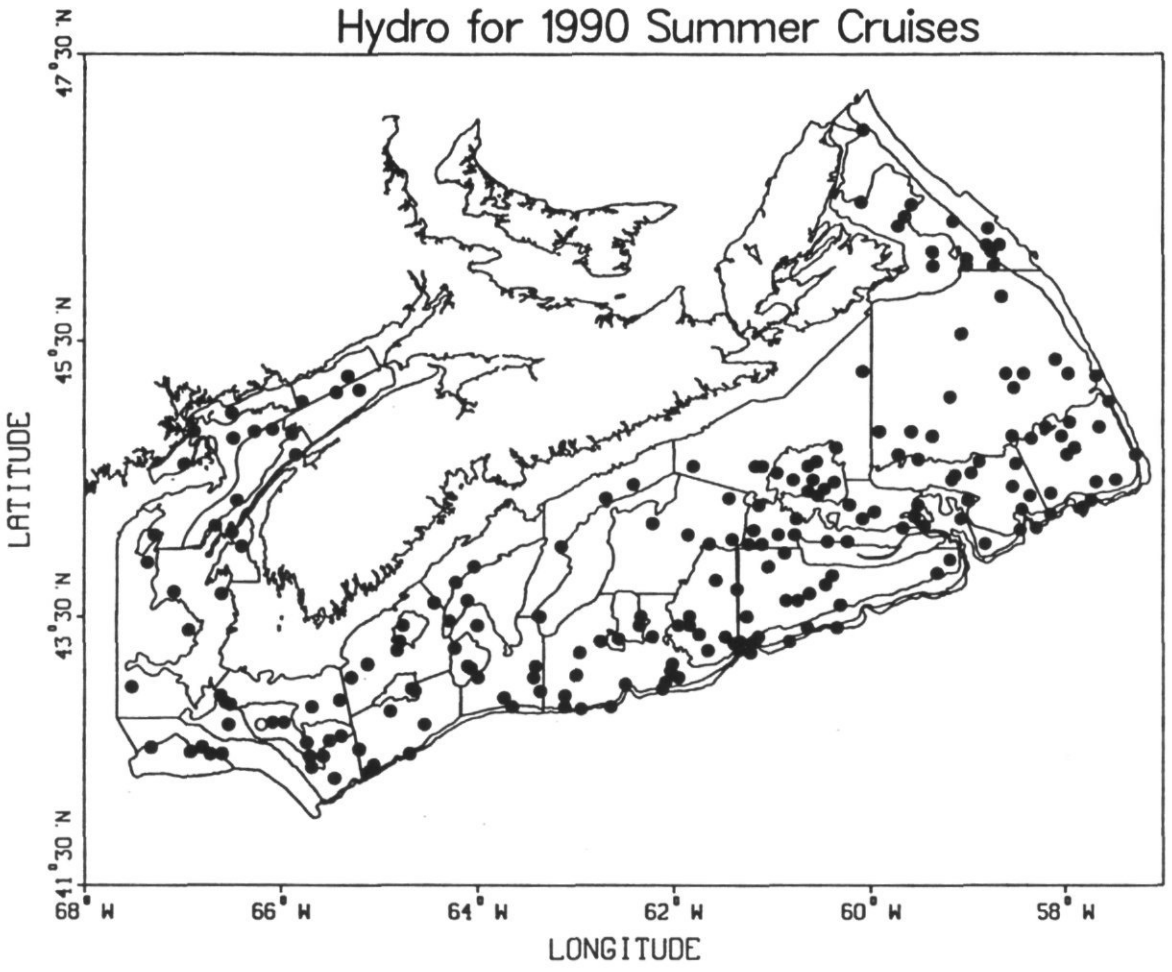


Figure 3. The location of near-bottom temperature sampling stations during the 1990 Canadian research vessel bottom-trawl surveys conducted during the summer on the Scotian Shelf within NAFO Divisions 4VWX. Within each panel a full circle indicates a station where a CTD cast was taken and an open circle indicates a station where near-bottom temperatures were measured with a reversing thermometer.

tively cool temperatures in the mid-1970s and late 1980s to early 1990s and relatively high temperatures in the late 1970s and early 1980s. Both show a trend toward changing temperatures from the mid-1980s to early 1990s.

These patterns reflect the trends in the time series shown in Figure 5. The strata on the eastern Scotian Shelf (ES group) are weakly related to PC I and more strongly related to PC II, whereas the strata on the western Scotian Shelf are consistently related to PC I and inconsistently related to PC II. In both groupings the trend is one in which the temperatures have declined throughout the mid-1980s and early 1990s.

Discussion

The general climatology and circulation of the continental shelf waters within the Scotian Shelf, Gulf of Maine, and Bay of Fundy region has been described by Hachey *et al.* (1954) and Sutcliffe *et al.* (1976). Annual updates on the climatology have been prepared since 1982 (e.g. Trites and Drinkwater, 1983). Reference to these can be found in Petrie and Drinkwater (1993). The distributions of temperature derived from the data examined here are consistent with the existing synthesis view (Petrie and Drinkwater, 1993).

The temperature time series within the region are characterized by a low frequency (decadal time period)

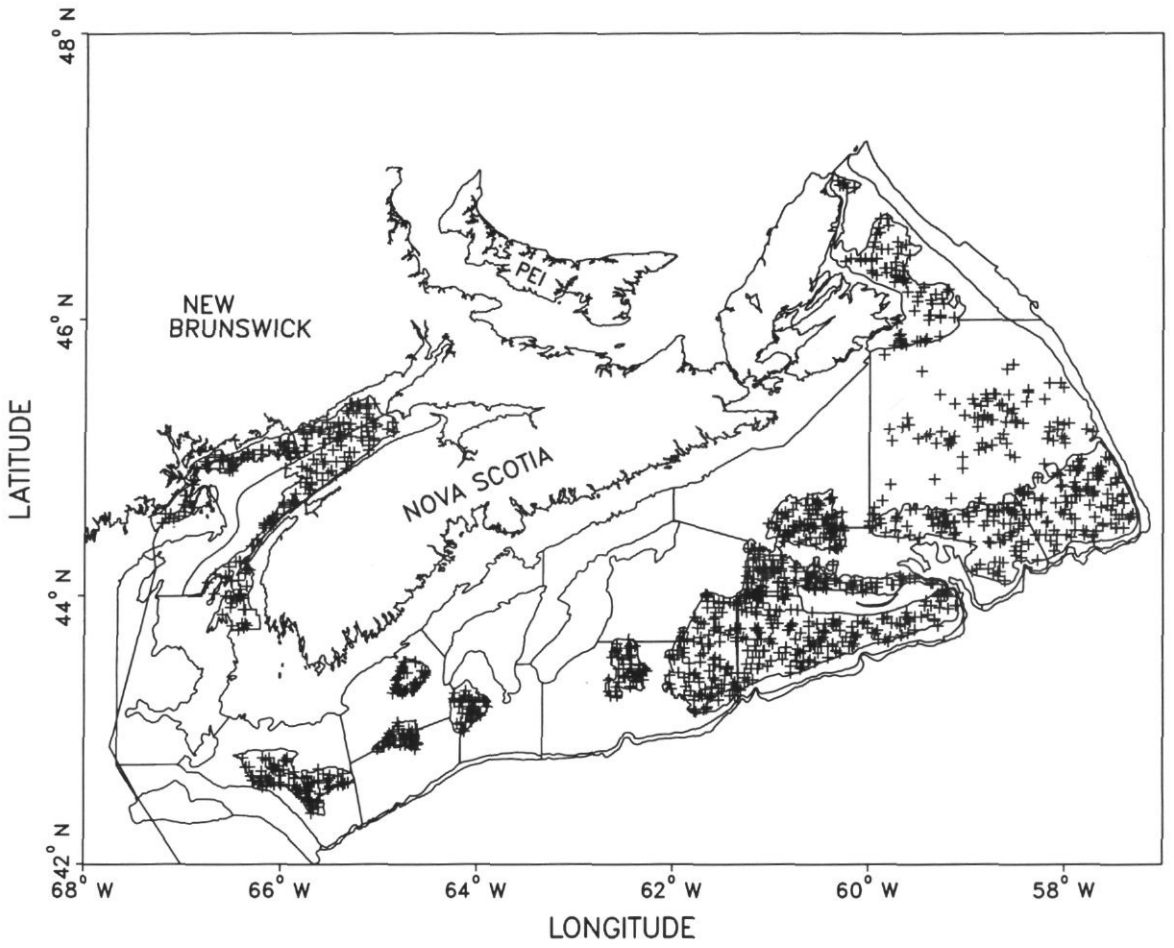


Figure 4. A composite of the location (crosses) of near-bottom temperature sampling stations within shallow strata sampled during the 1970–1992 Canadian summer research vessel bottom-trawl surveys conducted on the Scotian Shelf (NAFO Divisions 4VWX).

variation that is horizontally and vertically coherent throughout the region (Petrie *et al.*, 1991, Petrie and Drinkwater, 1993). The trend indicates that the late 1930s to early 1940s and the middle 1960s were relatively cold, whereas the late 1940s to early 1950s and the 1970s and 1980s were relatively warm. During the later 1980s temperatures have decreased such that in the early 1990s they are below the long-term mean.

The 1970–1992 period covered by the Canadian bottom-trawl surveys is short relative to the periods covered by the long-term monitoring stations (1921 – present at Prince 5; 1921 – present at St Andrews Biological Station; 1926 – present at Halifax Harbour; and 1905 – present at Boothbay Harbour). Therefore, the survey data do not include the low temperature period of the 1960s. However, they do show signs of the recent trend toward decreasing temperatures. In 1992 the near-bottom temperatures were below 1970–1992 means and dropped below zero within some strata. The frequency and horizontal extent of hydrographic stations in which below zero temperatures were recorded within the water column also reached historic highs (F. Page, unpubl.). In 1992 the extent of the sub-zero temperature extended over much of the north-eastern portion of the survey area (F. Page, unpubl.).

The Scotian Shelf is in a region with high variability in temperatures, both in amplitude of the seasonal cycle and in interannual variability. The amplitude and phase of the seasonal cycle changes with depth such that the amplitude decreases with increasing depth and the phase increases with depth. The seasonal cycle at the near-bottom depths sampled by the bottom-trawl surveys has

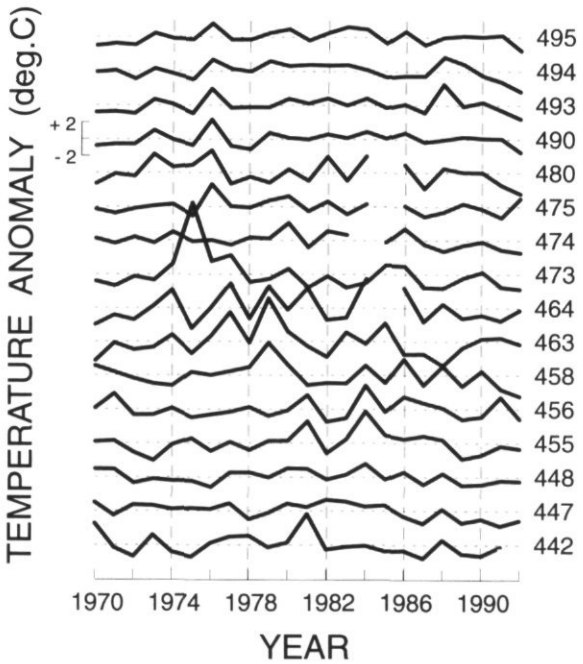


Figure 5. The time series of strata mean temperature anomalies within the shallow (<51 fathoms) strata sampled during the Canadian research vessel summer bottom-trawl surveys conducted over the Scotian Shelf (NAFO Divisions 4VWX). Anomalies are deviations from the long-term (1970–1992) strata means.

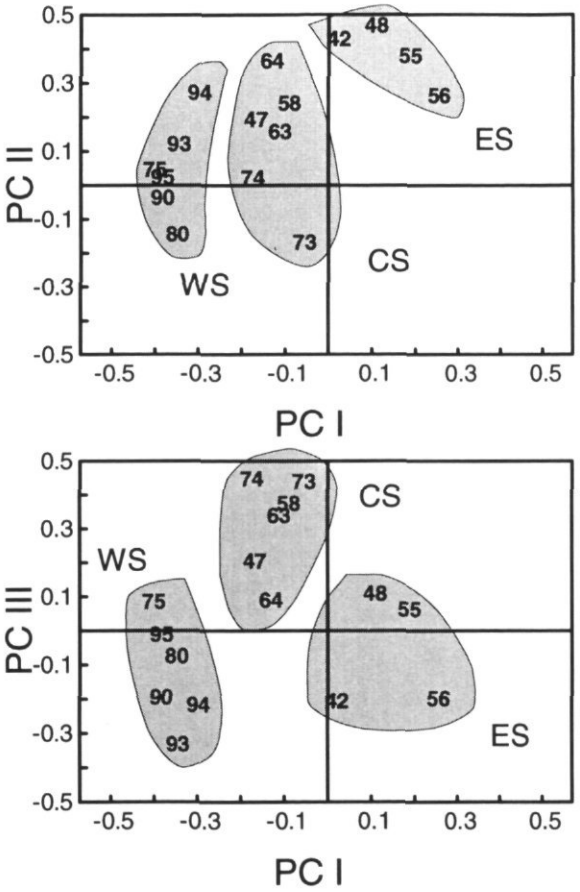


Figure 6. Scatter plots of principal components weightings calculated from the correlation matrix of the 1970–1992 time series of strata mean, near-bottom, summer temperatures from shallow strata. (Upper panel) PCI verses PCII, (lower panel) PCI verses PCIII.

an amplitude of 5°C at 50 m and less than 1°C at 100 m or greater (Colton, 1968; Petrie and Drinkwater, 1993). The seasonal minimum in temperature at 50 m occurs in March–April and the maximum in October–November. At 100 m the minimum occurs in May–June and the maximum in November–December (Colton, 1968). The rate of warming at 100 m during the summer period, when the bottom-trawl surveys are conducted, is approximately 0.5°C per month. Interannual variation in the timing of the surveys is in the order of several days and the duration of each survey is about 4 weeks. Therefore part of the interannual anomalies in temperature indicated by the time series is caused by interannual variation in the timing of the surveys. The surveys start at the western end of the Scotian Shelf and progress toward the east. The temperatures measured at the end of the survey are therefore at a later stage in the seasonal cycle than those measured at the beginning. This difference in timing corresponds to a 0.5°C difference in temperature. This is small relative to the 5–8°C gradient in temperatures along the shelf and the magnitude of the interannual temperature anomalies.

Despite these limitations the spatial pattern indicated by the PC analysis is consistent with the pattern identified by Thompson *et al.* (1988) in an analysis of sea surface temperatures. Both studies provide evidence for the separation of the eastern and western portions of the Scotian Shelf. The temporal pattern of the present analysis is not comparable to the Thompson *et al.* (1988) study because of the differences in the time periods covered by the data sets; 1970–1992 in the present case and 1946–1980 in the Thompson *et al.* (1988) analyses. In the present analysis the first and second principal components have low frequency trends that indicate decreasing temperatures in the late 1980s and early 1990s. This trend, although coherent throughout the Scotian Shelf, results in temperatures that are near the lower tolerance limit for cod on the eastern Scotian Shelf but not on the warmer western Scotian Shelf.

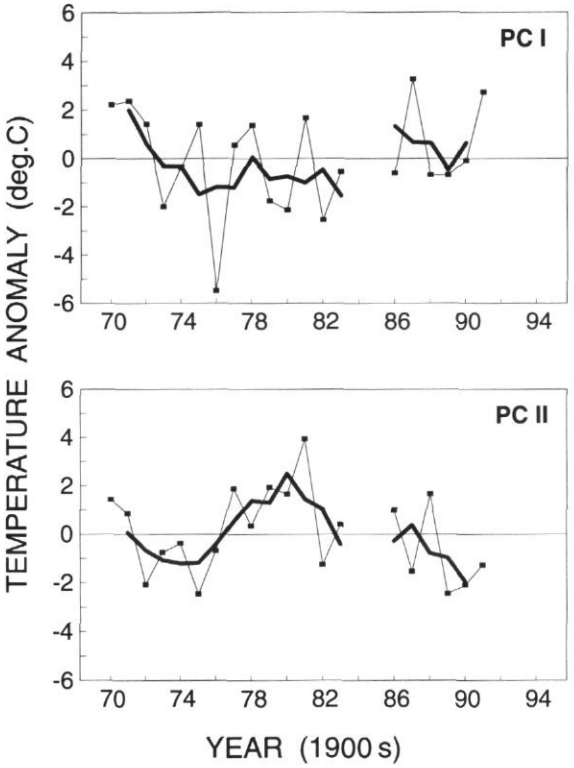


Figure 7. Time series plots of principal components I and II calculated from the correlation matrix of the 1970–1992 time series of strata mean, near-bottom, summer temperatures from shallow.

Acknowledgments

The temperature and salinity data were collected by numerous scientific staff and crew members of the Canadian Research Vessels "Alfred Cameron" and "Alfred Needler" and the charter Research Vessel "Lady Hammond". In recent years the hydrographic equipment was maintained, developed, and installed on board the research vessels by Jeff McRuer and Jim Reid. Assistance with the maintenance of computer hardware and software used for data storage and analyses was provided by Jim Gale, Shirley Fawkes, and Steve Bellis.

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ICES mar. Sci. Symp., 198: 332. 1994

Physical variability on the cod spawning grounds off southwest Iceland, 1990–1992 (Abstract)

Stefán S. Kristmannsson

Measurements of physical variables by CTD were carried out continuously over a 10-week period from the end of March to the beginning of June in 1990–1992. Results from mainly two sections, extending from the coast and beyond the 200 metre depth contour, are presented. The stratification of the water column was studied. In winter the water is well mixed but in spring a pycnocline is formed, due to both increased insolation and freshwater output from the land. The timing of the formation of the pycnocline was found to differ during the three years. In the beginning of May 1990 the formation of a pycnocline was due to fresh water on the inner half and to upwarming on the outer half. In 1991 the pycnocline had already formed in the coastal waters by the beginning of April as a result of freshwater outflow. The pycnocline on the outer part of the sections formed a few weeks later. In 1992, a pycnocline caused by fresh water close to the coast at the end of March had vanished by May. Finally, by the beginning of June the pycnocline had formed over the entire two sections. The amount of freshwater on the sections (as integrated equivalent freshwater thickness) varied on many time scales. There were extensive changes within the space of a few days and also from one month to the next. These were probably due to eddy motions, pulsating outflows from rivers and the ever-changing weather pattern. The change in the mean freshwater content during the 10-week period in 1990–1992 was 20% on the Krisuvik section and 50% on the Faxafloi section, reflecting the climate and water storage on land. Assuming a geostrophic balance of motion, the baroclinic part of the transport was computed. On the Faxafloi section the net flow was always northwards and ranged from 0.03 to 0.09 Sverdrups (million cubic metres per second). On the Krisuvik section, excluding an intermittent coastal jet, the geostrophic flow generally indicated an eastward direction coinciding with upwelling of heavier water onto the shelf. The freshwater coastal jet flowed westwards, reaching values of 0.09 Sverdrups. The net total flow, however, is westward, due to a large barotropic part, and is evident from drifters. Both sections indicated eddy motions most of the time, thus manifesting the prominent variability of these waters.

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Decadal transients in biological productivity, with special reference to the cod populations of the North Atlantic

B. J. Rothschild

Rothschild, B. J. 1994. Decadal transients in biological productivity, with special reference to the cod populations of the North Atlantic. – ICES mar. Sci. Symp., 198: 333–345.

The article discusses decadal transients in the ocean's biological productivity, with particular reference to post-1970s reductions in cod landings in the North Atlantic Ocean. A setting for the existence of decadal-productivity transients is developed from examples in the North Pacific and Humboldt Current. Determination of whether the decline in cod catch is a response to a multidecadal change in productivity depends on isolating "environmental" effects from "fishing" effects. A qualitative analysis of the environment and fishing suggests the possibility of an "optimum" environment for cod in the 1960s, which deteriorated in the 1970s and 1980s. To support this idea, evidence is presented that implies the existence of optimal conditions for phytoplankton, zooplankton, and herring during the 1960s in the Northeast Atlantic. These optimal conditions likewise declined in the 1970s. With regard to mechanisms, it is speculated that the key variable affecting the cod is biological productivity, and that indices such as temperature, windfield, etc., constitute a multivariate mix of factors that drives productivity.

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Introduction

A large number of fish stocks have exhibited significant declines in catch during the last several decades that have often been interpreted as resulting from overfishing. For example, the *New York Times* (3 August 1993 (C4)) reported that, "Scientists, industry experts and government officials agreed at a United Nations Conference that overfishing and the destruction of the habitat have caused alarming drops in marine populations". While the article mentions natural factors such as El Niño, it cites the depletion of the cod in the North Atlantic and goes on to say: "In 1989 the Food and Agricultural Organization [of the United Nations] said commercial fleets had driven some fish near commercial extinction."

This total attribution of stock-abundance variation to fishing implies *inter alia* that stock changes occur under conditions of "equilibrium" in a "constant" environment. The implication suggests a rather narrow and probably costly fishery-management strategy. Such a strategy implies: that reductions in fishing effort will cause declining stocks to increase in abundance; that management should be risk averse, or to put it another way, management should maintain fishing mortality at an arbitrary level that is less than the rational expected monetary value or EMV (see Keeney and Raiffa, 1976; also Rothschild and Heimbuch, 1983), and that in those instances when the stock "recovers" a "management success" should be claimed.

One reason for assuming that the environment is constant must be an explicit or implicit belief that it is only a noise component in fishery-data time series. This leads to the idea that the environment has little predictive value; it cannot be measured or observed, or usefully taken into account in the process of proferring management advice (see, e.g. Butterworth *et al.*, 1992). This view may be supported to some extent by a history of specious correlations (see the papers by Gulland, 1953; Carruthers *et al.*, 1951; and Saville 1959) or the fact that such relationships are difficult to verify (see, Shepherd *et al.*, 1984).

On the contrary, this article suggests that there is now enough information with which to determine the probability of a good or poor year class given the present state of ocean productivity *and* the size of the spawning stock. This is different from the more conventional approach, regressing year-class strength on environmental variables and then using the regression to forecast the following year's year-class strength. The state of productivity is an important characteristic of the "State of

Nature" used in adaptive and non-adaptive decision-theoretic approaches to fishery management (see Rothschild and Heimbuch, 1983). The state of productivity can also lend new insights to the stock and recruitment evaluation of the magnitude of recruitment-given stock size (see Rothschild and Mullen, 1985), as well as point toward the nature of variability contained in the relationship between spawning-stock biomass (SSB) and egg production (Rothschild and Fogarty, 1989).

The point of view maintaining the feasibility of forecasting recruitment derives from the observation that fish stocks have exhibited multidecadal changes in abundance for centuries, well before the advent of industrialized fishing. These fluctuations have continued to occur, apparently independently of fishing mortality, suggesting that they are not simply random occurrences but responses to changes in biological productivity, either in terms of primary production or in terms of the pathways by which primary production is transformed into fish biomass. If productivity is known, then it should be possible to judge whether any particular stock is at a relatively high or low level of abundance.

Evidence of multidecadal changes in productivity and a coupling of these transients with fish-stock abundance can be seen in a number of articles which are indicative of the phenomenon in the North Pacific, the Humboldt Current, and the Northeast Atlantic Ocean. In fact, this article asserts that the decline of the cod in the North Atlantic during the 1970s, while partly caused by fishing, was only one of a number of indices reflecting a general decline in productivity in the North Atlantic that began in the northeastern Atlantic in the late 1960s and 1970s eventually spreading to the northwestern Atlantic.

This article analyses the problem by first calling attention to examples of multidecadal transients in productivity coupled with fish-stock abundance in the North Pacific and in the Humboldt Current. With this setting in mind, the article takes note of the fact that cod catches in the Northeast Atlantic increased until 1950, but then declined steadily until 1990, while in the Northwest Atlantic, catches of cod increased until 1970 and then declined steadily over the next decade, remaining at constant low levels (Garrod and Schumacher, 1994). The article inquires whether the changes in catch are attributable to fishing or to the environment. While not denying the importance of fishing, it appears that the decline in cod catches on both sides of the Atlantic was also related to an environmental signal. Evidence is developed, principally from the eastern North Atlantic, that supports the notion of general biological productivity peaking in the 1960s and then declining in the 1970s.

Finally, the physical mechanisms that generate the changes in productivity are discussed, with a focusing particularly on the possible role of mineralized-nutrient changes and mesoscale variability.

Decadal transients in biological productivity in the North Pacific and the Humboldt Current

In 1982, Cushing collected evidence on multidecadal changes in productivity. Many of his examples concentrated on the North Sea and the northeastern Atlantic. Recent evidence sheds additional light on events in the North Pacific and the Humboldt Current.

The North Pacific

There is a growing body of literature (North Pacific climate symposium) reflecting an increase in biological production in the North Pacific in the 1970s. During this time, there was an increasing trend in chlorophyll-standing stocks north of Hawaii (Venrick *et al.*, 1987); a doubling of net zooplankton over much of the Subarctic Pacific (Brodeur and Ware, 1992); large increases in nekton and several fish stocks (Brodeur and Ware, MS) and a spectacular population explosion of the Far Eastern sardine, generating an annual yield of 3–4 million tonnes. In addition, Kawasaki (1989) has called attention to the parallel changes in clupeoid stocks at widely distant locations. A good summary is provided by Beamish and Bouillon (1993), who quantify major changes in salmon production and state:

> Because the increases in salmon survival [in the North Pacific] in the late 1970s occurred at the same time that year classes of a number of other commercially important marine fishes had exceptionally high marine survival (Beamish 1993), it appears that there was a general increase in production of commercially important marine fish species beginning in the late 1970s. The reason for the exceptionally strong year classes of marine fishes is believed to be the large increases in food for larval fishes that occurred in the late 1970s (Brodeur and Ware 1992; McFarlane and Beamish 1992; Beamish 1993). . . . We concluded that the trends in salmon production from 1925 to 1989 were not primarily a result of fishing effort, management actions, or artificial rearing, but rather that the trends in abundance were strongly linked to the environment.

These observations and others all point to an increase in the productivity of the North Pacific Ocean during the 1970s and 1980s.

The Humboldt Current

Prior to the 1940s there is little evidence of the spectacularly large Peruvian anchoveta stock centred in Peruvian waters. The catch increased during the early 1940s to the mid-1950s and then the population collapsed in the early 1970s. This sequence of events is supported by the

abundance of guano birds off Peru (Jordan and Fuentes, 1966), which seems generally to be correlated with the magnitude of the anchoveta stock. The bird population increased by a factor of four, beginning in the 1940s and reaching a peak in the mid-1950s, before declining dramatically in the mid-1960s, associated with the 1965 El Niño. Superimposed on this general trend in the bird population are four short-term decreases, during four El Niños between 1940 and 1965. It is likely that the bird population did not increase after the 1965 El Niño, because by that time the fishing had increased, landing 10 million tonnes, nearly the 12 million-tonne peak, reducing available food for the birds and limiting their capacity to increase in abundance (Fig. 1). The dramatic collapse of the fishery has generally been attributed to either the El Niño or to overfishing. However, in 1972 off Peru, the zooplankton stocks collapsed as well (see Carrasaco and Lonzano, 1989 and Alheit and Bernal, 1993) and have never recovered. It is unlikely that the zooplankton stocks had anything to do with fishing, so the implication is that the dramatic collapse of the anchoveta was not primarily caused by fishing intensity or the El Niño. The dynamics of the anchoveta are then consistent with the hypothesis of multidecadal transients in productivity. The increase evidently began in the 1940s and 1950s, reached a plateau and then declined sharply in the early 1970s. The El Niños which occurred before, during, and after the collapse seemed to have nothing to do with the evident increase or collapse, except for the 1972 coincidence. It is also interesting to observe that subsequent to 1972, observations of dinoflagellates dominating diatom abundance have been made (cf. Cushing, 1989). While it is true that an increase in sardine abundance followed the decline of the anchoveta, it still seems clear that the temporal change in anchoveta abundance reflected a change in the biological dynamics of the Humboldt Current region.

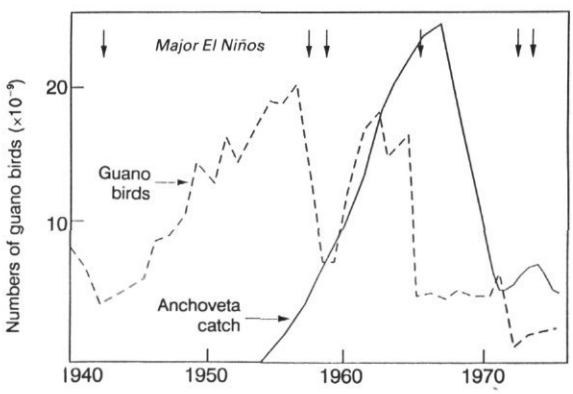


Figure 1. Number of guano birds and catch of anchoveta off Peru (redrawn from Cushing 1982).

The decline of the cod in the 1970s: fishing or the environment?

Was the decline in cod in the 1970s the result of intensive fishing or a multidecadal transient in the productivity of the North Atlantic similar to those that occurred in the North Pacific and in the Humboldt Current region? To begin to answer this question, it is necessary first to attempt to separate the effects of fishing from environmental change.

To make this separation in the most effective way would require a model that represents both fishing and environmental effects. The parameters associated with fishing and those associated with the environment could then be estimated establishing the relative importance of fishing and the environment.

However, representing both fishing and the environment adequately using a model is difficult. Well-known theories represent the effect of fishing (surplus production versus stock or effort, yield-per-recruit, and recruitment as a function of stock size). But, quantitative articulations of the stock–environment interactions, which need to span many variables and an extensive range of interacting time-and-space scales, are not generally available. Until the critical features of the environment are better understood, it is necessary to use the well-known theories on fishing to develop qualitative appraisals on environmental effects.

One such qualitative appraisal derives from comparing population abundance and fishing mortality time series. If fishing mortality is constant over a sufficiently long period, and the stock increases or declines in abundance, then it can be assumed that the increase or decrease is due to environmental factors. This assumes of course that non-equilibrium effects are adequately "averaged" because of the long-time period of observation. Also implicit is that the constant fishing mortality is not only constant over-all, but is constant over age or size groups too (eliminating the yield-per-recruit effect). A further assumption is that hidden strong non-linear effects are not operating. For example, suppose fishing mortality was constant, but sufficiently high to generate even a small decline in stock, then such a decline should be obvious over the span of the period of constant fishing mortality. One would tend to infer that a very rapid increase (or decrease) in a stock with relatively constant fishing mortality would arise from an environmental change even if fishing mortality was sufficiently high (or low) to produce a slow decline (or increase) in stock abundance.

In addition, certain ambiguities may arise when contrasting actual data with theoretical predictions. For example, an increase in egg production (i.e., stock) may result in a decrease in recruitment, and an increase in a high-level of fishing mortality may result in no decrease

in production, or yield-per-recruit. A complete discussion of this type of well-known problem is beyond the scope of this article. However, in considering the interaction between fishing mortality and stock size, the fact that fishing mortality and stock abundance estimates are generally derived from "cohort analyses" needs to be considered. The basic idea in cohort analysis is to estimate the decrements or increments in each age class from the catch of each age class using the yield function. The calculations result in an age-specific fishing-mortality rate and population abundance. However, the estimation of fishing-mortality rate is really developed from an estimate of total mortality rate from which some assumed constant value of natural mortality is subtracted. So, as pointed out by Gunnar Stefánsson (pers. comm.), the fishing mortality rate can contain an important component of variability that is due to unknown or unaccounted-for variability in the natural mortality rate.

In making qualitative and empirical inferences from fishing mortality and stock abundance time series, all of these conditions need to be considered relative to the magnitude of the observed effect (see Rothschild, 1986, p. 78, 1994).

For the cod stocks of the North Atlantic it is possible to compare the magnitude of fishing mortality to which the cod stock is exposed with estimates of spawning-stock biomass (SSB) recruitment, and indices of yield-per-recruit. Again, keeping in mind the above assumptions, if the environment is constant, over time, then these indices should on the average be constant over time. For example, plotting the relationship of SSB as a function of F (F is to be interpreted as a constant size or age-specific vector) and time, should yield a surface which only changes with F, and not with time.

While these assertions obtain theoretically and "on the average", they are not easily amenable to statistical inference. This has to do with sample size, the underlying distribution of the data, the fact that the data series possess different degrees of autocorrelation, and that the domain of the independent variables does not change in a consistent way over the entire data set. The best that can be done is to summarize the data by fitting some flexible surface through the data points and to assume that the number of data points is sufficiently large to mask recruitment variability and equilibrium adjustments, and in addition that reported "F" represents a fairly constant F vector. This should yield reasonable qualitative depictions of how the response surfaces depend upon the independent variables. This approach, even with its inherent shortcomings, must be close to extracting maximum information from the data.

To implement this qualitative appraisal, annual data on catch, fishing mortality, and SSB for the northern cod (1962–1986), the Icelandic cod (1963–1990), the North Sea cod (1970–1989), and the Northeast Arctic cod (1968–1990) were digitally interpolated from Jakobsson (1992). In addition, a yield-per-recruit *index* was computed. This index is simply the yield in any year divided by the recruitment for that year. The yield-per-recruit index is a function of stock biomass, and, when averaged over time, is a quick and rough index of actual yield-per-recruit.

Values of SSB, recruitment (R), and yield/recruitment (Y/R) were related to fishing mortality and year ("the environment") via a distance-weighted least-squares regression. Because the domain of the regression-smoothing procedure extends beyond the data domain, inferences are restricted to the data domain by the use of a kernel smoother. The implementations of these smoothed surfaces are plotted as contours in Figure 2. The contoured values are intended to be viewed as simply summarizing the data. The contour lines reflect the relative direction of the gradient in the SSB, R, and Y/R responses. If the contour lines are horizontal, then the responses are coupled with the theory of fishing; if, however, the contour lines are vertical, then the stock indices change with the "environment", or independently of the theory of fishing.

Effects of fishing and the environment on SSB

Changes in the SSB can be thought of as a point of departure for discussing environmental/fishing interactions. Referring to Figure 2, in the northern cod and in the North Sea cod, SSB declines sharply for any fixed level of fishing mortality: the contour lines are vertical. In the Icelandic cod, in contrast, environmental conditions appear to have improved since 1970. However, this improvement may not really have been an "improvement", but rather a relative increase generated by the negative effect of the "Great Salinity Anomaly" (GSA) in the mid-1960s. Jakobsson (1992) says that in May, 1965:

> It had become clear that survey conditions were completely different from previous years. The extension of the sea ice was much greater than had been observed since the cold year of 1918, the sea temperature was very low, there was hardly any sign of the important food species *Calanus finmarchicus* in the area west and north of Iceland. When coming to the area of the East Icelandic Current, temperatures below 0°C were common and on completion of the standard hydrographic sections northeast and east of Iceland there was no sign of the Polar Front. The hydrographic sections had therefore to be extended much further east than in any previous year of these surveys in order to find the Polar Front on the east side of the East Icelandic Current. This was in fact the beginning of the "Great Salinity Anomaly of the 1970's", which culminated in the Iceland Sea in 1968–1969. The immediate effect on the food chain and the herring migration pattern was obvious. Because of stratification of the surface layers, the

phytoplankton bloom lasted for only a very short period each spring. The populations of *C. finmarchicus*, the most important food species for the herring, disappeared almost completely. The highly productive area north of Iceland, which had sustained enough food for the largest herring stock in the world, was like a desert.

The effects of fishing mortality can nevertheless be observed in the Icelandic stock from the reduction in SSB in the mid-1970s at increased levels of fishing mortality.

The SSB of the northeast Arctic cod appears to be influenced partly by fishing and partly by environment. However, for fixed levels of fishing mortality, the stock has declined by a factor of 3 over three decades. In contrast, the Icelandic stock SSB increased from the 1960s to about 1980, when it began to decline. The stock appears to be coupled with the theory of fishing at its peak in the 1970s, because the SSB declined with increased fishing mortality (i.e., the contour line is horizontal).

With the exception of the Icelandic cod, the observations are consistent with the idea that there was an environmental optimum for cod in the 1960s with a subsequent deterioration of the environment for nearly three decades. The observations are also consistent with the negative effects of the Great Salinity Anomaly (GSA), as postulated by Cushing (1988) on demersal stocks.

Effects of fishing mortality and the environment on recruitment

These interrelationships are complex, involving the linkage between fishing mortality and SSB, *and* the linkage between SSB and recruitment. In this context it is necessary to account for the fact that there were no relatively large biomasses in the latter years of the time series. Taking these points into consideration, it might be thought that these relationships represent a net effect of SSB and recruitment.

With this interpretation a constant decline in recruitment occurs for all stocks except in the North Sea. In the North Sea, recruitment has tended to increase despite declining stocks and increased fishing mortality.

Effects of fishing mortality on yield/recruit index

Both the northern cod and the Northeast Arctic cod evidence peaks in Y/R which occur after the decline in the stock. There is something of a peak in the Icelandic cod. It seems as if the yield-per-recruit index is inversely proportional to biomass, reflecting compensatory mechanisms in the yield-per-recruit index, which is of course somewhat redundant with the SSB index. An explanation for the lack of response in the North Sea cod might be the cannibalistic dependence of adult cod on juvenile gadoids as food. As fishing mortality increases on the North Sea cod, the ratio of prey to predator size increases, reducing the catchability constant with which cod prey on juvenile gadoids.

Overview

Attempting to separate the effects of fishing from those of the environment is a difficult and elusive task. The classical stock assessment dilemma remains. Application of rigorous statistical procedure to data with uncertain statistical properties is certainly open to challenge, while at the same time generating a qualitative appraisal of such data is open to the criticism that rigorous statistical procedures have not been utilized.

It appears from the qualitative appraisal that the late 1960s was an environmental "optimum" for cod. The environment became subsequently suboptimum, as reflected by a decline in the populations, which for some stocks seems particularly uncoupled with fishing mortality.

Decades of high productivity in the Northeast Atlantic – the 1950s and 1960s

The above analysis implies that the decline of the cod stocks was induced by a deterioration in optimal environment and hastened by fishing. Were the seemingly optimal years for cod in the 1960s related to other components of the ecosystem?

Changes in the physical structure of the North Atlantic are evident from several sources. For example, the temperature series compiled by Smed *et al.* (1982) shows that much of the North Atlantic experienced a cooling trend from the turn of the century to about 1920. Then from about 1920 to 1930 the temperatures warmed and stayed warm until 1960 or 1965, when they dropped again.

There are differences in detail, however; the warming of the 1920s was dramatic, increasing sharply in the western Atlantic and gradually in the eastern Atlantic. In the post-mid-1960s there is a sharp peak in temperature in the western Atlantic. The abundance of northern cod was relatively high at this time. Subsequently the temperature and cod abundance declined in parallel.

In the central Atlantic the temperatures to the west of Iceland tended to peak in the late 1950s and then declined. There does not seem to be an obvious relation with the cod, but perhaps this has to do with the intervening effect of the GSA. In the northeast Atlantic temperatures have been declining since the early 1960s to the early 1970s, but appear to have increased again since 1975.

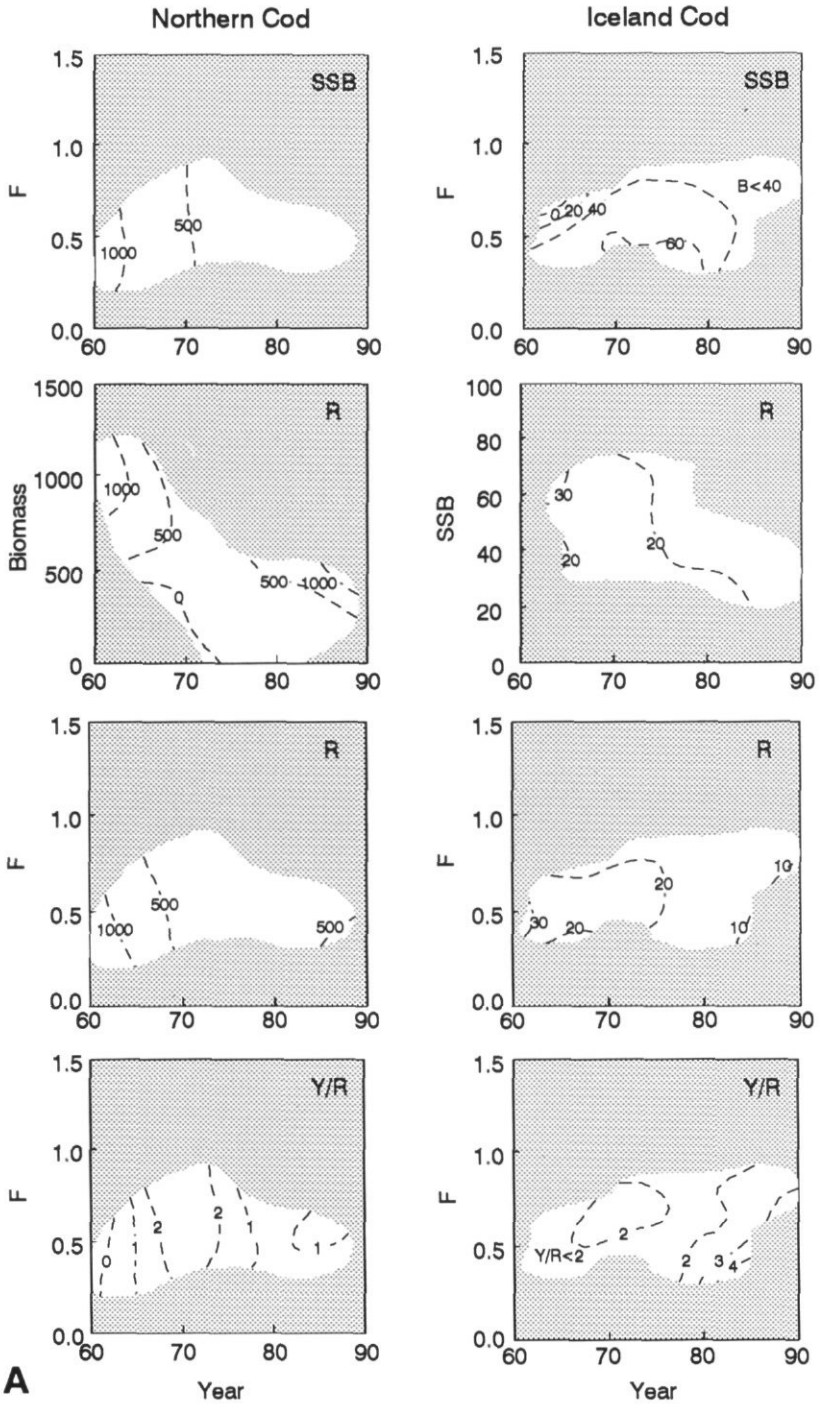


Figure 2. A, B. Population dynamics statistics for four populations of cod in the North Atlantic Ocean. Response surfaces of SSB, recruitment, and yield-per-recruit index as functions of fishing mortality, time, and spawning-stock biomass for four populations of cod in the North Atlantic.

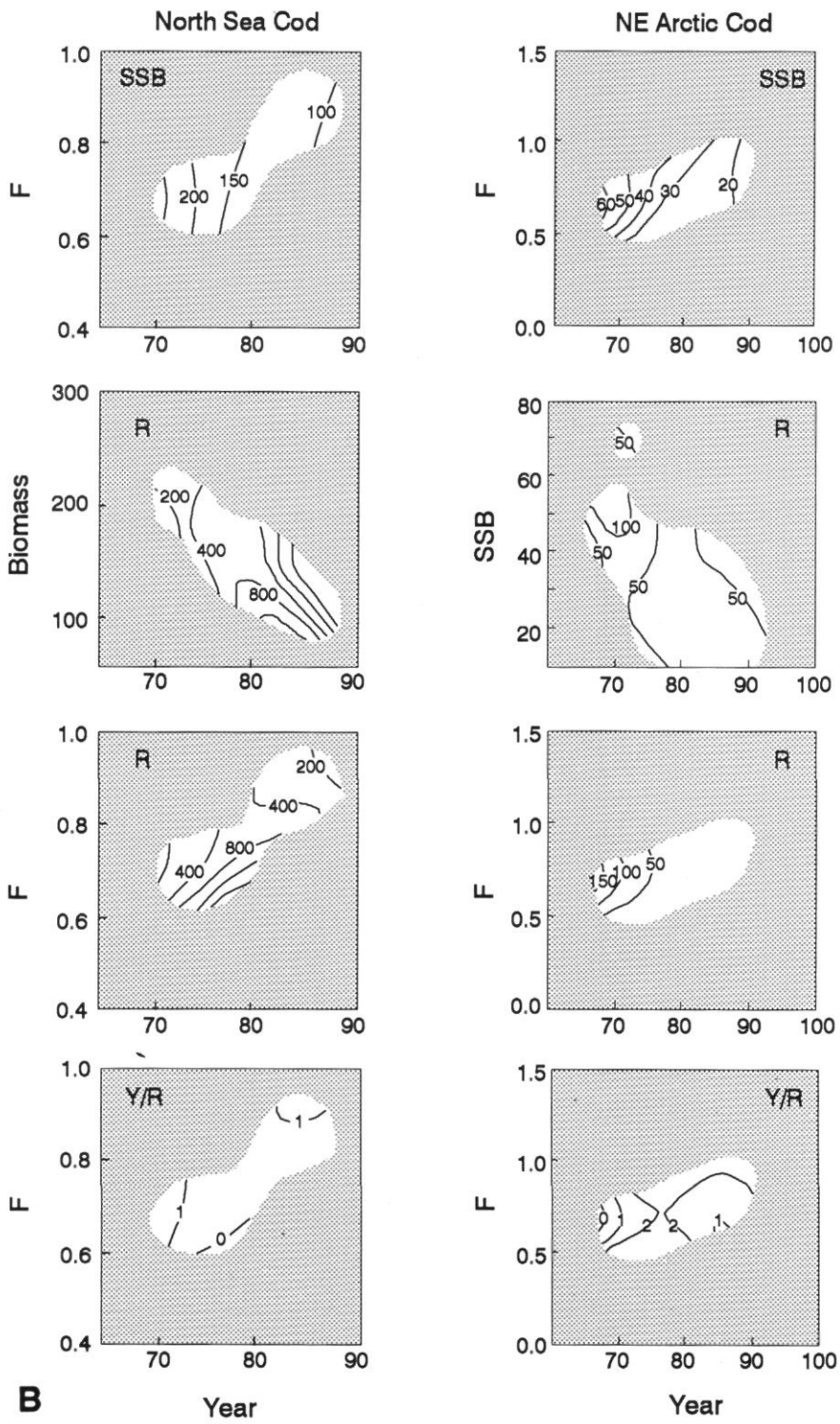


Figure 2. Continued.

Dooley *et al.* (1984) showed a somewhat parallel trend in salinity. In about 1920 the salinity of the Faroe–Shetland Channel increased substantially. The GSA of the mid-1960s and 1970s reflected a decrease in the salinities. Dickson *et al.* (1988) surveyed the advective track of the low salinity water around the North Atlantic. The anomaly had its onset just north of Iceland in 1965. However, in the eastern Atlantic, the anomaly spanned the years 1975 to 1979 (see Ellett and Blindheim, 1992).

Thus, with a very broad brush, the years from 1920 to about the mid or late 1970s comprised a period of relatively high salinity and temperature in the North Atlantic. Cushing (1982) called this period – the period between the 1920s and 1960s – "the recent period of warming". In summarizing the information about the period Cushing pointed to a dramatic faunistic change in the eastern North Atlantic (this basically amounted to northward shifts of warmer water fauna); a dramatic increase in the catch of the western Greenland cod; and the expression of a peak in the "Russell Cycle" in the English Channel.

While faunistic changes were evident at the onset of the period of warming, it is not clear, because of a lack of data in the early years, whether these events maintained themselves over the four warm decades, or whether they initiated a period of ecological succession. This succession may have resulted in the optimum environment. What is clearer is that the optimal period terminated in the late 1960s.

Cushing (1982) presents much of the available data on the decline of the productivity optimum in the eastern Atlantic (summarized in Figure 3, according to the figure numbers in Cushing's book). The average beginning year for the onset of these events was about 1950 and the average terminal date was about 1968. The beginning year is somewhat biased in the sense that some of the time series were initiated while the index was at a high level. Some of the key points are:

1. Many phytoplankton indices declined from the 1950s through the 1970s. Diatom abundance in the Continuous Plankton Recorder (CPR) indices of phytoplankton abundance reflect a substantial decrease beginning in 1970. The major feature of the decline is the disappearance of diatoms in the autumn (see Reid, 1978). Data on diatom abundance consonant with the CPR data are not available before the late 1950s, however; *Thalassiothrix* declined sharply in the Atlantic in 1970 (Reid *et al.*, 1992).
2. Important zooplankton species have declined in the eastern Atlantic and in the North Sea. For example *Pseudocalanus* abundance in the North Sea in the 1960s was one-third of that of the 1950s. Calanus abundance levels were lower between 1955 and 1963 than at other times (note that the Buchan stock of herring was exceptionally abundant in these years). At the same time the abundance of *Calanus* in the 1950s and 1960s was higher than in the 1930s, as indicated by time series samples taken on the Flamborough/Dogger Bank line.
3. The Buchan herring stock increased from the 1940s. It increased substantially, however, in the mid-1950s, reaching a peak abundance in the late 1960s before declining. The increase was due to very large recruitment. It is also of interest to note that the growth rate of herring increased during the years when the population was at a maximum. This suggests a relatively high abundance of food.
4. The gadoid outburst occurred at about the same time as the peak abundance of Buchan herring, and so, while cod and herring were negatively correlated in the southern North Sea, they were positively correlated in the northern North Sea. In addition, as pointed out by Holden (1978), the Y/R of cod was higher in the North Sea after WWII than before it, implying the possibility of increased growth and hence increased productivity of cod.
5. The Russell cycle was "turned on" in the mid-1960s, as well as peak abundance of *Sagitta elegans* in the channel. Pilchard eggs increased in the 1940s, but disappeared in the 1970s.

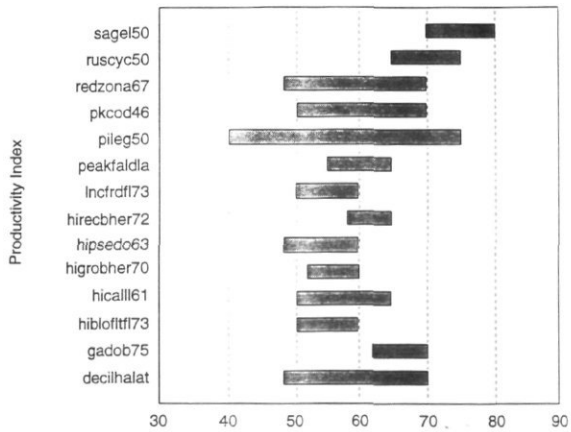


Figure 3. Indices of productivity decline in the Northeast Atlantic. The numbers following each code refer to figure numbers in Cushing (1982). Sage150 = peak *Sagitta elegans*; ruscyc50 = high fish larvae in Russell Cycle; redzona67 = reduction of peak zooplankton in Northeast Atlantic; pkcod46 = peak west Greenland cod 1950–1970; peakfaldla = peak fall diatoms; incfrdf173 = high recruitment of flatfish; hirecbher72 = high recruitment of Buchan herring; hipsedo63 = high densities of *Pseudocalanus*; higrobher70 = high growth of Buchan herring; hicall61 = high *Calanus* on Flamborough line; hiblofltfl173 = high biomass of flatfish; gadob75 = gadoid outburst; decilhalat = high *Thalassiothrix*.

The general conclusion from these observations is that some of the indices of heightened productivity may date back to the onset of warming and salinification in the 1920s, but this is not certain. Other indices reached peaks and then declined during the ca. 1950–1980 observation period. All of the indices certainly declined sharply during the late 1960s or early 1970s. It may be possible to find indices that behaved in a reverse pattern (e.g., Pilchard) but with the exception of a few cases, it is not clear what these are.

There is not nearly as much data for the western Atlantic as there is for the eastern Atlantic. Was the decline of the northern cod under the same environmental influence as in the western Atlantic? This would of course imply a basinwide control of productivity.

Mechanisms

The analysis at this point has led to the observations that (1) the multidecadal fluctuations in fish-stock abundance have occurred in recent decades and appear to be coupled with changes in zooplankton abundance and other indices of productivity; (2) the decline of cod in the North Atlantic appears to have been coupled with environmental change as well as fishing; and (3) the decline of cod stocks in the Northeast Atlantic which began in the late 1960s or early 1970s was coincidental with the decline in indices of biological production in the Northeast Atlantic Ocean.

To move these observations – of what are essentially "effects" – into a predictive mode, it is necessary to study the mechanisms or the causal chain that leads to these effects. A number of mechanisms have been proposed. For example, Cushing (1982) has maintained that temperature controls the timing of the spring bloom and that the coincidence of this timing with secondary production controls recruitment success in North Sea cod. Cushing (1988) tracks the salinity anomaly around the North Atlantic and shows how it is related to declines in cod stocks. Mertz and Myers (1993) doubt the effect of the salinity anomaly on cod in the Northwest Atlantic. Dickson and Brander (1994) point out how the pan-Atlantic windfield affects the migration and drift of cod colonizing new areas, giving the appearance of increased stocks. Cushing, in a series of articles, discusses the increase in gadoids in the North Sea as a result of variations in spring-bloom timing. Cushing (1980) discusses the relation between cod and herring in the North Sea, finding that the evidence is inconclusive as to whether the herring decline or the environment was related to the increase of the 1960s. Brander (1992) on re-examining the data for the North Sea did not find a relation between *Calanus* and cod. Loeng (1990) showed that the recruitment of Northeast Arctic Cod was temperature-dependent in the sense that good year classes required relatively warm water. Ellertsen *et al.* (1989) showed that there was a 30-day range in maximum abundance of *Calanus* (stage I), the primary food of young cod in the eastern Atlantic, as a function of a 2°C change in temperature. Sundby and Fossum (1990) have shown how turbulence is affected by the windfield and stratification and how these variables influenced feeding of larval cod.

It is reasonable to assume that some or all of these indices are linked, in some fashion, with the variability of cod stocks. However, because some of the mechanisms are strictly physical in nature, it is appropriate to ask whether, in fact, their mode of action is physiological (e.g., temperature affecting physiological rates) or trophodynamic (e.g., the effect of small-scale turbulence on feeding rates), or whether there is some more fundamental mode of interaction?

The broad decline in indices of productivity suggests that this more fundamental mode might involve the amount of primary production and/or the nature of the pathways by which primary production is converted to fish biomass. Measurements of primary production or trophodynamic pathways are really not available in terms of geographical or temporal scope or frequency to determine whether the decline in the "effects" observed in the late 1960s really resulted from changes in biological productivity, except for the fact that some of these effects are of themselves indices of productivity.

However, it is possible to speculate upon the causes, the actual mechanisms that drive the implied changes in productivity. It would seem natural to begin by hypothesizing that basin and sub-basin scale multidecadal changes in the planetary windfield influence the biological productivity of the North Atlantic in a complex way. For example, Wallace and Gutzler (1981) discuss the teleconnections that link the windfield in the North Pacific with the North Atlantic and the northern North Atlantic with the southern North Atlantic, etc. Among these teleconnections, North Atlantic spatial oscillation is of particular interest, since it implies that a relatively high pressure over Greenland is coupled with a relatively low pressure over the Azores and vice versa. Specifically, Wallace and Gutzler (1981) show that there are loci of strong negative spatial correlations in sea level and 500 mb pressure for 45 winter months for the winters of 1963 to 1977, which appear consistently over the entire northern hemisphere.

The spatial negative autocorrelations appear to oscillate temporally and are therefore evidently not distributed at random with respect to time. A specific exemplification of the temporal oscillation in the North Atlantic is computed by Rogers (1984) and is based on the pressure difference between Iceland and the Azores. When Rogers' index is high, the Icelandic low is rela-

tively strong, and there is a relatively high pressure along lat. 40°N, strong North Atlantic westerlies; below normal temperatures in the Greenland–Labrador area, and the eastern US and western Europe will be relatively warm. When the index values are low, the opposite will be true. In other words, there is a multidecadal periodic variability in the forcing of windstress vector.

So the windstress forcing at the sea surface varies coherently over basin and sub-basin space scales and over multidecadal time scales. The critical question is how this variability in windstress forcing interacts with the internal dynamics of the ocean with regard to motion and the distribution of properties that affect ecosystem dynamics. On the one hand, there must be a virtually linear component to these processes that results in the direction and strength of the wind simply fortifying or diminishing some climatic current pattern. On the other hand, the more general manifestation of the variability in windstress relates to the ocean–atmosphere heat engine. There is no simple way of describing the dynamics of any particular component of the engine, because one component has a non-linear dependence on all other components. It would be a considerable oversimplification to say that the basic idea is that the combination of ocean/atmosphere interactions, which serve to warm or cool and increase or decrease salinity, interact with wind-driven stress at the sea surface to create instabilities that cause the water to flow with respect to the earth's surface. The large-scale flows result in vorticity which is eventually expressed in the eddy field which is typified by both large eddies being transformed into small eddies and vice versa. The smallest eddies are eventually dissipated into heat.

The three-dimensional eddy structure both results from and is formed by important one-dimensional special case representations of the eddy structure. These include the depth of convection in winter, the depth of mixing, and intensity of stratification in summer.

There are many aspects of how this physical structure affects biological processes. Two seem particularly relevant to multidecadal transients in productivity. The first relates to the injection of remineralized nutrients into the photic zone and the second to the effect of transient mesoscale eddies on trophodynamics.

Nutrients

An important issue involves the total amount of remineralized nutrients (e.g., nitrate) available each year to fuel the annual production cycle. The incorporation of nitrate into the production cycle might be thought of as occurring in two modes. The first involves the quantity of nitrate available at the onset of stratification and the spring bloom, the second the quantity of nitrate injected into the photic zone after the onset of stratification.

With regard to the amount of nitrate available at the onset of the spring bloom, it is reasonable to postulate that interannual variations in the intensity of stratification and the depth of the mixed layer would result in interannual variations in the absolute quantity of nitrate available each spring.

Even if the intensity of stratification was constant and also the depth of the mixed layer, it is possible that variations in the concentration of spring nitrate might vary. This could occur if there were interannual differences in the intensity of winter convection. Meincke *et al.* (1992) and Clarke *et al.* (1990) have noted that very deep convection in the Greenland Sea has been turned off in the 1980s. Some variations in winter convection may be due to the presence of the GSA. Large variations in nitrate concentrations could arise depending on the degree to which convective mixing intercepted any deep nitrate maximum.

With regard to the second mode, nitrate can be injected into the photic zone after stratification by transient and semipermanent eddies, coastal upwelling, and divergent processes.

What is interesting is the possibility that the relative importance of these processes changes. The implication is that the balance between nitrate and ammonium-based production changes. In fact, it could be speculated that the analyses of Cushing (1989), Le Fèvre and Frontier (1988), and Goldman (1988), reflecting a shift to a more dinoflagellate than diatom-dominated primary production, involve a more ammonium-driven production base. A decline in surface nitrate would be consonant with the downward trend in fall diatoms in reaches of the Northeast Atlantic, such a downward trend could have a negative effect on the production of large zooplankters, which in turn would have a negative effect on cod. Note also that the decline of zooplankton in the Humboldt Current was typified to be a decline in diatoms.

Eddies and trophodynamics

The effects of the eddy structure on trophodynamics operates in at least two modes. The modification of nutrient injection into the photic zone is well known. A mode which is little understood involves how eddies mix-and-stir volumes of water that at the outset of the mixing-and-stirring process have different concentrations of predator/prey or nutrient acceptor/nutrient-donor organisms.

Haidvogel (1983) reviews the physics of eddy structures while Angel and Fasham (1983) consider the biology. In essence, it is possible to think of the organisms that are relative to the flow as passive tracers. The evolution of the distribution of passive tracers is discussed by Haidvogel *et al.* (1983).

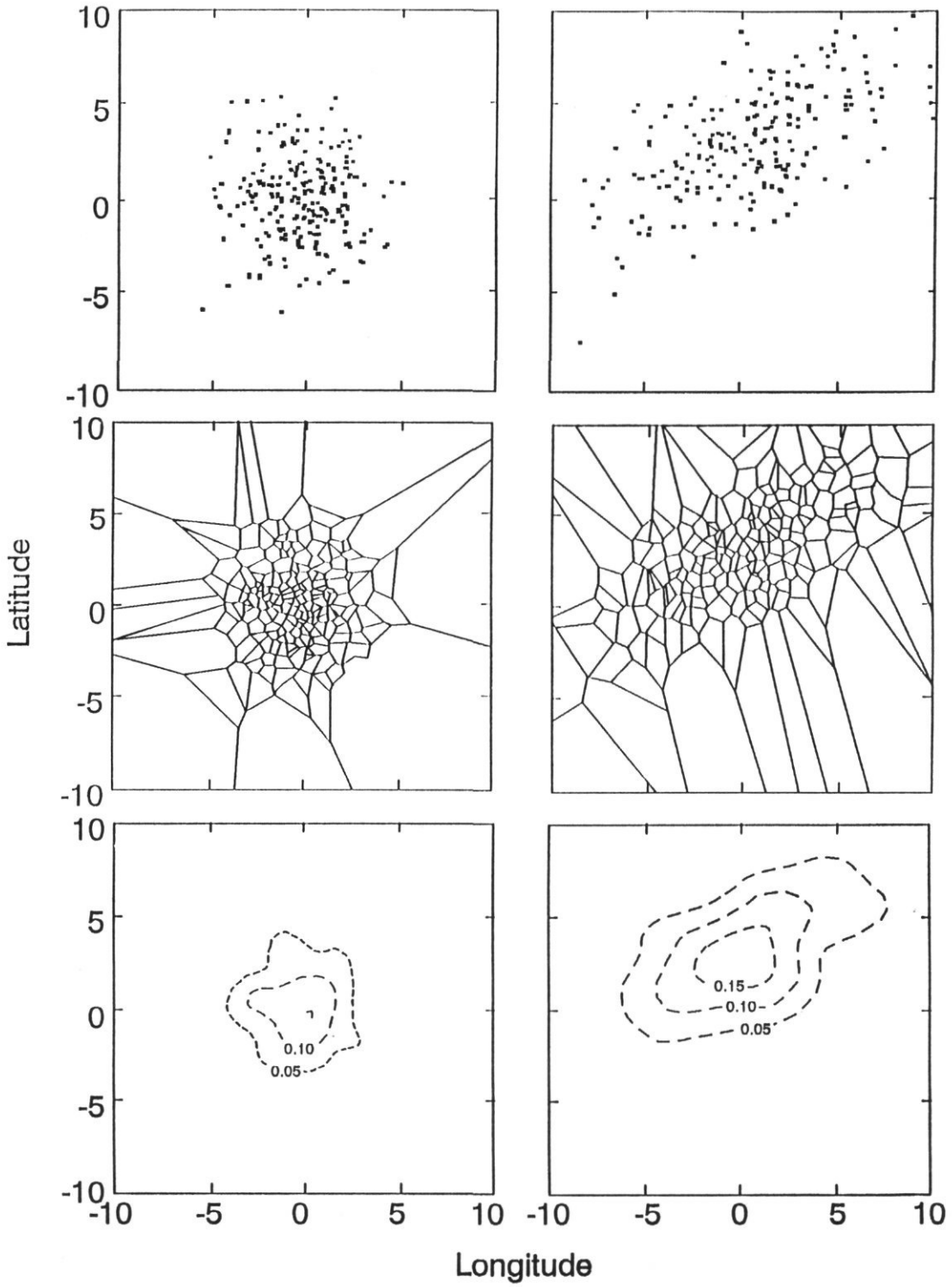


Figure 4. Stretching of a random distribution of particles according to Corrsin (1953). Top panel shows particles, middle panel shows Voronoi tessellations accompanying the particles, and bottom panel shows smoothed distribution of particles.

As Haidvogel *et al.*, point out, and as further discussed by Tennekes and Lumley (1982) and others, the effects of turbulent flow are generally to draw the tracer particles into streaks, causing a relatively rapid dispersal along the length of the streaks and an increase in the concentration along the gradient normal to the main axis of the streaks. Haidvogel *et al.* (1982) also point out that two-dimensional turbulence can account for the filaments as dispersive rather than advective processes. A "real world" implementation of the theoretical results is given by Robinson (1993).

One of the most important points to be made is that the dispersion of tracers in a turbulent setting is quite different from the dispersion of tracers that would occur if the dispersion was driven only by diffusive processes, as implied in a considerable body of ecological literature (Okubo 1980). To demonstrate this point, the spatial dispersion of particles can be thought of in terms of a bivariate normal distribution (Corrsin, 1953). In order to visualize the mixing-stirring vortex stretching effect as postulated by Corrsin, undispersed and dispersed particle configurations were constructed by randomly drawing 2-tuples from a specified bivariate normal distribution (Fig. 4). The density of the contour maps of the 2-tuples was calculated using kernel smoothing techniques to show how point distributions underlie the "density pictures" developed by numerical simulation, and to show that the density at any point contains only part of the information required for particle–particle interaction. One piece of information is the volume of any particle. To study this problem, consider the Voronoi tessellations associated with the particular sets of 2-tuples.

The size of each "tile" in the tessellation can be thought of as the availability of nutrients for each particle. In the centre of the patch, competition is large and growth is limited; in a band around the centre competition is neutralized; on the edges there is no competition for nutrients and growth is maximized. Each eddy structure will result in a different mix of these phenomena and thus contribute differently to the overall metabolism of the upper ocean.

This puts into perspective the continuum of scales. The basin scale sets up the basic physiological and metabolism settings – the temperature and nutrients and primary production. With these as given, the mesoscale sets limits on the interactions among predators and prey via exquisitely complicated mixing and stirring mechanisms, and finally the small-scale turbulence modifies the interactions set up by mixing and stirring. This is in effect a functional biological cascade. The basin scale represents the signal, the microscale drives the noise, and the mesoscale represents the transition in information between signal and noise. This helps to clarify the relation of signals and noise in the biological system and further serves to articulate its practical implication: because the planetary and basin-scale events associated with the teleconnections are relatively slow moving, once established, frequent events such as year classes should be predictable. This can be seen because the changes in plankton structure that seem to be associated with the productivity optimum in the North Atlantic can be determined, in principle, in virtually real time. It thus seems potentially possible to develop predictions of year-class strength from the slow-moving teleconnections and from plankton abundance.

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Modelling retention of cod eggs and larvae (*Gadus morhua* L.) on the Newfoundland Shelf

Brad deYoung and Fraser Davidson

deYoung, B., and Davidson, F. 1994. Modelling retention of cod eggs and larvae (*Gadus morhua* L.) on the Newfoundland Shelf. – ICES mar. Sci. Symp., 198: 346–355.

An analytical model is developed to describe retention ratios for passive particles on a shelf. This general model is applied to the drift of cod eggs and larvae on the Northeast Newfoundland Shelf, using observed winds measured at St John's, to hindcast retention of eggs from 1960 to 1990. Sensitivity tests show the potential influence of spawning location on the interannual variability of the retention ratio. A significant but weak correlation is found between the retention ratio time series and the observed recruitment of cod. It is suggested that retention of eggs and larvae on the shelf, as influenced by interannual variations in the windstress, may be an important factor in determining successful recruitment of cod in this area.

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Introduction

In spite of a recognition of the general characteristics of the recruitment problem, an understanding of the factors which control recruitment remains a fundamental goal of population biology (Rothschild, 1986; Hilborn and Walters, 1992). The importance of egg and larval success to recruitment has been recognized for a long time (Hjort, 1914). Two hypotheses were put forward by Hjort, (1) that of food availability, an idea later developed by Cushing (1975) as the match-mismatch hypothesis and (2) retention of the larvae in zones favourable for their development. The second hypothesis underlies the work of Iles and Sinclair (1982), who rejected match-mismatch for Atlantic herring (*Clupea harengus harengus*) and argued that the crucial factor was the link to the physical environment rather than to planktonic food. In this paper, we develop an analytical model as a tool for exploring one factor that might control recruitment variability of cod on the Northeast Newfoundland Shelf – retention of eggs and larvae on the shelf.

Many different types of models have been developed in recent years for application to the problem of egg and larval transport. There have been convincing studies to show the influence of wind as a mixing agent (Peterman and Bradford, 1987), but direct links to transport have been harder to prove (Sinclair *et al.*, 1985). Hofmann *et al.* (1992) developed a one-dimensional model of Antarctic krill (*Euphausia superba*) to explain the influence of the thermal structure of the water column on the reproductive strategy of the krill. Bartsch *et al.* (1989) applied a baroclinic numerical model to explain how herring larvae reach their nursery grounds in the North Sea. Working on a dynamically similar problem to that of egg drift, Hofmann *et al.* (1991) used a semi-spectral baroclinic model to simulate drift of phytoplankton in the California coastal current system. Models of the transport of Japanese sardine larvae (*Sadinops melanostictus*) have used both observational data, as obtained from Geomagnetic ElectroKinetograph (GEK) surveys (Kobayashi and Kuroda, 1991), and also numerical models (Kasai *et al.*, 1992). On the Newfoundland Shelf, Helbig *et al.* (1992) have applied a simple Ekman model, superimposed on a barotropic velocity field, to investigate some of the features of the transport of cod (*Gadus morhua*) eggs and larvae. They showed that some regions of the shelf were biologically separated by the circulation field.

The model which we develop is an extension of one first proposed by Kasai *et al.* (1992), who developed a simple one-dimensional model to explain some aspects of the retention of Japanese sardine larvae (*Sardinops melanostictus*) inside the Kuroshio Current. They also developed a two-dimensional numerical model with

which they successfully simulated the year-to-year variation in larval survival ratios. Our goal is to develop a two-dimensional, analytical, time-dependent model which we shall force with observed winds. Although there are limitations to this approach, we believe its simplicity to be advantageous and that the model solution is general enough to be applicable to other problems.

This paper is organized as follows. In the next section, the two-dimensional model is developed, based upon the earlier work of Kasai *et al.* (1992). "Study area and model results" contains a brief discussion of the geographical application of the model, to the Newfoundland Shelf, together with the model results. In the final section we discuss the results and the implications for future work.

Two dimensional analytical model

The model as developed by Kasai *et al.* (1992) was one-dimensional and applied to the Kuroshio Current to give the retention ratio of the larvae on the shelf side of the Current. An advection diffusion equation was solved for the larval concentration which was used to determine the proportion of larvae found inshore of the Kuroshio Current. Here, we extend this model by making it two-dimensional, including a time-dependent windstress. We have in mind a region based upon the Newfoundland Shelf (Fig. 1) which we consider to be an infinite half-plane in the alongshelf direction. In our model, we define the retention ratio as the proportion of larvae found on the shelf. Later, we limit our interest in the half-plane to an alongshore distance of about 1000 km, roughly the length of the Northeast Newfoundland Shelf. Although we have greatly simplified the topography, we have maintained the basic features of the system, a long shelf that is still relatively broad, i.e. hundreds of kilometres.

The time rate of change of larvae concentration in a given volume is equal to the advection and diffusion of larvae out of this volume. The two-dimensional advection diffusion equation is:

$$\frac{\partial C}{\partial t} + u\frac{\partial C}{\partial x} + v\frac{\partial C}{\partial y} = \kappa_h\left(\frac{\partial^2 C}{\partial x^2} + \frac{\partial^2 C}{\partial y^2}\right) \tag{1}$$

where C (x, y, t) is concentration, t is time, u(t) and v(t) are the x and y components of velocity, and κ_h is the horizontal diffusivity. The advection diffusion equation can be solved by analogy to the simple one-dimensional diffusion equation

$$\frac{\partial C}{\partial t} = \kappa_h \frac{\partial^2 C}{\partial x^2} \tag{2}$$

which has solution:

$$C = \frac{1}{\sqrt{4\kappa_h t}} e^{(-x^2/4\kappa_h t)} \tag{3}$$

To solve the advection diffusion equation we use the following transformation of coordinates.

$$\hat{x} = x - \int_0^t u(t')\,dt' \tag{4a}$$

$$\hat{y} = y - \int_0^t v(t')\,dt' \tag{4b}$$

$$\hat{t} = t \tag{4c}$$

By the chain rule of differentiation, we find:

$$\frac{\partial}{\partial x} = \frac{\partial}{\partial \hat{x}} \tag{5a}$$

$$\frac{\partial}{\partial y} = \frac{\partial}{\partial \hat{y}} \tag{5b}$$

$$\frac{\partial}{\partial t} = \frac{\partial}{\partial \hat{t}} - u\frac{\partial}{\partial \hat{x}} - v\frac{\partial}{\partial \hat{y}} \tag{5c}$$

In the modified coordinates, the advection diffusion equation is expressed as a simple diffusion equation:

$$\frac{\partial C}{\partial \hat{t}} = \kappa_h\left(\frac{\partial^2 C}{\partial \hat{y}^2} + \frac{\partial^2 C}{\partial \hat{y}^2}\right) \tag{6}$$

The solution approach that we follow is similar to that taken by Kasai *et al.* (1992), except that we make fewer simplifying assumptions. We assume, as do they, that the initial distribution of the spawning eggs is given by a Gaussian distribution. This produces solutions for the retention ratio in terms of error functions. We do not assume that the velocities u and v are constants, though we do add a constant term to the v- component of velocity. Both of the velocity components vary in time, though they are fixed in space.

Transforming the standard solution of the diffusion Equation (6) into the original coordinates x and y, as well as making the substitution $t = T + t_o$ yields:

$$C = \frac{1}{\sqrt{4\kappa_h(T + t_0)}} \times \exp\left(\frac{-(y - \int_0^{T\times t_0} v(t)\,dt)^2 - (x - \int_0^{T+t_0} - u(t)\,dt)^2}{4\kappa_h(T + t_0)}\right) \tag{7}$$

T is the time after the initial spawning when the variance

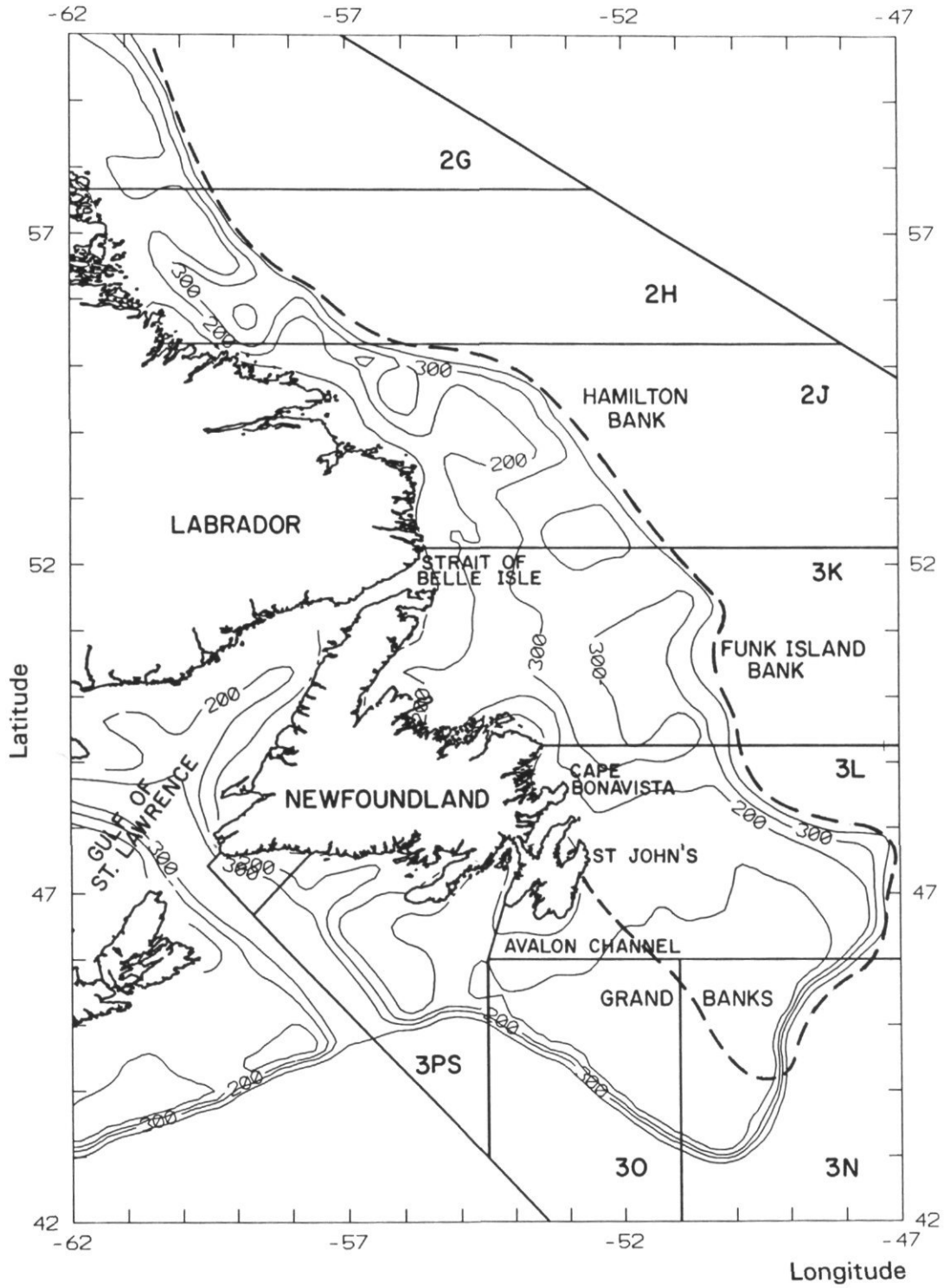


Figure 1. The bottom topography in the Newfoundland Shelf. The NAFO divisions from 3Ps to 2G are shown and the range of the Northern cod (deYoung and Rose, 1993) shown with a dashed line.

of the patch of larvae is $4\kappa_h t_0$. Letting $\alpha = 4\kappa_h t_0$, and then simplifying the solution we obtain:

$$a = 4\kappa_h t + \alpha \tag{8}$$

$$cx = \int_0^T u(t')\,dt' + x_0 \tag{9}$$

$$cy = \int_0^T v(t')\,dt' + y_0 \tag{10}$$

and allowing for reflection at the coast x = 0 gives

$$C = \frac{1}{\sqrt{a}} \exp\left(\frac{-(y - cy)^2}{a}\right) \times \left\{\exp\left(\frac{-(x - cx)^2}{a}\right) + \exp\left(\frac{-(x + cx)^2}{a}\right)\right\} \tag{11}$$

where a is the time-dependent variance of the larval distribution and cx and cy are the coordinates of the patch centre. The retention ratio is the proportion of eggs on the shelf to the total number of eggs and is given by:

$$R(t) = \frac{\int_{As} C(x, y, t)\,dA}{\int_{Aw} C(x, y, t)\,dA} = \frac{\int_0^L \int_0^l C(x, y, t)\,dx\,dy}{\int_{-\infty}^{\infty} \int_0^{\infty} C(x, y, t)\,dx\,dy} \tag{12}$$

where As and Aw represent the area of the shelf and the whole region respectively, l is the cross-shelf width and L is the alongshelf length (Fig. 2). Note that the coordinate system is set such that y is alongshelf and x is cross-shelf (cf. Fig. 1). Making the substitution

$$\sigma = (y - cy)/(\sqrt{a})\ dy = \sqrt{a}d\sigma$$

$$\phi = (x - cx)/(\sqrt{a})\ dx = \sqrt{a}d\phi$$

$$\varphi = (x + cx)/(\sqrt{a})\ dx = \sqrt{a}d\varphi$$

$$y = L \rightarrow \sigma = (L - cy)/\sqrt{a}$$

$$y = 0 \rightarrow \sigma = -cy/\sqrt{a}$$

$$x = l \rightarrow \phi = (l - cx)/\sqrt{a}$$

$$x = 0 \rightarrow \phi = -cx/\sqrt{a}$$

$$x = l \rightarrow \varphi = (l + cx)/\sqrt{a}$$

$$x = 0 \rightarrow \phi = cx/\sqrt{a}$$

For the model domain the retention ratio is:

$$R(T) = \int_{-cy/\sqrt{a}}^{(L-cy)/\sqrt{a}} e^{-\sigma^2}\,d\sigma \times \left(\int_{-cx/\sqrt{a}}^{(l-cx)/\sqrt{a}} e^{-\phi^2}\,d\phi + \int_{-cx/\sqrt{a}}^{(l-cx)/\sqrt{a}} e^{-\varphi^2}\,d\varphi\right) \tag{13}$$

If we define the error function such that

$$\text{erf}[a, b] = \frac{2}{\sqrt{\pi}} \int_a^b e^{-z^2}\,dz \tag{14}$$

where z is just a dummy variable, then the retention ratio becomes

$$R(T) = \frac{\pi}{4} \text{erf}\left[\frac{-cy}{\sqrt{a}}, \frac{(L - cy)}{\sqrt{a}}\right] \times \left\{\text{erf}\left[\frac{-cx}{\sqrt{a}}, \frac{(l - cx)}{\sqrt{a}}\right] + \text{erf}\left[\frac{-cx}{\sqrt{a}}, \frac{(l - cx)}{\sqrt{a}}\right]\right\} \tag{15}$$

where a, cx, and cy depend on T, as in Equations (9) and (10). Note that we are primarily interested in the region close to the shelf break. The reflection condition is negligible since the wind-driven current cannot trans-

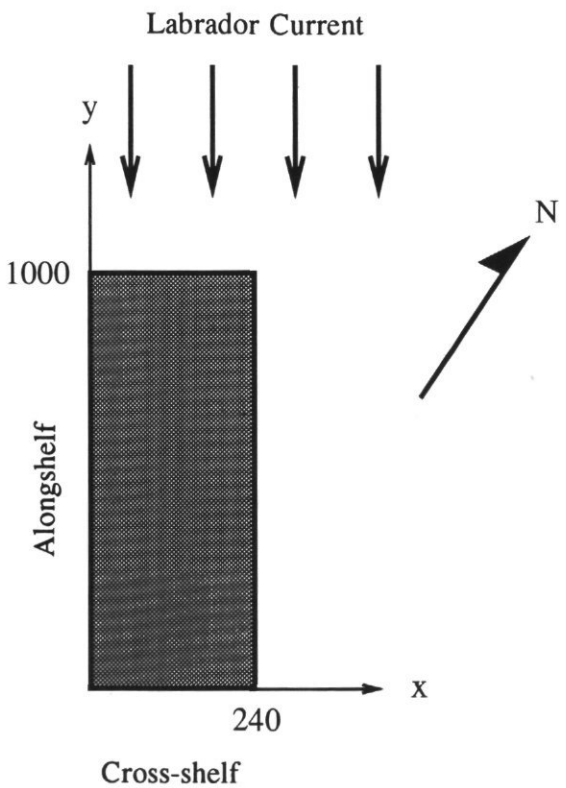


Figure 2. The model domain and axis orientation showing the shelf (the shaded region) and the direction of the mean flow (0.20 m s^{-1}), representing the southward flowing Labrador Current.

port particles across the width of the shelf in the time frame that we are considering, approximately 50 days. The average wind-driven currents are from 1 to 10 cm s^{-1}.

Study area and model results

The circulation in the Newfoundland Shelf region (Fig. 1) is dominated by the influence of the Labrador Current, which has both an inshore and an offshore branch (Petrie and Anderson, 1983). One way to obtain the velocity field is via a diagnostic model (deYoung *et al.*, 1993) applied to density data from the shelf. Figure 3 shows the velocity field for the Northeast Newfoundland Shelf obtained from a diagnostic model applied to an objectively analysed density data set, covering all available data from 1910 to 1989. This plot shows the circulation pattern on this shelf, with two strong flows visible, one at the shelf break and one on the inner part of the shelf (Greenberg and Petrie, 1988).

We treat the southward flow in this region as constant, with a fixed southward velocity of 0.2 m s^{-1}. Thus the shelf is a simplified two-dimensional analogue of the real shelf. As did Helbig *et al.* (1992), we assume that the eggs are in the surface Ekman layer, hence we use an average wind-driven Ekman velocity, averaged over the top 50 m of the water column (Gill, 1982). Anderson and deYoung (1994) showed that eggs take from 5 to 10 days to reach the surface layer, after which they remain in the surface layer until after hatching. Anderson and deYoung (1994) do show that there is some vertical structure to the cod egg distribution, but that most of the eggs are found in the surface waters. In our model, all

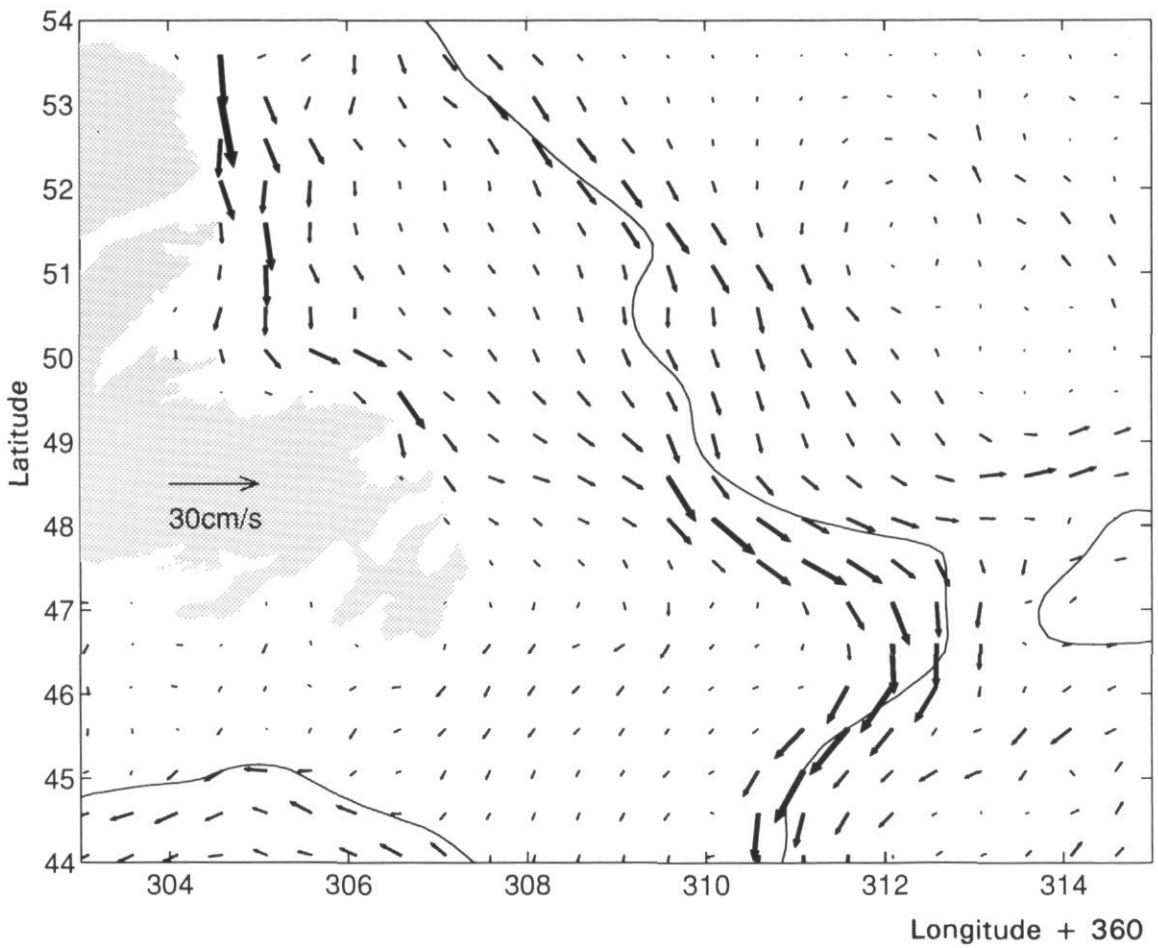


Figure 3. Surface circulation on the Northeast Newfoundland Shelf as determined from a diagnostic model (deYoung *et al.*, 1993) applied to density data objectively analysed for the region. This plot is similar to that derived from the barotropic model of Greenberg and Petrie (1988). The 500 m isobath is shown as a solid line.

the eggs are assumed to be trapped in the mixed layer. From spawning to hatch is about 20–30 days at the observed temperatures of 0–3°C. Young larvae can also be treated as passive drifters early in their lives; we treat the eggs and the larvae as passive drifters for the 50 days of our model runs. One important factor ignored in this model is the influence of the vertical migration of the larvae (Sclafani *et al.*, 1993), for which we have no data.

Detailed information on the spawning location of cod is sparse, though in a summary of cod recruitment and distribution deYoung and Rose (1993) concluded that most of the spawning occurs in water 300–600 m deep, near the shelf break. A recent paper by Hutchings *et al.* (1994) questions this conclusion, using trawl catch data to show that spawning cod have been found on the inner part of the shelf as well. Although we consider the cod to spawn on the outer part of the shelf, near the shelf break (Templeman, 1966), we test the sensitivity of the results to spawning location. Recruitment data were obtained from the Department of Fisheries and Oceans sequential population analysis (Hilborn and Walters, 1992) of the cod in the 2J3KL region (Fig. 1) of the Newfoundland Shelf (Baird *et al.*, 1992).

The primary source of data used in this analysis is wind data, measured at St John's. Windstress is computed using the drag formulation developed and tested by Large and Pond (1981). The raw wind data were measured at hourly intervals. We filtered this data, with a low-pass filter, to remove energy at periods below half-a-day, since the model time step was 12 h. Averages of the retention ratio over time are carried out from May until July, covering the spawning period of the cod (Templeman, 1966; May, 1966). We also ran the model for an earlier time window, 1 April to 20 May. Results from this analysis show greater variability than the retention reported here. Correlation results with recruitment were similar to those reported here.

The model was run with different size areas for the starting egg mass, from 5 to 100 km radius, and with different values of the horizontal diffusivity, from 0 to 100 $m^2\ s^{-1}$ (Csanady, 1982). The centre point for the initial distribution was also varied, located either at the shelf break or 50 km inshore of the shelf break. We found relatively little dependence upon the horizontal diffusivity, with the retention ration changing by about 10% for a change of κ_h from 0 to 100 $m^2\ s^{-1}$. For all the runs reported here, we chose $\kappa_h = 50\ m^2\ s^{-1}$.

The location and size of the egg mass did, however, play an important role in the model results. In Figure 4a and b we plot the retention ratio for 39 different years (1953–1992). The models are run for 50 days starting at 21 May in each year. Figure 4a shows that there is extreme sensitivity if the egg mass is started at the shelf break. The sensitivity is greatest for small patch sizes, since movement over a small distance implies a big change in the retention ratio. For a radius of 5 km, the mean retention ratio is 0.3 with a standard deviation of 0.2. As the radius increases, the mean retention increases and the standard deviation decreases by a factor of three. For an initial location 50 km inshore of the shelf break, the mean retention ratio decreases with increasing radius (Fig. 4b).

Sample trajectories in Figure 5 show the location of the centroid of the egg patch. These runs show the location of the patch for 50-day model runs, from 25 May to 10 July. Most of the transport driven by the wind is across the shelf break. The strong southward transport is because of the mean southward flow that we put into the model to represent the mean flow of the Labrador Current. The two plots in Figure 5 show trajectories for years when the retention was high (1975) and low (1981), illustrating the differences in the trajectories for these two years. The halfway point of the drift curves, marked with a circle in Figure 5, show that 1975 and 1981 are different in the first half of the period, but are similar in the second half. This sensitivity to the timing of the analysis somewhat complicates the interpretation of our results.

A plot of the retention ratio over the period 1960 to 1990 shows the interannual variability in the retention ratio, normalized by the maximum since it is the variability itself in which we are interested (Fig. 6). Does this retention ratio relate somehow to recruitment for cod? Also plotted in Figure 6 is the recruitment index for the 2J and 3KL cod (Fig. 1). This recruitment index has been normalized by the number of spawning adults (i.e. the 6+ fish), thus population size effects are removed, and also by the maximum in the record. The two time series shown in Figure 6 have an r^2 of 0.34, which is marginally significant at the 90% level. There is not much difference in the result if we do not normalize by the population size (Fig. 6b). There is a weak significant correlation in this case as well. One other way to look at these results is via a scatter diagram plotting normalized recruitment versus the retention ratio (Fig. 7). This plot confirms the regression analysis of Figure 6 showing that although the correlation between recruitment and retention may be significant it is weak.

Summary and conclusions

We have developed a two-dimensional analytical model to simulate the time-dependent retention of eggs and larvae on the Newfoundland Shelf. The model retention ratio for the shelf shows significant, but weak, correlation with the measured recruitment of cod in the 2J and 3KL region of the Newfoundland Shelf. These results are consistent with the recent model of deYoung and Rose (1993), who argue that retention of eggs and larvae

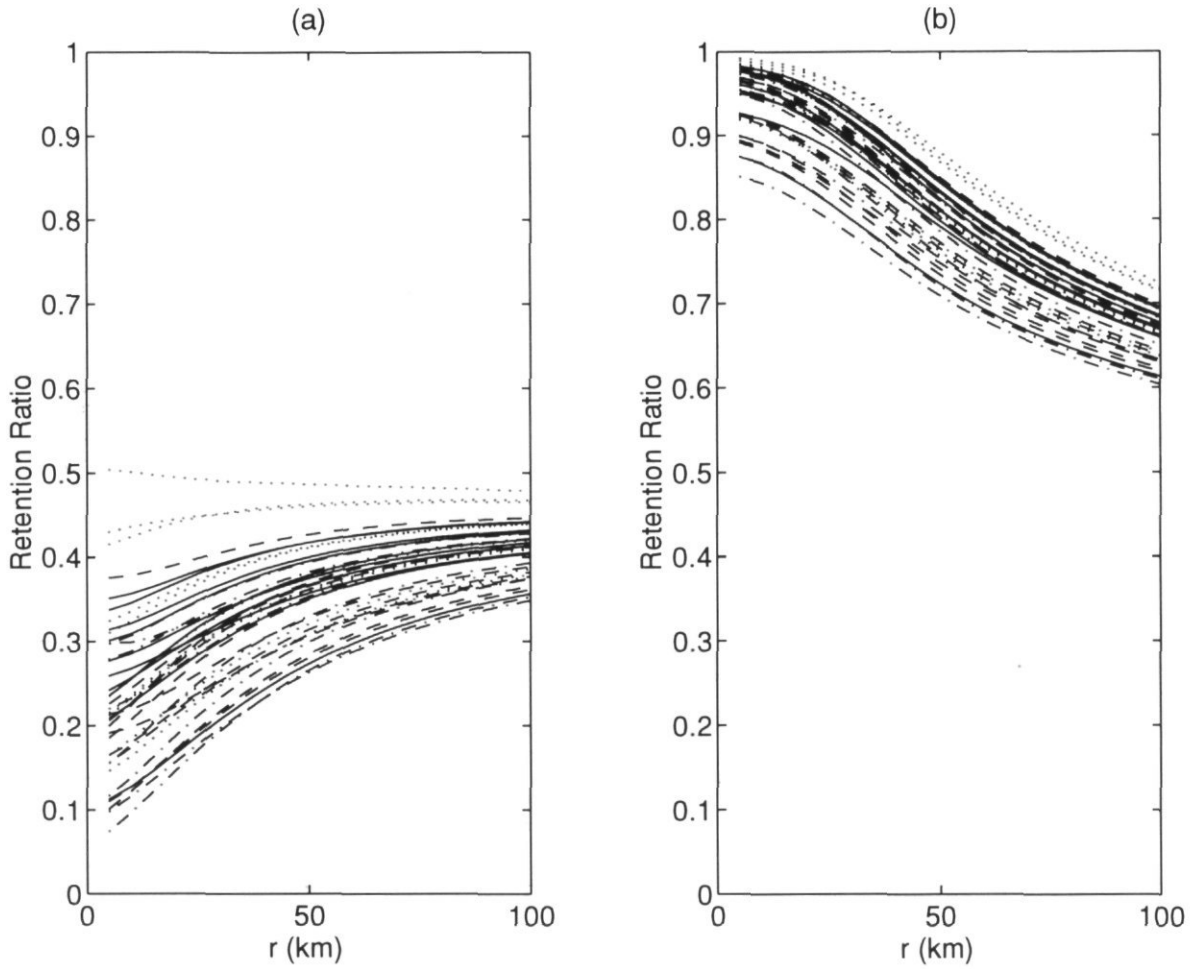


Figure 4. Dependence of the retention ratio upon the starting egg mass radius, which ranges from 5 to 100 km. In (a) the egg mass is started at the shelf break. In (b) the egg mass is started 50 km inshore of the shelf break.

on the shelf is important for successful recruitment for cod in this region. The model also shows that the initial location and size of the egg patch is crucial in determining the retention of eggs on the shelf.

If 2J and 3KL cod do spawn at the shelf break, then increasing the patch size will normally increase their chance for retention on the shelf. In a year with strong onshore advection, however, a small patch size can serve to increase the retention, which would already be high. If cod spawning is widely dispersed over the shelf, as argued by Hutchings *et al.* (1993), then the retention of eggs on the shelf is significantly increased and the interannual variability of the retention ratio is dramatically reduced.

One potential difficulty with the analysis presented here is that the spawning does not occur simultaneously throughout the 2J and 3KL regions. Cod in the northern part of the 2J region are thought to spawn earlier than those in the south (3L). Analysis using winds from different times of the year shows that retention is sensitive to the timing of the forcing. Since the retention ratio will depend upon the time window that we choose (see Fig. 4), our results may be confounded by this time variability. Unfortunately, the only reliable recruitment data are for the entire 2J and 3KL regions (deYoung and Rose, 1993).

Another model limitation is that the eggs are considered to be trapped in a homogeneous surface layer. As Anderson and deYoung (1994) show, the eggs take 5–10 days to reach the surface layer, and there is some structure to the vertical distribution of the eggs. A three-dimensional model, including stratification, is required to account for this effect. Vertical migration of the larvae, which hatch 40–50 days following egg release,

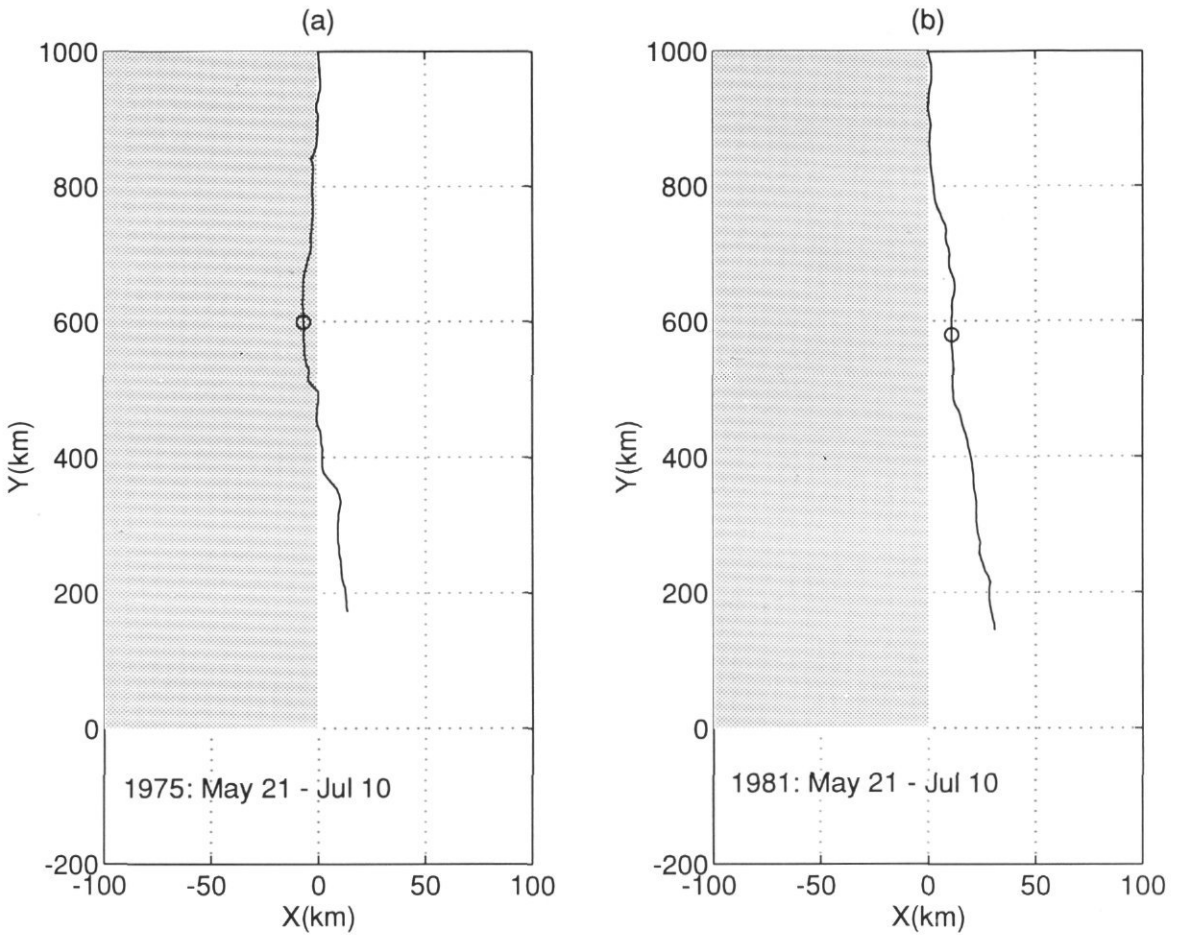


Figure 5. Sample trajectories of the egg patch for (a) 1975 and (b) 1975. The period for the simulation is from 1 April to 10 July. The halfway point in the simulation is shown with an open circle.

may also be an important factor in determining recruitment variability (Sclafani *et al.*, 1993). One potential effect of vertical migration could be to further disperse the larvae because of vertical gradients of the horizontal currents in the water column through which the larvae are migrating.

Recent work shows a relation between salinity and cod recruitment (Myers *et al.*, 1993; Sutcliffe *et al.*, 1983) and temperature and cod recruitment (deYoung and Rose, 1993); however, clear mechanistic links remain elusive. Myers *et al.* (1993) could find no mechanism explaining the correlation; however, deYoung and Rose (1993) related the temperature effect to changing spawning locations of the fish in warm and cold years. They suggest that cod respond to the interannual changes in the temperature field which they experience during their cross-shelf migrations. Their altered spatial distribution, a southward shift during cold years, leads to reduced recruitment because of lower retention of eggs and larvae owing to the spatial pattern of the circulation field.

The influence of the residual field (Cushing, 1975), Ekman transport (Bailey, 1981), diffusion (Koutsikopoulos *et al.*, 1991) and internal waves (Kingsford and Choat, 1986) have all been suggested as mechanisms for the transport of eggs and larvae. There is evidence that this drift is often passive (Bailey, 1981; Koutsikopoulos *et al.*, 1991) and some suggestion that it may at times be active (Werner *et al.*, 1993). One of the difficulties in relating the recruitment of the fish to environmental variables is the strong cross-correlation that exists among almost all environmental variables in the Northwest Atlantic (Petri *et al.*, 1992). Thus deterministic models are difficult to verify.

Our model does show significant correlation, although the percentage of explained variance is small. Such weak correlations are not unexpected when attempting to explain recruitment variations, since there

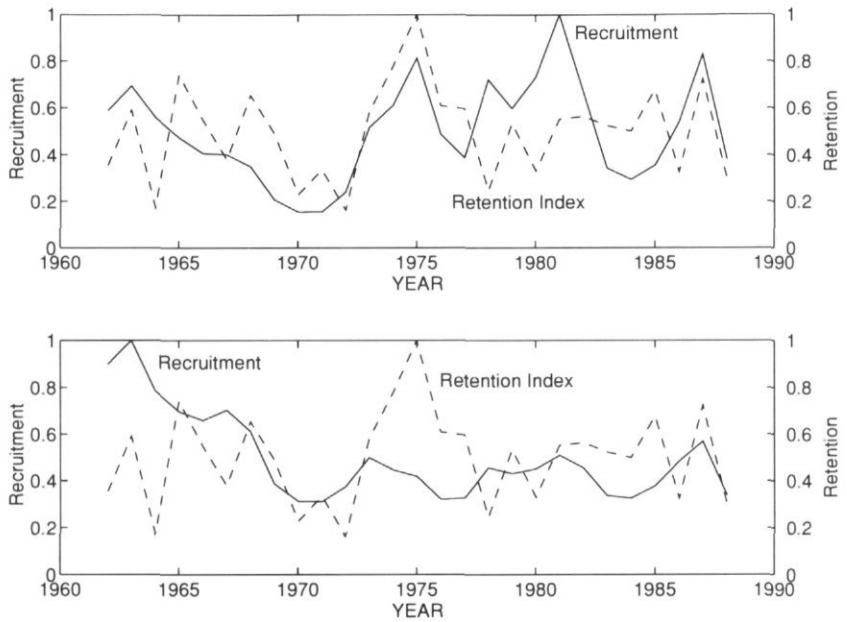


Figure 6. Retention ratio (dashed line) and recruitment of three-year-olds (solid line) for the period 1960 to 1990. The recruitment data are from a virtual population model applied to the cod trawl survey data (Baird *et al.*, 1992). In the upper panel (a) the recruitment data are normalized by the number of spawning adults, but in (b) simply the recruitment itself is plotted. All time series have been normalized by their maxima to make comparisons easier. The period for the simulation is from 21 May to 10 July.

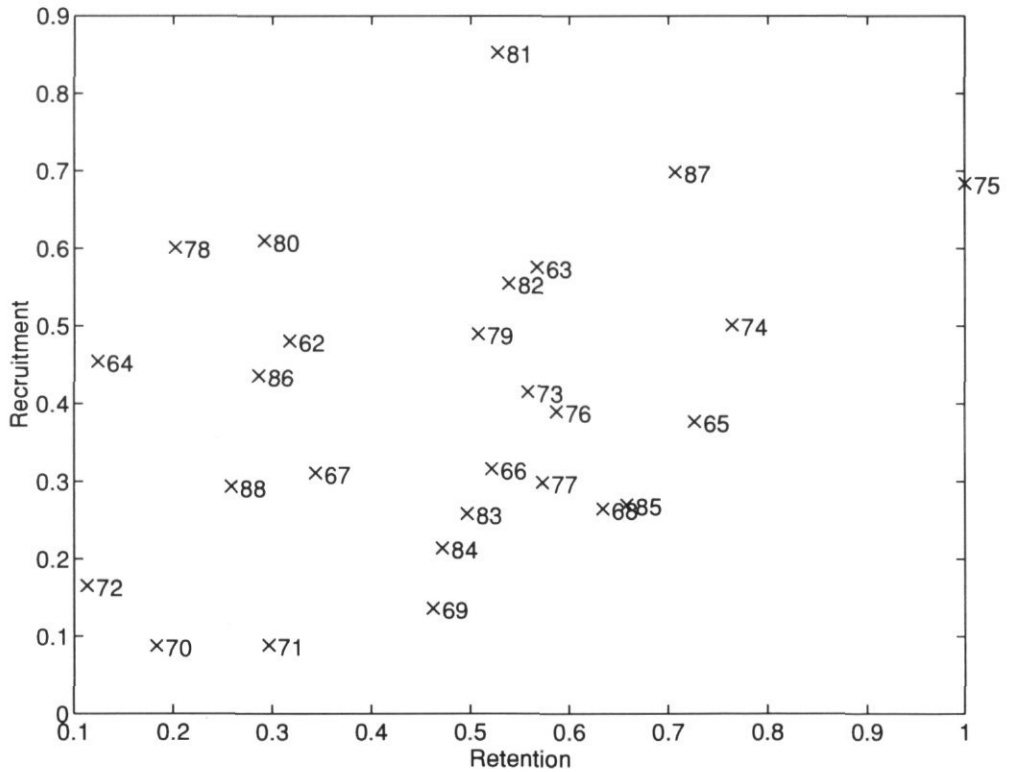


Figure 7. Scatterplot of recruitment, normalized by spawning population size, and the retention ratio. The last two digits of each year are shown beside each point.

are so many factors that influence recruitment. Our simple model is proposed as a tool for testing sensitivity of retention in a shelf or bank region. Although retention may not be a dominant mechanism in every system, it is likely to play a role, even if only in extreme years. We propose to apply a more sophisticated numerical model, which uses a diagnostic velocity field (Fig. 3), together with a wind-forced component that will allow us better to resolve the spatial variability of the residence time on the shelf.

Acknowledgments

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ICES mar. Sci. Symp., 198: 356–378. 1994

Influence of wind-driven advection on interannual variability in cod egg and larval distributions on Georges Bank: 1982 vs 1985

R. G. Lough, W. G. Smith, F. E. Werner, J. W. Loder, F. H. Page, C. G. Hannah, C. E. Naimie, R. I. Perry, M. Sinclair, and D. R. Lynch

Lough, R. G., Smith, W. G., Werner, F. E., Loder, J. W., Page, F. H., Hannah, C. G., Naimie, C. E., Perry, R. I., Sinclair, M., and Lynch, D. R. 1994. Influence of wind-driven advection on interannual variability in cod egg and larval distributions on Georges Bank: 1982 vs 1985. – ICES mar. Sci. Symp., 198: 356–378.

Two contrasting spawning years of Atlantic Cod (*Gadus morhua*) were studied for influences of physical circulation processes on larval distributions: 1982, when there was an apparent offshore loss of eggs and early larvae during April; and 1985, when there was westward displacement of eggs and larvae from the northeast spawning grounds but little evidence of offshore loss. Particles were tracked in monthly-mean flow fields generated by a three-dimensional numerical circulation model in response to the M_2 tide, high and low Scotian Shelf inflows, and the 1982 and 1985 monthly-mean windstresses from February through May. Passive particles were released each year in the northeast Georges Bank spawning area on 1 February, 1 March, or 1 April and tracked until 1 June. The resulting Lagrangian description of the circulation was used to examine the effects of variable advection and spawning date on larval distributions for the two years. In all cases, significant numbers of particles remained on the Bank at the end of each month, suggesting that there is high potential for some larvae to remain on the Bank under a wide range of flow conditions. Greater losses from the Bank occurred for particles in the surface layers (<25 m) and greater retention for particles in deeper layers (>25 m). The impact of different windstresses on the loss or retention of larvae depended on their magnitude, direction, and timing relative to spawning. Off-bank losses in the surface layer were greatest for windstress with a significant along-shelf component towards the northeast when larvae were on the Northeast Peak or the southern flank. The results were qualitatively consistent with MARMAP observations of cod eggs and larvae for the two years, with greater losses in 1982 associated with strong eastnortheastward windstress in April. For the 1 February and 1 March spawning dates, the largest contrast between 1982 and 1985 was obtained in the low Scotian Shelf inflow cases, with only 10% of the starting particles remaining inside the Bank's 70-m isobath at the end of May in 1982, compared with 20–30% in 1985. Off-bank losses for 1 April releases were greatest for particles released in 1982, with only 10% of the starting particles remaining inside the 70-m isobath after 30 days.

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Introduction

Background

Atlantic cod (*Gadus morhua*) stocks on Georges Bank have declined dramatically in the last 30 years, primarily owing to increased fishing effort (Brown, 1987). During this same period there have been noted decadal changes in environmental conditions, such as the change in bottom-water temperatures on Georges Bank (Holzwarth and Mountain, 1990). While environmental variations can affect the seasonal and interannual distributions of

adults and juveniles, recruitment is most likely to be affected by conditions during the early life history from eggs and larvae through recently settled juveniles. A review of the possible effects of environmental factors on fluctuations in cod stocks in the Georges Bank and Gulf of Maine region is given in Serchuk *et al.* (1994).

In a recent modelling study, Werner *et al.* (1993) explored the influences of physical advection and biological migration on the distribution of cod and haddock early life stages on Georges Bank. They used a late-winter/early-spring 3-D circulation field driven by the M_2 tidal current, climatological mean windstress and Scotian Shelf inflow to simulate the distribution of larvae spawned on the Northeast Peak of the Bank (see Fig. 1). Werner *et al.* (1993) found that, while larvae remaining in the surface Ekman layer are generally advected off-bank, larvae below the surface layer are transported southwestward along the southern flank of Georges Bank and are retained on the Bank if their position immediately upstream of the Great South Channel is shoalward of approximately the 70-m isobath. These results were found to apply to passive larvae and to those with specified vertical distributions and migration based on field observations.

Here we build on the climatological mean results of Werner *et al.* (1993) and consider effects of the variability in windstress and Scotian Shelf inflow for two contrasting years. There was a marked difference in the windfields, as well as in the distribution patterns of cod eggs and larvae, between winter–spring of 1982 and 1985. Cod had relatively good recruitment at age 1 for the 1985 year class (43.3 million fish) and poor recruit-

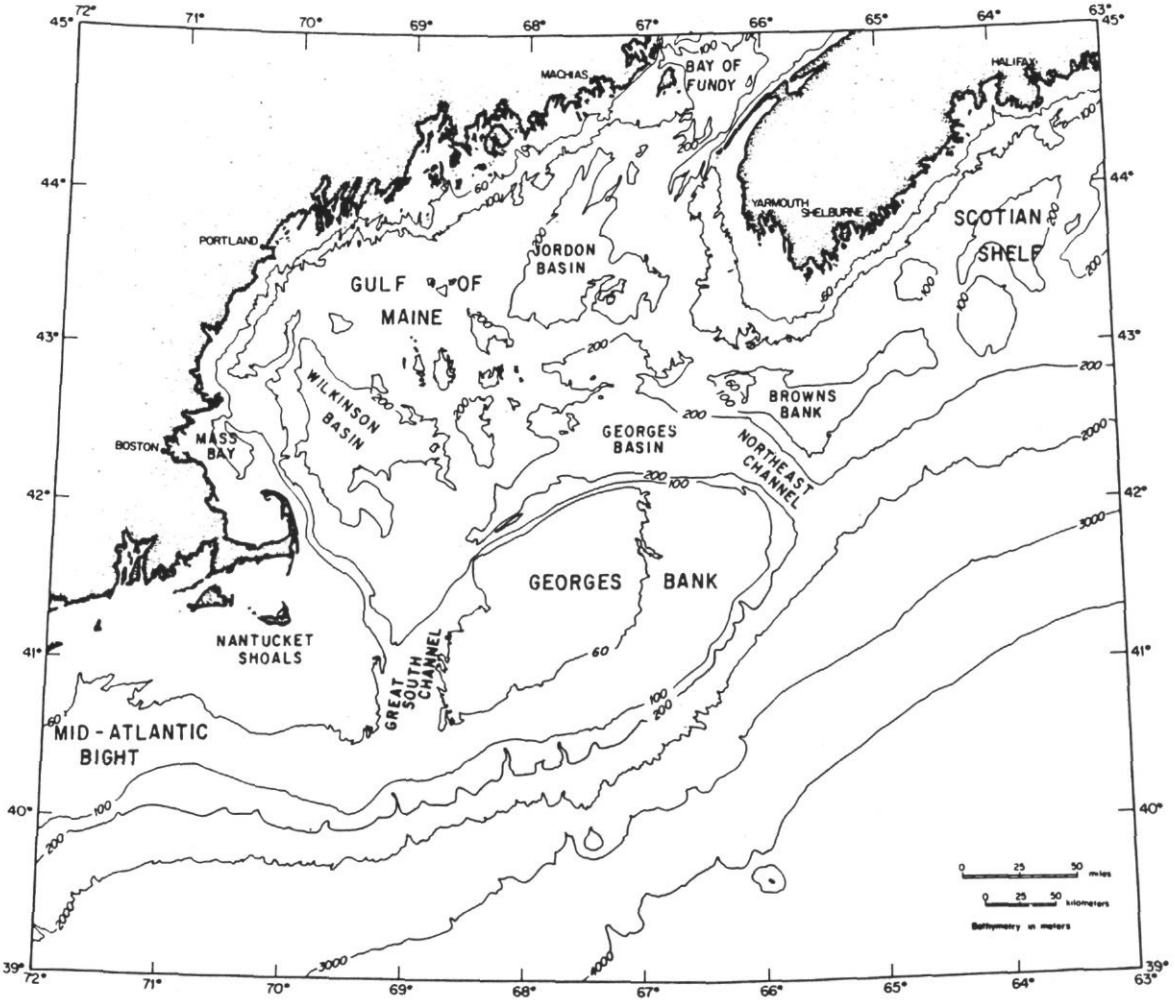


Figure 1. Map of the Georges Bank–Gulf of Maine region showing major topographic features.

ment for 1982 (9.6 million fish) (Serchuk and Wigley, 1992).

Information on the distribution and abundance of cod eggs and larvae was obtained from a comprehensive fisheries ecosystem study conducted by the Northeast Fisheries Science Center (Sherman, 1986; Smith, 1988). This program, known as MARMAP (Marine Resources Monitoring Assessment and Prediction), included standardized year-round surveys of fish eggs and larvae in the Northeast Shelf Ecosystem to provide base lines against which shifts in species composition and diversity within the finfish community could be observed and evaluated. These surveys continued for 11 years, from 1977 to 1987.

Observed MARMAP egg and larval distribution data of cod for 1982 and 1985 are described for these two years. Model results, i.e., particle tracks, for these two years are then used to examine the potential influences of interannual windstress differences and Scotian Shelf inflow variations on larval advection and the observed MARMAP distributions.

Georges Bank circulation

Descriptions of the circulation on Georges Bank may be found in Butman and Beardsley (1987), Butman *et al.* (1987), and for March–April, Werner *et al.* (1993). Topographic rectification of the strong M_2 tidal currents results in a persistent clockwise gyre which is intensified in summer–fall by the Bank's density field (e.g., Loder and Wright, 1985). The large-scale coastal current (Chapman and Beardsley, 1989), seasonal-mean windstress (e.g., Greenberg, 1983) and the shelf/slope front (e.g., Flagg, 1987) contribute to through-flow in the region, while storms (e.g., Brink *et al.*, 1987) and Gulf Stream rings (e.g., Garfield and Evans, 1988) contribute to episodic outflows from the Bank. During February–May, stratification on the Bank is weak and gyre strength and recirculation in the Great South Channel are near their seasonal minima. The mean flow is strongest along the Bank's northern edge, while the southwestward flow on the southern flank and into the Middle Atlantic Bight increases approaching the shelf/slope front at the shelf break. Near-surface drifter studies during December–April indicate an offshore flow component with an estimated average residence time of near-surface water on Georges Bank of 45 days (Flagg *et al.*, 1982). Key features of the Bank's physical regime, from the perspective of the modelling strategy used in this paper are the interannual persistence of the major circulation features and the dominance of forcing by tides, wind, and large-scale through-flow in winter and early spring.

Methods

Egg and larval data

MARMAP surveys were conducted at monthly to bimonthly intervals in the 260 000 km^2 shelf area from Cape Hatteras, North Carolina to Cape Sable, Nova Scotia. A 61-cm bongo fitted with 0.505 mm and 0.333 mm mesh nets sampled ichthyoplankton and zooplankton, respectively. Tow profiles were smooth oblique to a maximum depth of 200 m. Towing speed varied between 1 and 2 knots to maintain a 45° wire angle. The bongo was lowered at 50 m min^{-1} and retrieved at 20 m min^{-1}. Sampling methods for all aspects of the MARMAP Program are described in detail by Sibunka and Silverman (1984, 1989). A summary of the MARMAP surveys for the 1982 and 1985 seasons is listed in Table 1. Larval abundance estimates were adjusted to reflect day/night/twilight differences in vulnerability to capture using correction factors derived by Morse (1989). All catches were standardized to number per 10 m^2 sea surface area. Maps of contoured numbers of egg stages and larval size classes per 10 m^2 were created using Surface III software (Sampson, 1988).

Fish eggs were identified and separated into three

Table 1. Summary of winter–spring MARMAP Ichthyoplankton Surveys of the Georges Bank–Southern New England region, 1982 and 1985 seasons.

Survey	Year	Date	Mid-date	No. of stations	Survey days represented
35	1982	17 Feb–17 Mar	3 Mar	52	84
36		31 Mar–2 May	16 Apr	60	44
37		18 May–10 Jun	30 May	52	44
57	1985	11 Jan–30 Jan	18 Jan	56	51
58		13 Mar–4 Apr	24 Mar	41	39
59		2 Apr–10 Apr	6 Apr	55	25
60		9 May–18 May	14 May	57	31

developmental stages: Stage I – spawned to before blastopore closure; Stage II – blastopore closed to before tail bud lifts free from yolk surface: and Stage III – tail bud free to before hatching (Berrien and Sibunka, 1994). Cod and haddock eggs can only be separated in Stage III, so the species partitioning of the earlier stages was approximated according to relative proportions of the later stage. Incubation rates for haddock eggs are essentially the same as for cod (Page and Frank, 1989), and loss rates for the two species are assumed to be the same. The duration of the cod egg stage is about 19 days at 5°C (Thompson and Riley, 1981) and 60% of the incubation time occurs for Stages I and II, and 40% for Stage III (Table 2). The larvae were separated into four length classes: 3–5 mm, 6–8 mm, 9–11 mm, and 12–15 mm. The mean age and duration of the length classes were determined from the age–length relationships derived by Bolz and Lough (1988) and are listed in Table 2. The mean age of egg and larval stages was based on average incubation/growth rates and assumed to be constant for both years 1982 and 1985.

The survey area was divided into four subareas: <70 m and 71–200 m on Georges Bank, <200 m on the Southern New England Shelf west of 69°00′W (Great South Channel to Montauk), and >200 m water depth. For each subarea, the mean density of the egg and larval stages was estimated by the method described by Pennington (1983), which is based on the delta distribution. The mean density of each stage was multiplied by the area of the subarea and the number of days represented by the survey for a seasonal abundance estimate. Stage- and age-specific loss rates were estimated from exponential regressions by the methods of Lough *et al.* (1985). Loss rates too were estimated for selected egg and larval stages between surveys when the time interval matches the approximate durations between stages.

Circulation model and forcings

Using a harmonic finite element method, the circulation model solves the 3-D non-linear shallow water equations with eddy viscosity closure in the vertical, and forcing by tides, surface stress, inflow at the boundaries and a prescribed density field (Lynch *et al.*, 1992; Lynch and Naimie, 1993). The equations of motion at two frequencies are solved using an iterative method to represent non-linearities, including tidally induced residual currents and influences of both winds and tides on the horizontally and temporally varying eddy viscosity. The baroclinic flow component is not included in the model solutions used here because of difficulties in its computation (and reliability) given sparse density data, and indications that the major winter–early-spring flow features on Georges Bank can be approximated with barotropic solutions (e.g. Werner *et al.*, 1993). The model mesh and bathymetry are the same as in Werner *et al.* (1993), extending from the Scotian Shelf into the Middle Atlantic Bight and deep ocean, with 6756 nodes in the horizontal and 21 unequally spaced nodes in the vertical providing greater resolution in the surface and bottom Ekman layers. The horizontal resolution also is variable, with grid size under 5 km over most of Georges Bank.

Table 2. Average duration and age of cod egg and larval stages used in this study. Egg development schedule is based on 5°C.

Developmental stage		Duration (days)	Age (days)
Egg	I	5	2.5
	II	6	8
	III	8	15
Larva	3–5 mm	5	24
	6–8 mm	13	37
	9–11 mm	14	51
	12–15 mm	9	60

Four sets of year-specific model flow fields (two sets in each of 1982 and 1985) were used to obtain the particle trajectory results presented here. Each set comprised barotropic solutions at both the M_2 tidal and zero (monthly-mean) frequencies for individual months from February through May. In each set, the M_2 tidal forcing was specified as in Lynch and Naimie (1993), spatially uniform monthly-mean windstresses were prescribed, and monthly-mean inflows onto the Scotian Shelf were specified. Open and solid-wall boundary conditions, and the parameterization of friction were as in Werner *et al.* (1993).

The monthly-mean windstresses were obtained from the Comprehensive Ocean-Atmosphere Data Set (Woodruff *et al.*, 1987) for the area 40–42°N 64–68°W, centered near the southeastern end of Georges Bank. Stresses were computed using an approximation to the method of Wright and Thompson (1983), and the neutral-stability speed-dependent drag coefficients of Isemer and Hasse (1987). The stresses for the two different years and the climatological (long-term) means are listed in Table 3.

To investigate the influence of the uncertain large-scale through-flow, the two sets of solutions for each year differed in the amount of inflow onto the Scotian Shelf, specified through a mean set-up on the coastal node in Cabot Strait (upstream boundary). In the first set of solutions, referred to henceforth as the "low through-flow" cases, a set-up value of 0.124 m was used in all months. This value was chosen to give, in model solutions (not presented here) forced with the climatological windstresses, transports on the inner Scotian Shelf which approximated the observational estimate of 0.59 Sv for the Halifax section in March–April (based on

Table 3. Monthly windstress (Pascals) and direction (degrees from true N) used for computed flow fields.

Month	Mean	1982	1985
Feb	0.120 @ 119.7	0.098 @ 148.5	0.054 @ 94.6
Mar	0.089 @ 126.6	0.043 @ 111.0	0.153 @ 115.6
Apr	0.039 @ 116.7	0.165 @ 78.5	0.063 @ 85.0
May	0.014 @ 84.9	0.044 @ 181.6	0.059 @ 63.4

Drinkwater *et al.*, 1979 and Anderson and Smith, 1989). However, with the exception of April, the resulting climatological flow fields significantly underestimated the observed southwestward flow at Station A (40°51.4′N 67°24.1′W) on the southern flank of Georges Bank, based on moored measurements from 2–4 years in 1975–1979 (e.g. Butman *et al.*, 1982). Consequently, the second set of solutions, referred to henceforth as the "high through-flow" cases, was obtained using set-up values of 0.55 m and 0.37 m for February and March, respectively, and the original value (0.124 m) for April and May. The revised values for February and March, while unrealistically high for the Scotian Shelf because of the neglect of baroclinic effects there, were chosen so that alternative climatological flow fields for these months (not presented here) approximated the observed mid-depth mean currents at Station A. The set-up value of 0.124 m was retained in the May solution, since the addition of a baroclinic flow component (not included here) indicated that the discrepancy with observed Station A currents in May was a baroclinic effect which could not be approximated with a barotropic solution; hence, the solutions for May are probably less reliable than the others.

The resulting sets of monthly flow fields for 1982 and 1985 with the alternatives of low and high through-flow provide contrasts through both the known (different) windstresses and the uncertain through-flows in these years. The high through-flow solutions for February–April can be argued as most appropriate for the vicinity of Station A on the southern flank, assuming that forcings other than windstress in 1982 and 1985 were close to their climatological averages and that the measured mean currents in 1975–1979 are representative of the climatological means. The along-shelf transports on the southern flank in the various flow fields (Table 4) are scattered about the climatological average of 0.43 Sv for winter (Flagg *et al.*, 1982).

Table 4. Along-shelf (southwestward) transports (Sv) on the southern flank of Georges Bank in 1982 and 1985 based on low and high estimates of inflow from the Scotian Shelf.

	1982		1985	
	Low inflow	High inflow	Low inflow	High inflow
Feb	0.44	0.76	0.24	0.56
Mar	0.29	0.50	0.28	0.49
Apr	0.01	0.01	0.20	0.20
May	0.42	0.42	0.17	0.17

Particle tracking model

Particle trajectories were computed in the above flow fields for release dates of 1 February, 1 March, and 1 April, and an end-date of 31 May. Since cod spawning is protracted, the different release dates test the sensitivity of loss or retention of eggs and larvae to the timing of the spawning. The particles were fully passive, with no imposed behaviour. Tracking in the 3-D flow fields followed a standard 4th-order Runge-Kutta integration scheme with adaptive step-size control (Blanton, 1992). Particle displacements in a particular month were based on the tidal and mean flow fields for that month, with the end-of-month particle positions used as initial positions for the next month. In order to isolate the influences of variable advection in the cases considered, a standard spawning grid (see Werner *et al.*, 1993, Fig. 10) was used, composed of 726 particles distributed in six horizontal layers at depths of 1 m, 10 m, 20 m, 30 m, 40 m, and 50 m. Particles were tallied each month for four subareas used in summarizing the MARMAP observations.

Results

Timing of spawning

The peak abundance of cod eggs by MARMAP survey number is shown for the 1978–1987 time series in Figure 2. Spawning of cod began in the autumn and peaked in February–April, but eggs can be found in all seasons except summer. It is difficult to detect interannual differences in the timing of spawning because of the generally wide spacing in survey times. Also note that there was no January MARMAP survey in 1982 to compare egg and larval distributions and abundances with 1985 Survey 57 (Table 1).

1982 survey distribution of cod eggs/larvae

On Survey 35 (3 March middate), Stage I cod eggs were distributed broadly across Georges Bank, with high concentrations extending from the Northeast Peak westward across the shoals (Fig. 3). Stages II and III eggs and the recently hatched 3–5 mm larvae were located more central to the bank, mostly within the 70-m isobath. On Survey 36 (16 April), the highest densities of Stages I, II,

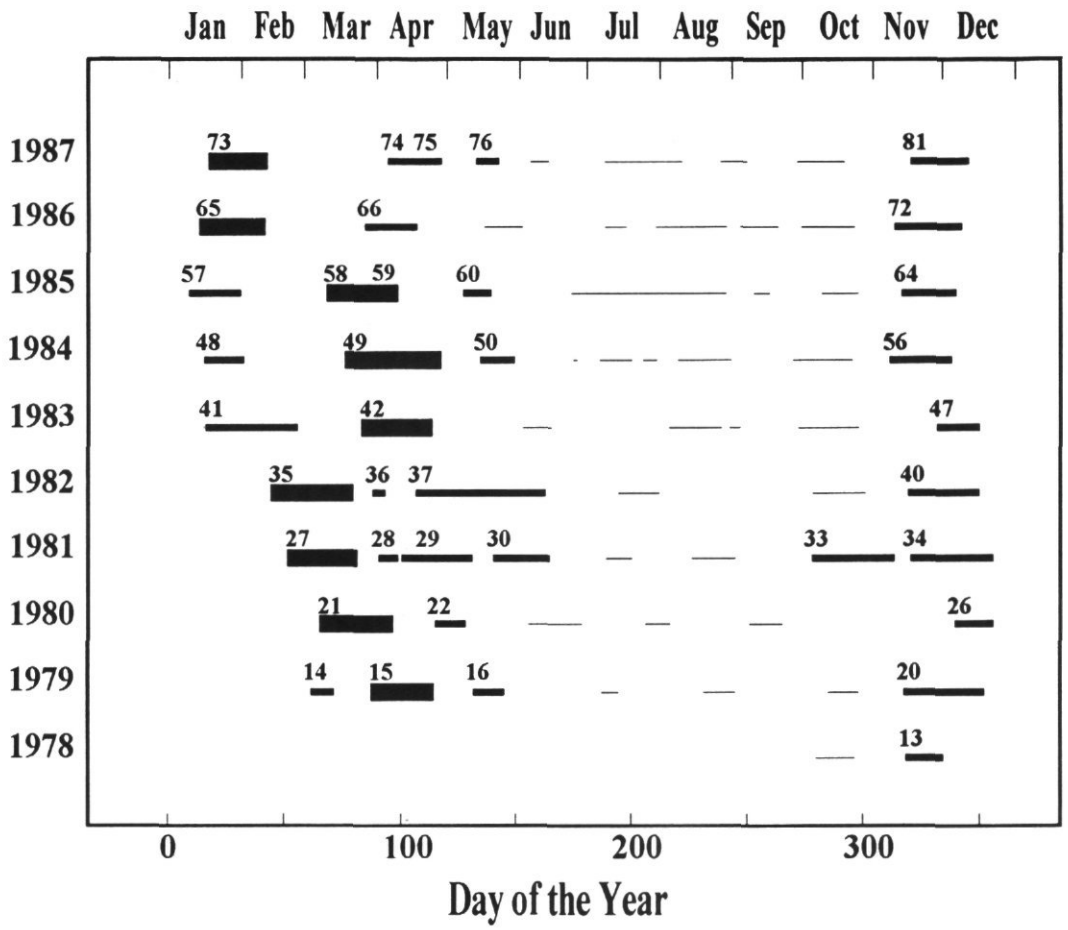


Figure 2. Scored abundance (bars) of cod eggs (Stage III) by MARMAP survey (number over bar) for the years 1978–1987. Egg abundance: —— none, ▬▬ Low, ▬▬ peak.

and III eggs were located on the flank of eastern Georges Bank, extending across the 100-m isobath. Relatively few larvae were caught; the smallest size classes of larvae were distributed along the southern flank. Assuming that the 6–8 mm larvae in Survey 36 came from Stage III eggs in Survey 35, these larvae would have been advected southeastward to the edge of the bank in about 45 days, or approximately at the rate of 2.5 km d^{-1} (2.9 cm s^{-1}). By the last Survey 37 (30 May), even fewer larvae were caught. Some spawning of cod was still evident on Northeast Georges Bank based on the occurrence of Stages I–III eggs (also see Table 5).

1985 survey distribution of cod eggs/larvae

Cod eggs on Survey 57 (18 January) were distributed from eastern Georges Bank westward across the central shoals and the Great South Channel onto Nantucket Shoals (figure not shown for this survey). Based on the distribution patterns of eggs, spawning was most intense on eastern Georges Bank and Nantucket Shoals. Larvae of the 3–5 mm and 6–8 mm size classes were most abundant on Nantucket Shoals. On Survey 58 (24 March), egg and early larval abundances were high and widely distributed across Georges Bank and Nantucket Shoals (Fig. 4). The highest densities of eggs were located on eastern Georges Bank, but the 3–5 mm and 6–8 mm larvae mostly resided along the southern flank. A few 9–11 mm larvae were caught on Nantucket Shoals. On Survey 59 (6 April) egg densities were lower but the distributions were similar to the previous survey. The highest concentrations of larvae, 3–5 mm, 6–8 mm, and 9–11 mm, were located along the southern flank of Georges Bank, extending across Great South Channel to Southern New England. Comparing the approximate egg to larval displacement rate between centers of mass for Surveys 58 and 59 suggests an advection rate of 6.7 km d^{-1} (7.7 cm s^{-1}) southwestward. Very little spawn-

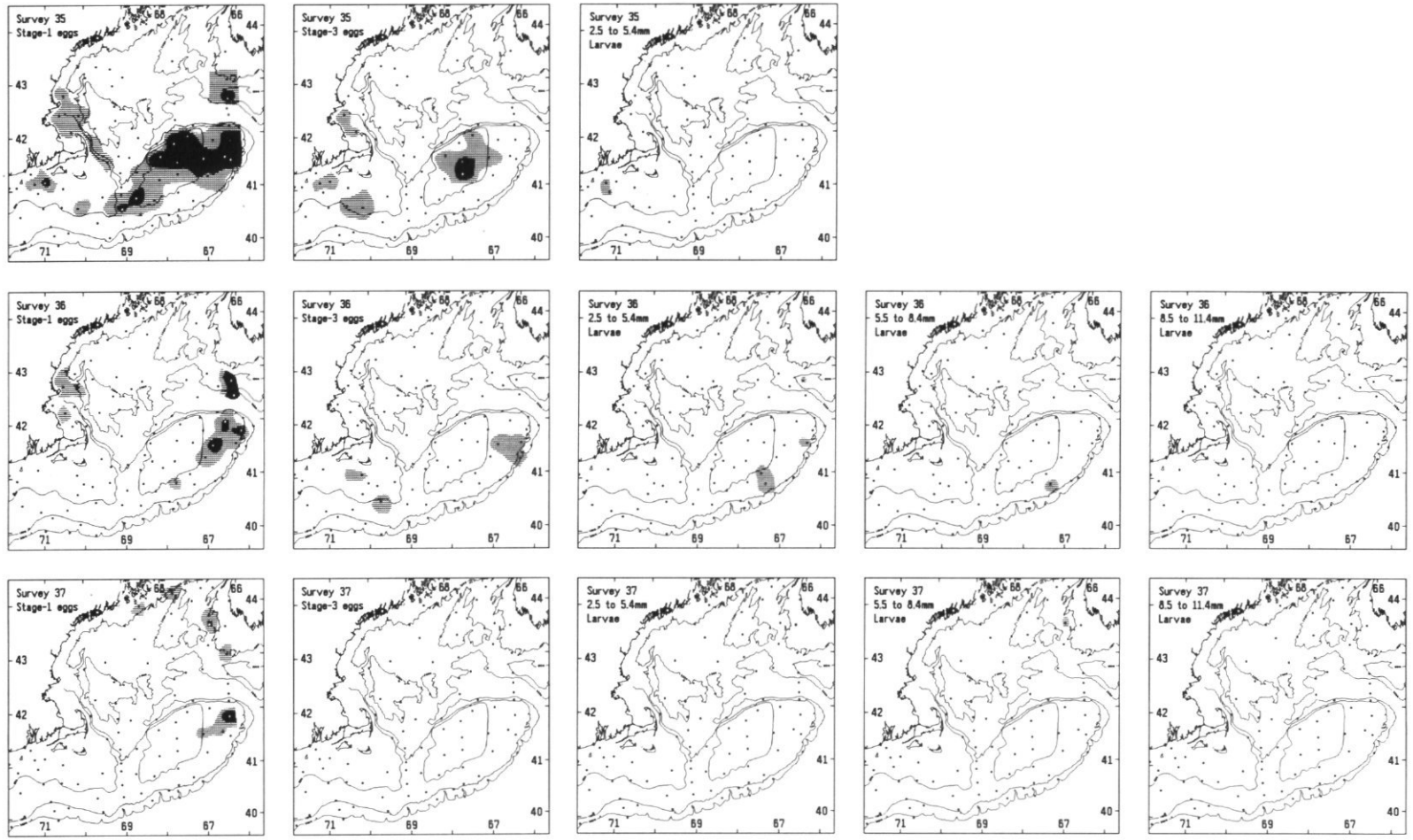


Figure 3. Selected cod egg and larval distributions for three surveys (35, 36, 37) during the 1982 season. Abundance (no./10 m^2) shadings are by order of magnitude. No./10 m^2; None, 1–10, 11–100, 101–1000, >1000.

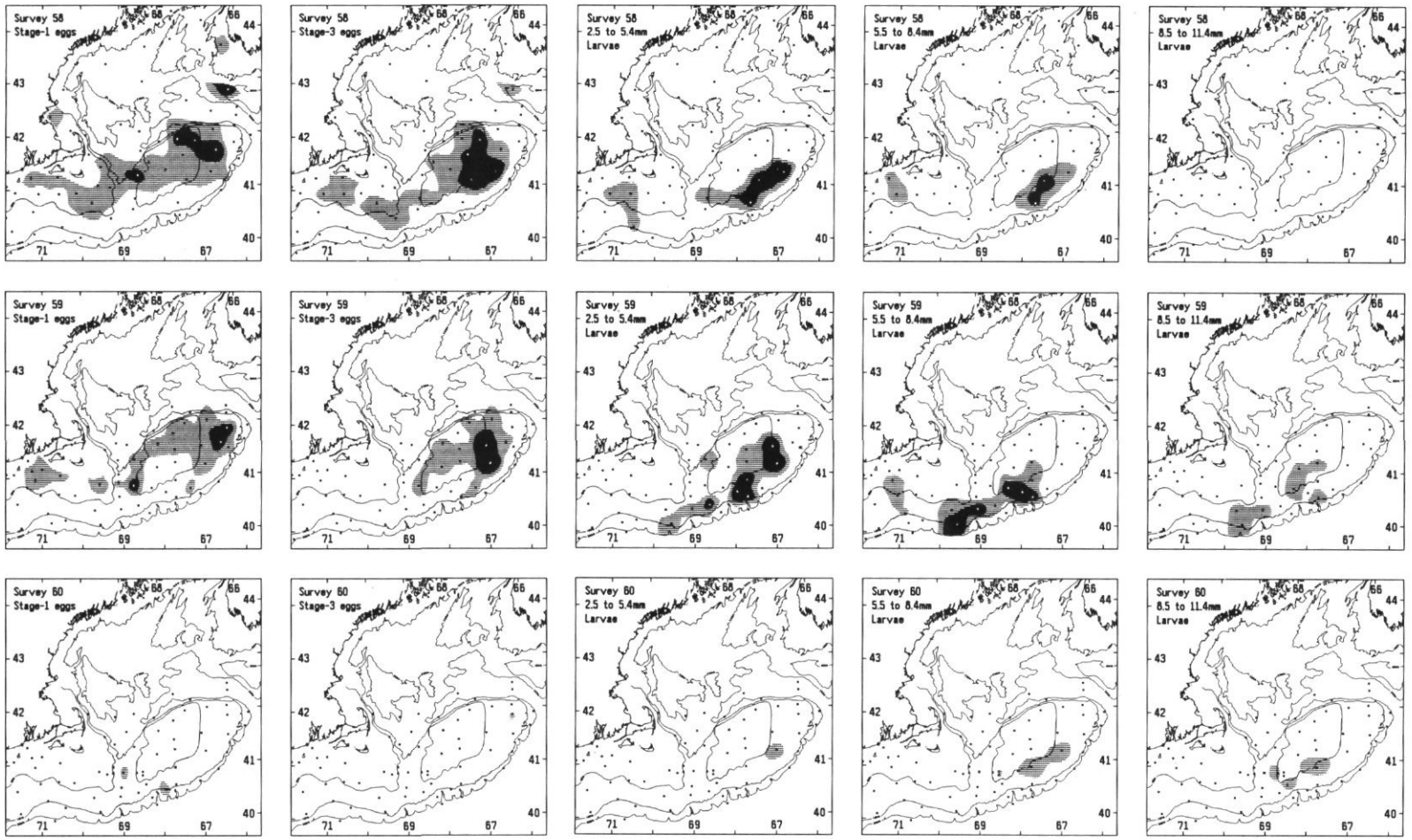


Figure 4. Selected cod egg and larval distributions for three surveys (58, 59, 60) during the 1985 season. Survey 57 is not shown. Abundance (no./10 m^2) shadings are by order of magnitude. No./10 m^2; None, 1–10, 11–100, 01–1000, >1000.

Table 5. Abundance estimates ($\times 10^{-9}$) for egg and larval stages of cod in the Georges Bank–Southern New England area, 1982 and 1985 seasons.

	Egg stage			Larval size class (mm)			
	I	II	III	3–5	6–8	9–11	12–15
1982 Survey							
35	85 830	43 294	9 996	561	0	0	0
36	3 410	1 964	1 086	335	128	27	0
37	1 475	394	88	0	84	25	0
Total	90 715	45 652	11 171	896	212	56	0
1985 Survey							
57	4 667	5 272	4 624	3 474	650	24	0
58	10 412	10 927	12 573	12 752	2 603	50	0
59	3 795	5 137	4 406	5 134	6 492	994	106
60	305	212	149	197	540	448	187
Total	19 178	21 549	21 751	21 556	10 284	1 515	293

ing was evident on Survey 60 (14 May) based on the low egg catches. The more abundant larval size classes, 6–8 mm and 9–11 mm, were located mostly on the southern side of Georges Bank in waters <70 m.

Abundance and loss rates: 1982 and 1985 spawning seasons

Cod egg and larval abundance estimates for the 1982 and 1985 surveys are given in Table 5. Survey totals represent the seasonal production estimates for each stage, which are plotted on a logarithmic scale in Figure 5. Production of Stage I eggs was 90.7×10^{12} in 1982 and 19.2×10^{12} in 1985. That is, spawning was 4–5 times higher in 1982 than in 1985. About 90% of the eggs produced in 1982 occurred on Survey 35; less than 10% occurred in the April and May surveys (Table 5). In 1985, egg production appeared to be more protracted compared to 1982 (note, no survey in January 1982, however): 50–60% of the eggs produced occurred on Survey 58 (24 March) and about 20% in the January and April surveys. Therefore, the peak spawning period appeared to be March in both years. In 1982, abundance of the subsequent egg and larval stages declined rapidly; few larvae were found on Surveys 36 (16 April) or 37 (30 May). The exponential regression of stage abundance against the mean age (Fig. 5) produced an average 1982 loss rate of 17.6% d^{-1} ($Z = -0.194$). In 1985, the abundance of cod egg stages and the 3–5 mm and 6–8 mm larval size classes remained at a high level before declining in the later larval stages. The 1985 average loss rate was 7.2% d^{-1} ($Z = -0.075$).

Loss rates for selected egg and larval stages between surveys also show a similar pattern between the two years (Table 6). Loss rates were generally high (8–16% d^{-1}) in 1982 and low (1–9% d^{-1}) in 1985. Later larval stages usually had higher loss rates than earlier stages. The largest losses in 1982 occurred between Surveys 35 and 36, 3 March to 16 April, where the cohort loss rate was estimated at 12–16% d^{-1} between Stage I eggs and larval stages 6–8 mm and 9–11 mm.

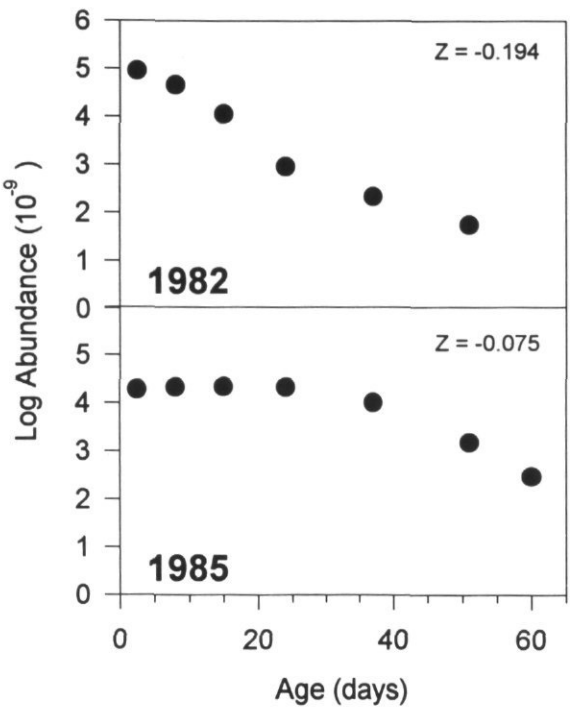


Figure 5. Cod abundance versus stage mean age for the 1982 and 1985 seasons. Instantaneous loss rates (Z) are included in the plots.

Table 6. Loss rates of selected cod egg and larval stages between surveys for the 1982 and 1985 seasons.

Surveys	Mid-dates	Days	Stages compared	Loss rates (Z = %/day)
35 & 36	3 Mar–16 Apr 1982	44	EI-L6	12.4
			EI-L9	15.5
36 & 37	16 Apr–30 May 1982	44	EI-L6	8.0
			EI-L9	10.1
57 & 58	18 Jan–24 Mar 1985	65	None	
58 & 59	24 Mar–6 Apr 1985	13	EI-L3	1.1
			L3-L6	5.4
			L6-L9	9.3
59 & 60	6 Apr–14 May 1985	38	EI-L6	5.1
			EII-L6	6.2
			EII-L9	8.4
			EIII-L9	8.1
			EIII-L12	8.5
			L3-L12	8.8

Horizontal and vertical structure of the flow fields

The spatial structure of the monthly-mean flow fields is illustrated by horizontal sections at 30 m and vertical sections across the southern flank (see Werner *et al.*, 1993, Fig. 10) for the various months using the high through-flow cases (Figs. 6–9). Focusing on selected months in conjunction with the transports in Table 4 as an index of along-shelf flow variability, key flow features and the influences of wind and through-flow can be discussed.

In general, the major elements of the underlying tidally induced gyre remain important in the various monthly-mean fields: clockwise drift with a northern-flank jet, saddlepoint in Great South Channel and outflow towards the Southern New England Shelf (Lynch and Naimie, 1993; Ridderinkhof and Loder, 1994). The primary exceptions to this are: (i) in the near-surface region where the Ekman drift generally dominates under moderate-to-strong wind stresses, (ii) the April 1982 field in which the southern-flank southwestward drift and saddlepoint are dominated by wind-driven currents, and (iii) the high through-flow fields for February and March, in which the saddlepoint is dominated by southward flow in the Great South Channel.

In describing the influences of variable windstress and through-flow, it is instructive to recognize the basic characteristics of these flow components in the present solutions. The through-flow, which is vertically uniform outside the bottom Ekman layer, supplements clockwise drift on the northern and southern flanks of Georges Bank, and is southward in the Great South Channel region (e.g., Fig. 12 of Lynch *et al.*, 1992). The response to windstress has two components: the surface Ekman layer driven by the local stress, and the large-scale pressure-field response involving vertically uniform currents and associated bottom Ekman layers. The net surface Ekman transport is directed 90° to the right of the windstress with magnitude proportional to the stress, while the large-scale response involves currents primarily along isobaths with greater strength for along-shelf (compared with cross-shelf) stress (e.g., Wright *et al.*, 1986). For the southern flank of Georges Bank, the net results are that the largest offshore (essentially surface Ekman) transport occurs for along-shelf stress towards the northeast, while the strongest along-shelf currents towards the northeast (southwest) occur for stress towards the northnortheast (southsouthwest). By corollary, windstress towards the eastsoutheast or west-northwest has little influence on the along-shelf flow.

Contrasting the 1982 and 1985 solutions for selected months, these basic characteristics can be seen to account for the variability in flow fields. In March of 1982 and 1985 the windstress was directed approximately eastsoutheast, but with a much greater magnitude in 1985. In spite of this difference the along-bank currents and transports on the southern flank are similar (for particular through-flow cases; e.g., Table 4). The (weaker) currents in the cross-bank direction (Figs. 8, 10) are more sensitive to the different windstress magnitudes in these months. The cross-bank patterns are similar to that in the climatological seasonal mean (Fig. 8b of Werner *et al.*, 1993), with offshore flow in the near-surface region and downwelling below the surface layer over the shelf break; however, the flow speeds are significantly larger in 1985.

In April of 1982 and 1985, the windstresses again had similar directions, this time directed eastnortheastward and eastward (i.e., more along-shelf) with much greater

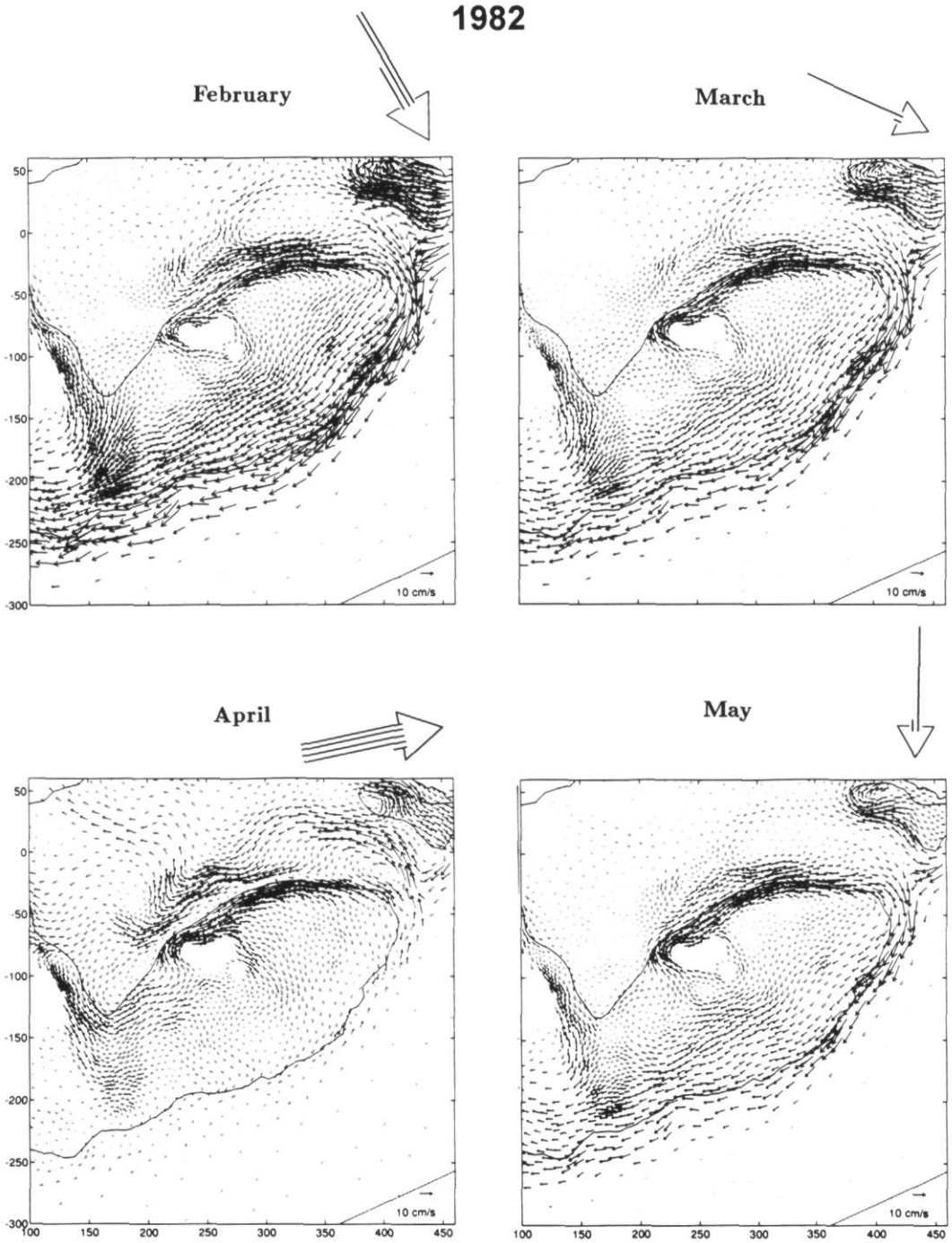


Figure 6. Horizontal section at 30 m of the monthly-mean flow on Georges Bank for February and March (high through-flow), April and May of 1982. Each full shaft of the monthly-mean wind vector above each panel corresponds to a stress of 0.04 Pa. The 100 m depth contour is shown. The blank region on Georges Bank indicates depths shallower than 30 m. Axes in km.

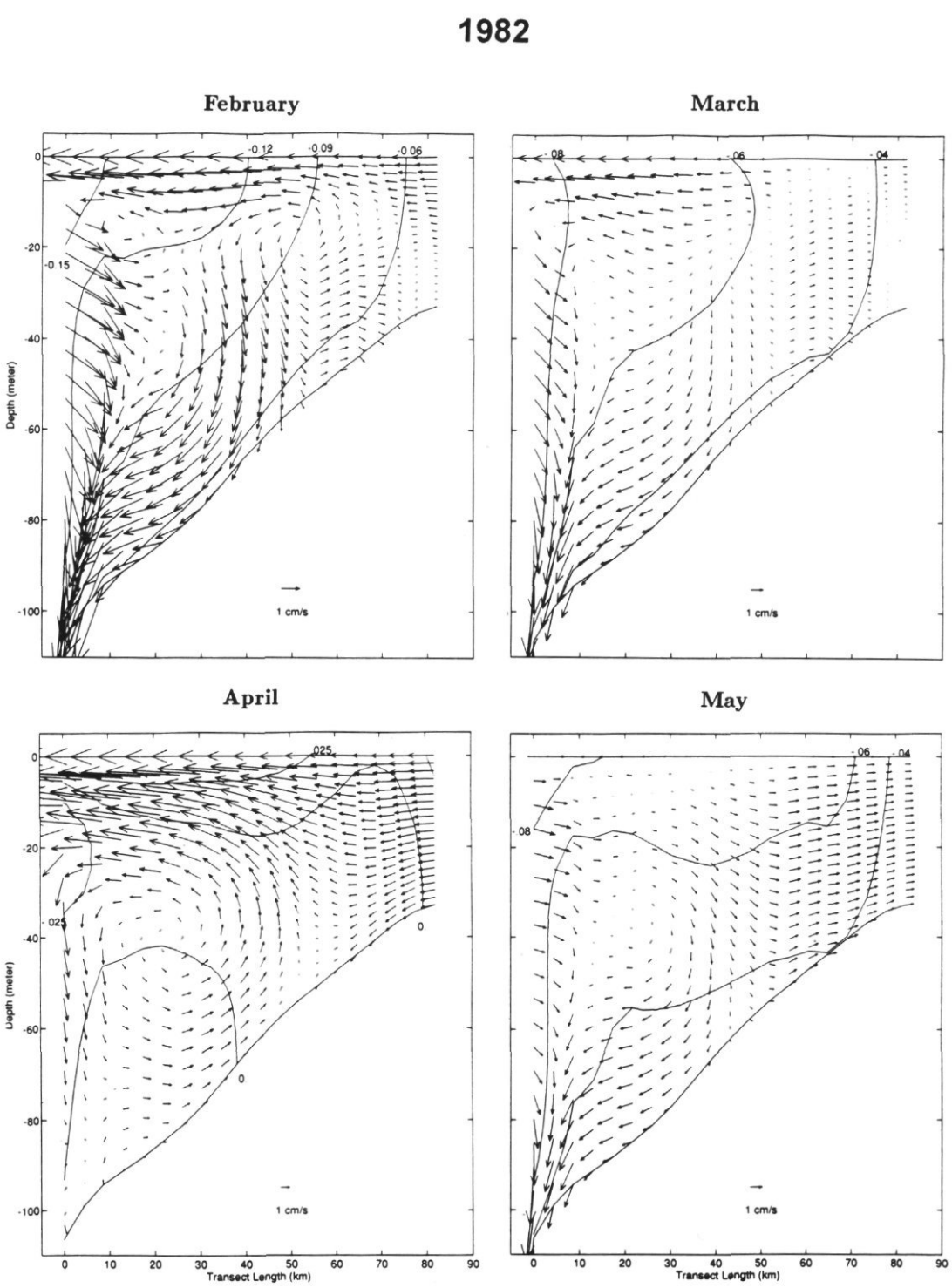


Figure 7. Vertical section across the southern flank of the monthly-mean flow for February and March (high through-flow), April and May of 1982. Isotachs (in m s^{-1}) of the along-bank component are negative into the page. Vector scale at the bottom of each panel is provided for the horizontal velocity component. Depth in m, horizontal distance in km.

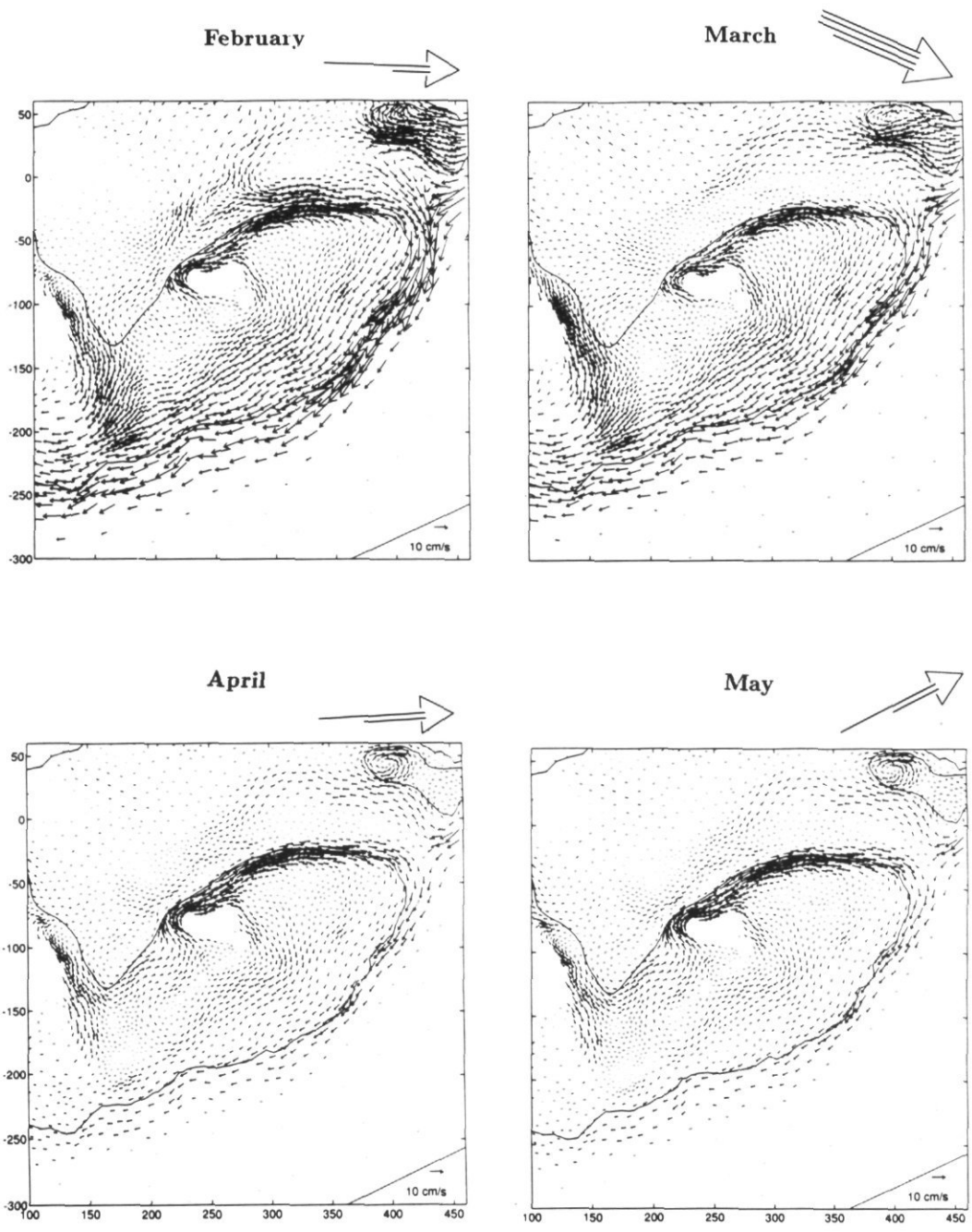


Figure 8. Horizontal section at 30 m of the monthly-mean flow on Georges Bank for February and March (high through-flow), April and May of 1985. Format is the same as for Figure 6.

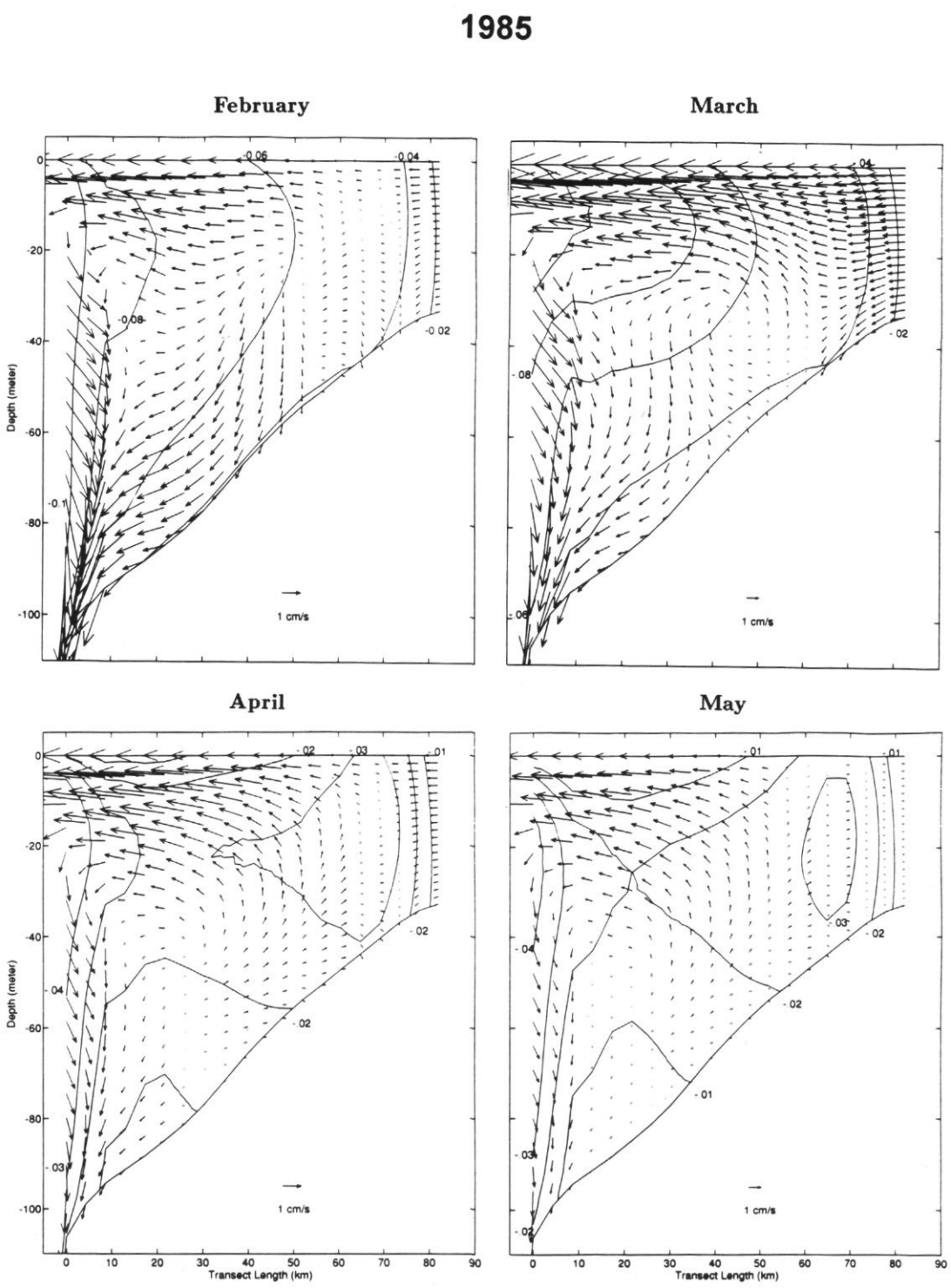


Figure 9. Vertical section across the southern flank of the monthly-mean flow for February and March (high through-flow), April and May of 1985. Format is the same as for Figure 7.

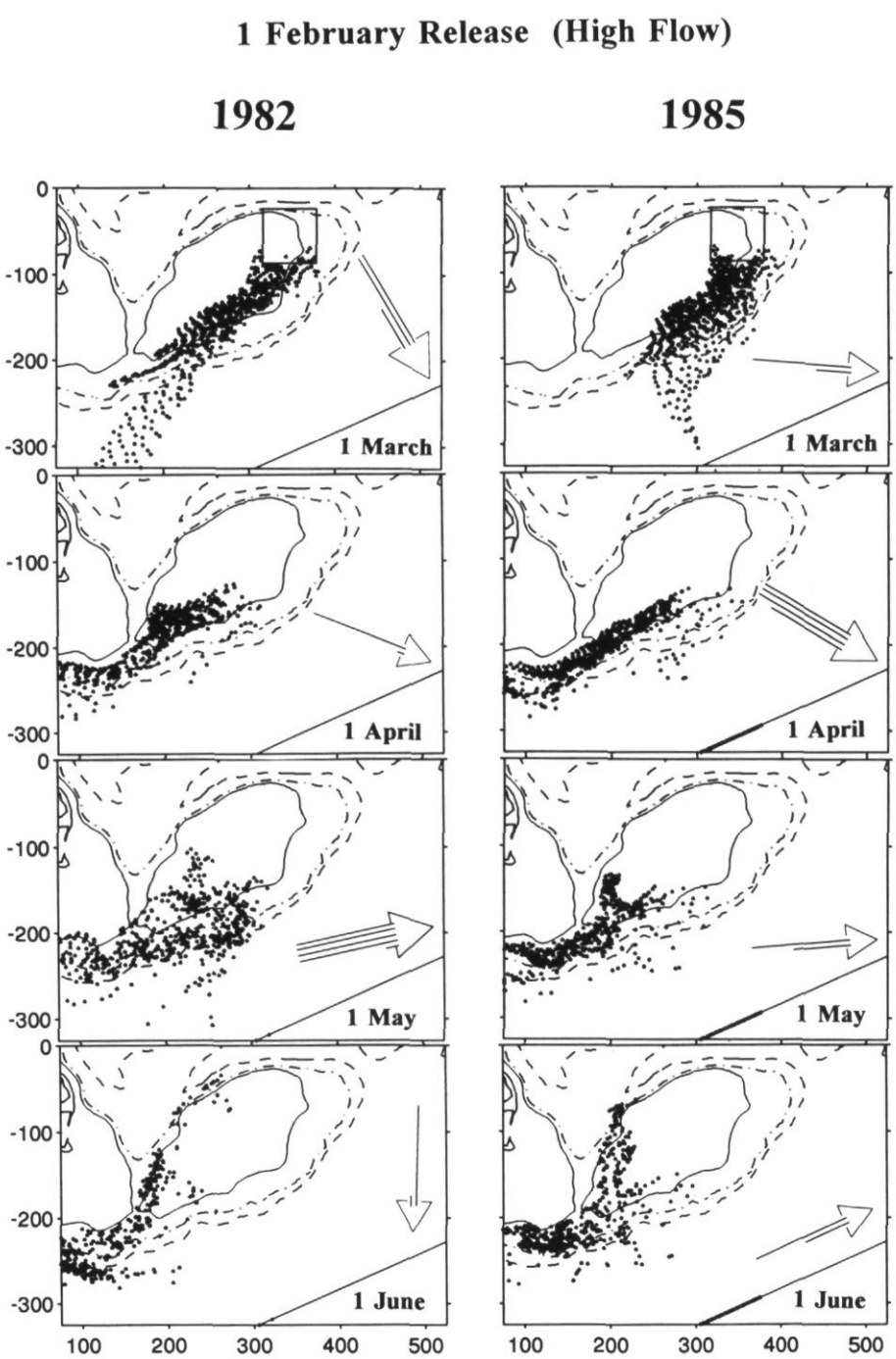


Figure 10. Monthly particle locations, from 1 March to 1 June, for the 1 February 1982 and 1985 releases in the high through-flow field. The rectangle on northeastern Georges Bank in the first plot represents the model spawning grid. Monthly-mean wind vectors are drawn in the bottom right of each panel. Each full shaft on the wind vector corresponds to a stress of 0.04 Pa. Horizontal axes in km. Depth contours are the 70 m (solid), the 100 m (dash-dot) and the 200 m (long dash).

magnitude in 1982. The influence of the different windstress magnitudes on the along-shelf transports is much greater than in the March solutions, with the along-shelf drift on the southern flank largely arrested by the strong winds in April 1982. The cross-shelf flow patterns in these months also show similarities to the climatological seasonal-mean, except for increased on-bank flow in the lower water column between the 50- and 80-m isobaths. The cross-bank flows are stronger in April 1982 consistent with the stronger windstress and offshore Ekman transport.

The flow fields for February and May also illustrate the sensitivity to wind direction. The strong southsoutheastward stress in February 1982 (similar to the climatological mean used in Werner *et al.* (1993)) yields the largest along-shelf flow to the southwest of any case, through the combination of Ekman transport and the large-scale response. Although the windstresses were only moderate in May of 1982 and 1985, the different directions result in different overall current responses. In May 1982 the southward windstress results in increased southwestward flow (again, through both Ekman transport and the large-scale response), whereas the eastnortheastward stress in May 1985 results in a substantial reduction in the along-shelf flow on the southern flank. The cross-shelf flow patterns for May also have significant differences. In May 1982 there is no offshore surface drift on the section, while in May 1985 there is substantial offshore Ekman transport, as in April of 1982 and 1985.

Particle tracking runs

The detailed differences in model trajectories for the two years are illustrated by the monthly particle distributions for the 1 February and 1 March releases in the high through-flow cases (Figs. 10, 11), the 1 March release in the low through-flow case (Fig. 12), and 1 April release (Fig. 13). The effects of variations in the windstress, through-flow, and release date are best summarized by bar graphs of the number of particles in the various subareas, for all release depths (Fig. 14), and the upper ($\leq$20 m) and lower water column in the 1 March high through-flow case (Fig. 15).

Despite the different windstresses and through-flows, the particle distributions show broad similarities in the different cases, illustrating the persistence and stability imposed on the Georges Bank physical regime by tidal forcing and significant prevalence in the windstress and through-flow directions. The qualitative features of the climatological pattern described in Werner *et al.* (1993) generally hold, with general southwestward drift towards the Southern New England Shelf, offshore loss of near-surface particles, and recirculation of some particles in the Great South Channel region after 2–3 months. However, there are also significant differences associated with the variations in windstress, through-flow, and release date.

February 1 releases

For both years and through-flows (Figs. 10, 14), about 10–15% of the particles (near-surface ones) are lost offshore during the first month, with further offshore losses in subsequent months. On the other hand, about 20% or more of the particles (deeper ones) remain on the Bank after 4 months. Among the latter, at least 8% remain inside the 70-m isobath on the Bank on 1 June, many of which recirculate northward in the Great South Channel region (e.g., Fig. 10). The number of particles remaining inside the 70-m isobath by May–June is less in 1982 for both through-flows, owing primarily to increased offshore particle displacement during the April 1982 eastnortheastward windstress forcing. The number of particles remaining both inside the Bank's 200-m isobath and on the shelf as a whole on 1 June is also less in 1982 for both through-flows. The primary influence of through-flow strength is that more particles reach the Southern New England Shelf with stronger through-flow. The through-flow also affects the number of particles lost offshore during adverse wind events as a result of influences on their along-shelf position. For example, more particles are lost offshore during April 1982 in the low through-flow case, because fewer particles reach Great South Channel by 1 April. In contrast, deep particles that reach the Channel in the high through-flow case are displaced onto the central Bank by the April 1982 wind forcing.

March 1 releases

The greatest change in the particle distributions for this release date is the large reduction in the number of particles inside the Bank's 70-m isobath during April 1982 (for both through-flow cases; Figs. 11, 12, 14). In contrast to the 1 February releases there is a corresponding reduction in the number of particles inside the Bank's 200-m isobath. The result is that fewer particles remain inside both the 70-m and 200-m isobaths on 1 June in 1982 than 1985. The influences of through-flow on the results for this release date are less than for the 1 February releases, with fewer particles reaching the Southern New England Shelf (as a result of the shorter tracking period) and less effect on offshore losses during April 1982 (because fewer particles had reached Great South Channel). The displacement of particles into the Northeast Channel in April 1982 is associated with the wind-driven counterclockwise flow along the southeastern shelf break, but may be exaggerated because of the underestimation of clockwise (baroclinic) through-flow along the shelf break in the present barotropic solutions.

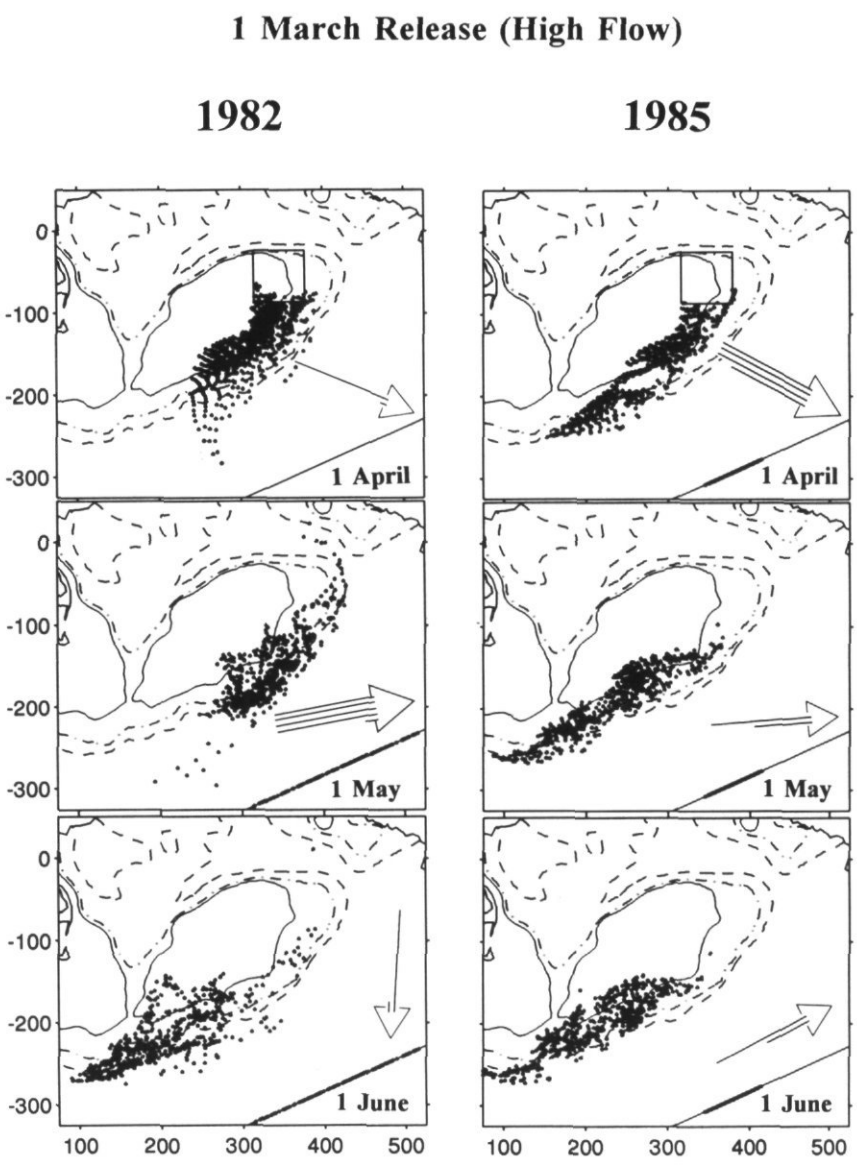


Figure 11. Monthly particle locations, from 1 April to 1 June, for the 1 March 1982 and 1985 releases in the high through-flow field. Format is the same as for Figure 10.

The importance of vertical position to particle displacements and losses is illustrated by the particle counts for the 1 March releases with high through-flow (Fig. 15). In both years the majority of upper-level (≤20 m) particles are lost offshore, in 1982 owing to the April winds and in 1985 owing to the March winds, while the majority of lower-level particles remain on the Bank on 1 June. The greater losses from inside the Bank's 70-m isobath in 1982 (compared to 1985) are primarily associated with lower-level particles being displaced to the outer Bank in April 1982.

April 1 releases

For this release date too, the greatest change in particle distributions is associated with the April 1982 winds, with a 50% reduction in the number of particles on the Bank and a fivefold reduction in the number inside the 70-m isobath (Figs. 13, 14). These reductions, associated with both the offshore Ekman transport and reversal of the along-shelf flow, are the greatest monthly reductions during all the simulations, further illustrating the sensitivity to the timing of adverse wind events (relative to

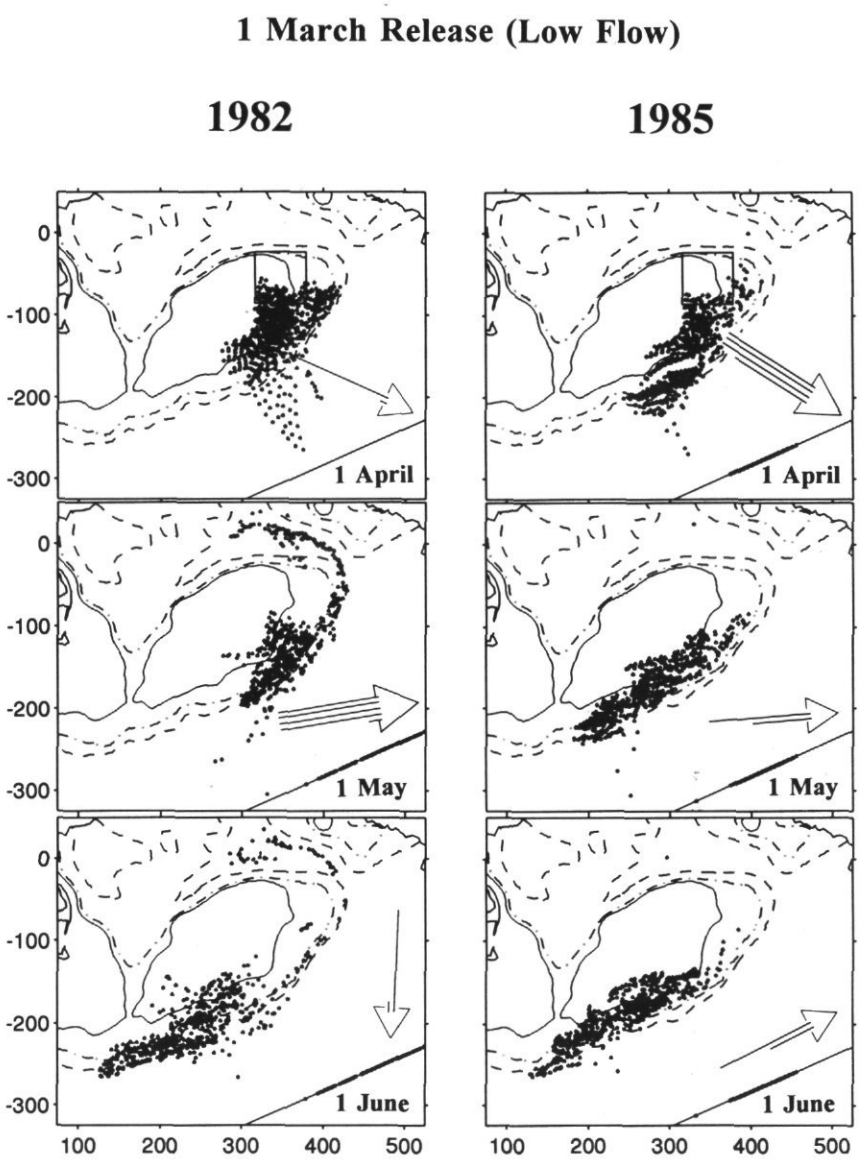


Figure 12. Monthly particle locations, from 1 April to 1 June, for the 1 March 1982 and 1985 releases in the low through-flow field. Format is the same as for Figure 10.

release/spawning time). There are similar but significantly weaker reductions in April and May of 1985, associated with the weaker along-shelf windstress towards the east and eastnortheast. The increase in the number of particles on the Bank on 1 June 1982 is influenced by the May flow field over the shelf break and hence is probably sensitive to the absence of the baroclinic flow component.

Discussion

In all cases considered, significant numbers of particles remained on the Bank at the end of each month, suggesting that there is high potential for some larvae to remain on the Bank under a wide range of flow conditions. However, particles in the upper 10–20 m were generally lost eventually, either to the deep ocean or to

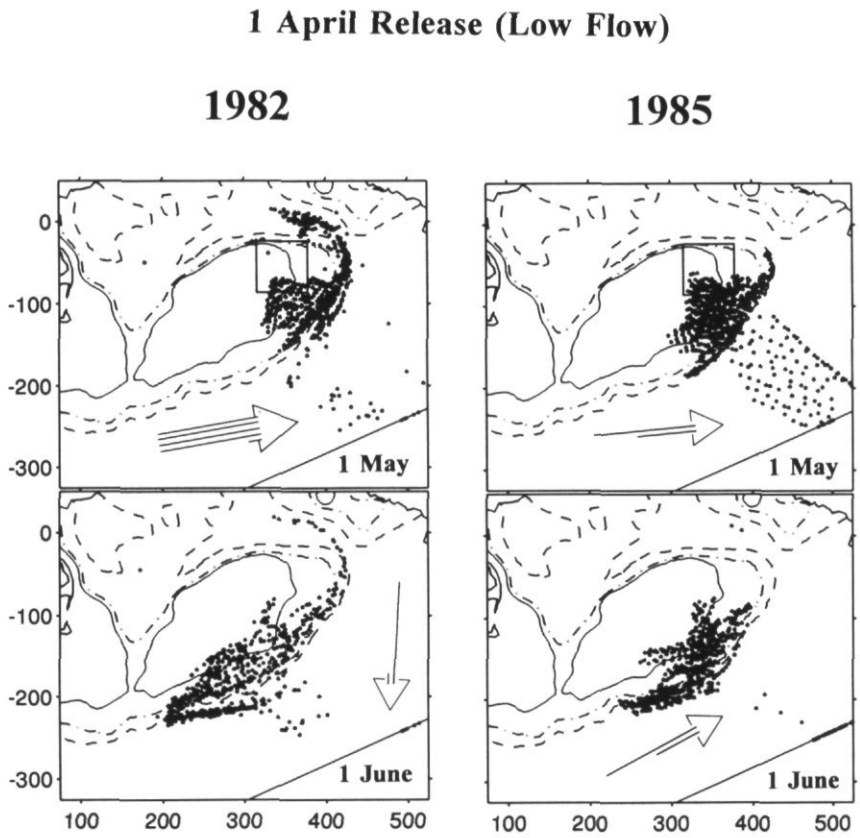


Figure 13. Monthly particle locations, from 1 May to 1 June, for the 1 April 1982 and 1985 releases in the low through-flow field. Format is the same as for Figure 10.

the Southern New England Shelf. In contrast, particles released at 40 m or 50 m were generally advected (southwestward) along the southern flank more slowly and had the greatest potential for retention via recirculation in Great South Channel. These findings for 1982 and 1985 are consistent with Werner *et al.*'s (1993) seasonal-mean results that suggested the existence of a "two-layer system" on Georges Bank during winter and spring, with greater losses from the Bank for particles (larvae) in the surface layers (<25 m) and greater retention of particles (larvae) in deeper layers (>25 m). A related result is that particles released most shoalward are the most likely to be retained (recirculate).

The different model simulations elucidate the mechanisms through which windstress and through-flow affect the retention of particles on Georges Bank, and support an important contribution from the April 1982 windstress to the higher loss rates in the MARMAP observations. The windstress contributes to particle displacements from the Bank most directly through transport in the surface Ekman layer, but also through the large-scale pressure response (and associated bottom Ekman layers) and vertical mixing. Since the net Ekman transport is directed to the right of the windstress direction, offshore losses of near-surface particles on the southern flank of Georges Bank are generally largest for windstresses with a large component directed alongshelf to the northeast. Offshore Ekman transport was the major contributor to particle loss from the Bank in April 1982, which was the month with the greatest northeastward windstress during years considered. In contrast, for cross-shelf windstress, the net Ekman transport is directed along-shelf and is generally less significant to particle retention on the southern flank (except in the Great South Channel region). However, cross-shelf stress does result in offshore Ekman flow at some depths, as well as downwelling from the Ekman layer over the shelf break, which can be very important to particle retention on the shelf (Werner *et al.*, 1993).

Other mechanisms through which windstress influences particle displacements on Georges Bank are the barotropic flow component associated with the regional

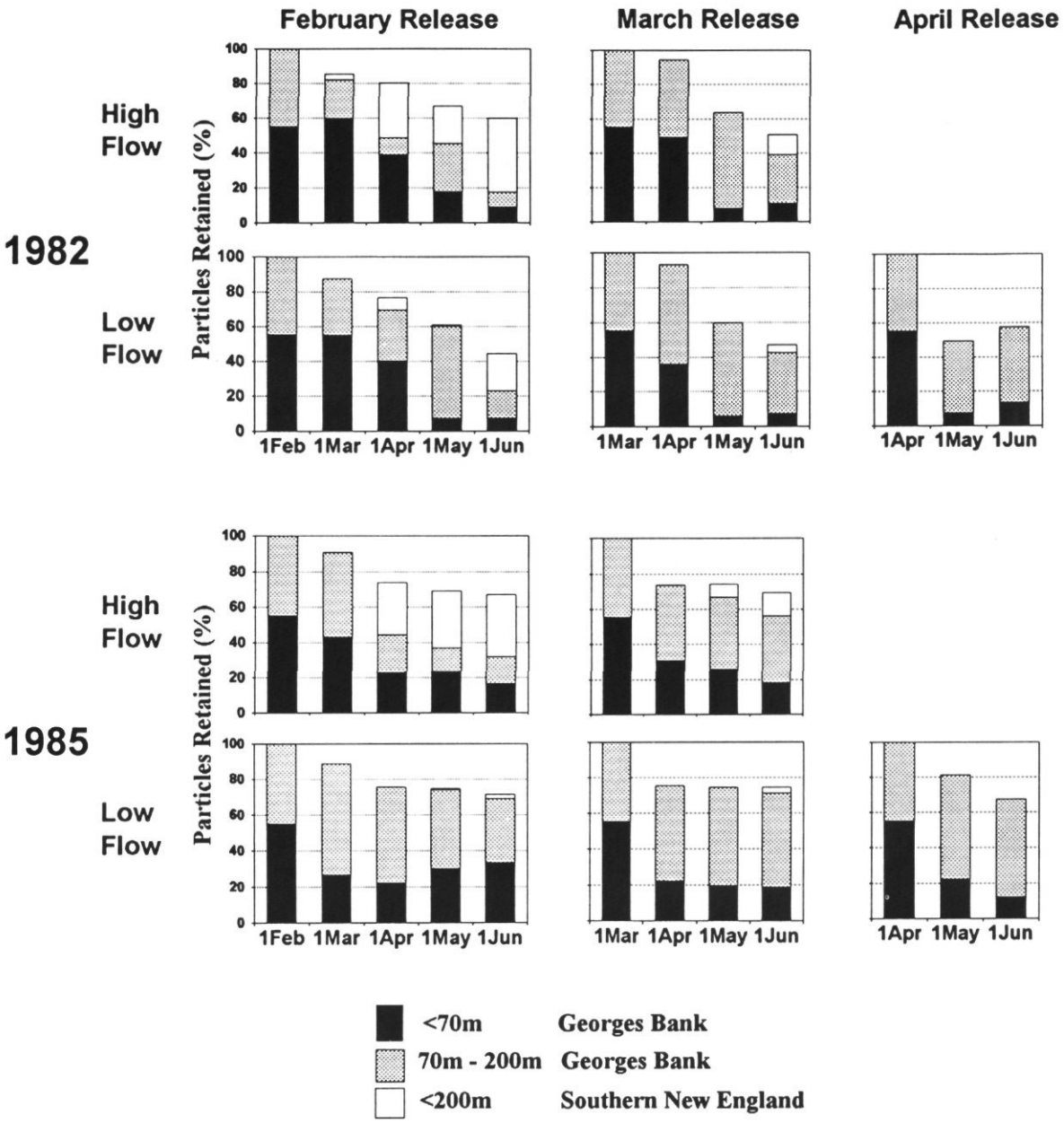


Figure 14. Monthly percentage of particles located in three subareas (Georges Bank <70 m and 70–200 m, Southern New England Shelf <200 m) for the 1982 and 1985 February, March, and April releases in high and low through-flow fields.

pressure-field response, the related bottom Ekman layer transport, and windspeed contributions to the vertical eddy viscosity and hence the Ekman layers' vertical structure. In the present simulations, the most important of these mechanisms is the barotropic flow field which, as shown in previous studies (e.g., Wright *et al.*, 1986), is generally directed along isobaths with greater magnitude for along-shelf (compared to cross-shelf) windstress. Through this mechanism, the eastnortheastward stress in April 1982 disrupted the southwestward flow on the southern flank and retarded the movement of particles to the Southern New England Shelf, and also displaced deep particles in the Great South Channel onto the central Bank. Significant barotropic-flow influ-

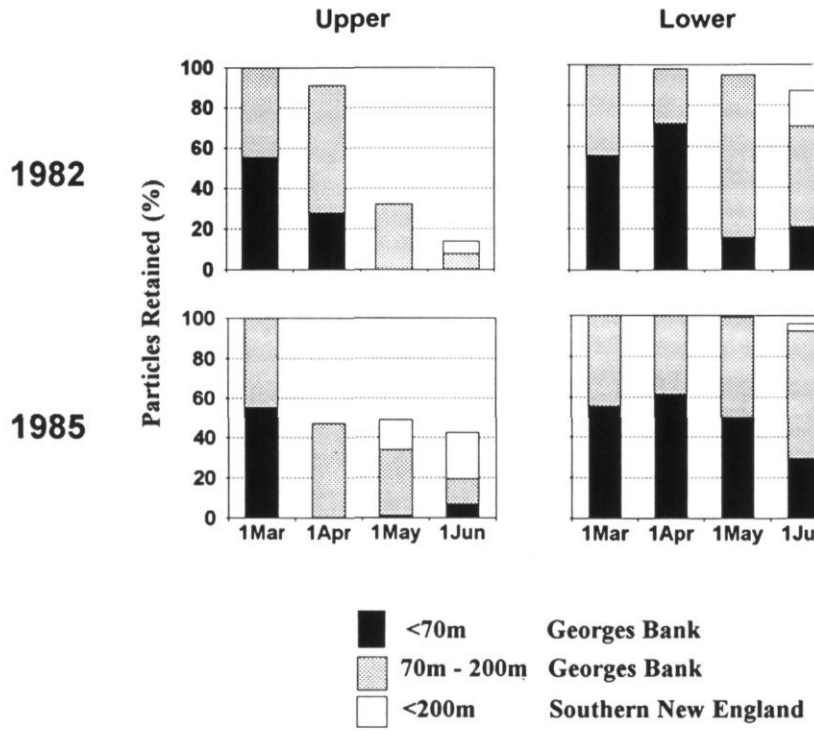


Figure 15. Monthly percentage of particles located in three subareas (Georges Bank <70 m and 70–200 m, Southern New England Shelf <200 m) for the 1982 and 1985 March releases in the upper (1, 10, 20 m) and lower (30, 40, 50 m) parts of the water column in the high through-flow field.

ences from along-shelf stress also occurred in February–May of 1985, with the influence in all cases being reduced advective losses to the Southern New England Shelf. While the barotropic flow response to cross-shelf windstress is weaker, the influence can be significant; for example, in February 1982, above-average cross-shelf stress contributes to increased along-shelf particle movement towards the Southern New England Shelf.

While along-shelf windstress towards the northeast is unfavourable to particle retention in the surface Ekman layer on the southern flank of Georges Bank, the on-bank flow in the bottom Ekman layer (e.g. April 1982 in Fig. 7) contributes favourably to particle retention on the Bank. The importance of this mechanism is related to the strength (and direction) of the barotropic current, and hence primarily to the along-shelf component of windstress. Another mechanism for wind influences is windspeed contributions to the vertical eddy viscosity magnitude, and hence the Ekman layer thicknesses. This influence is relatively small in the present solutions (e.g., compare April panels of Figs. 8 and 10) because of the strong tidal currents and the particular viscosity formulation used, although it should be more important with vertically varying eddy viscosity and more sophisticated turbulence closure.

The strength of the through-flow has two influences on particle retention. In the absence of wind influences, increased through-flow generally leads to greater particle movements towards the Southern New England Shelf and reduced recirculation in the underlying tidal residual circulation. However, in more realistic situations with significant windstress, the primary influence of the through-flow is on the transit time of particles from the Northeast Peak to the Great South Channel, and hence on their vulnerability to cross-shelf displacement in the wind-driven Ekman layers. In the upper water column, faster through-flow can lead to increased retention through reduced exposure to the generally unfavourable Ekman transport, while in the bottom Ekman layer, faster through-flow can be unfavourable since the wind-driven bottom Ekman layer flow is generally on-bank for the prevailing winter–spring wind directions. This interdependence of the wind and through-flow influences also involves the relative timing of wind and through-flow variations, with respect to both each other and particle release times (i.e., spawning time), since influences can vary with particle positions (e.g., southern flank vs Great South Channel).

Overall, the results provide support for a significant adverse influence of the strong eastnortheastward winds

in April 1982 on the retention of larvae on Georges Bank. The number of particles remaining inside the 70-m isobath at the end of April was lower in 1982 than in 1985 for all cases (different through-flows and release dates), which is consistent with the high loss rate between the egg and larval stages from survey 35 to 36 (Table 6). In view of our previous findings that the recirculation in Great South Channel has a critical separation line near the 70-m isobath on the southern flank (Werner *et al.*, 1993; Ridderinkhof and Loder, 1994), it can be concluded that the different windstresses resulted in a lower potential for larval occurrence and retention on the central Bank in 1982, for spawning prior to early April. This is consistent with the observed egg and larval abundances and distributions in 1982 and 1985, which indicated higher losses in 1982.

However, the model results also point to complexities and areas requiring further investigation. While the strong eastnortheastward windstress in April 1982 was adverse to larval retention on the whole, it "flushed" the Bank in the surface layers only and the resulting circulation had features which were favourable to retention for some locations (on-bank flow at depth on the southern flank and in the Great South Channel). For example, the number of particles remaining on the Bank inside the 200-m isobath at the end of April in the 1 February releases was not much lower in 1982 than in 1985, with many particles remaining between the 70- and 200-m isobaths. While such particles should have a lower probability of eventual retention on the Bank, they probably should not be regarded as lost in a recruitment sense. Secondly, the number of particles retained inside both the 70- and 200-m isobaths had some sensitivity to the uncertain through-flow, pointing to the need for further information on this flow component. Thirdly, the May results in general are probably less reliable because of the neglect of baroclinic flow and absence of additional through-flow. These issues point to the need for various improvements in the model flow fields (baroclinicity, interannual through-flow variations, temporal resolution of wind forcing) as well as consideration of other MARMAP years such as those with current measurements. In addition, detailed analyses of existing data (Noble *et al.*, 1985) suggest strong directional, frequency, seasonal, and vertical dependences in the wind-current coupling on the southern flank, pointing to the need for careful interpretation of model predictions.

The model simulations suggest that variability in the wind strength and direction contributed to the variable retention of eggs and larvae on Georges Bank in 1982 and 1985. However, other physical mechanisms also may have contributed, such as the position of the shelf/slope front and the influences of warm-core rings. Cohen *et al.* (1986) examined the possible factors responsible for recruitment of the 1981, 1982, and 1983 year classes of haddock on Georges Bank, documenting the passage of an intense storm during 6–9 April 1983 with windspeeds of 34–64 knots. The normal southwestward current on the outer southern flank abruptly changed to southeastward for a period of three days with an implied displacement of about 40 km offshore at 5 m below the surface. While this storm was a major contributor to the anomalous monthly-mean windstress used in the model for April 1982, its influence is probably not fully represented. It is possible that additional eggs and larvae of cod residing in the surface water are advected off Georges Bank and lost during such brief and intense storms. While many biological and physical factors contribute to recruitment variability in nature, and make comprehensive modelling difficult, the present study illustrates how three-dimensional numerical circulation models can be used to understand the potential role of selected environmental factors.

Acknowledgments

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Modelling the transport of cod larvae from the Lofoten area

Bjørn Ådlandsvik and Svein Sundby

Ådlandsvik, B., and Sundby, S. 1994. Modelling the transport of cod larvae from the Lofoten area. – ICES mar. Sci. Symp., 198: 379–392.

Arcto-Norwegian larval and juvenile cod have five months of pelagic drift with the currents from the spawning areas at the Norwegian coast to the nursery grounds in the Barents Sea. During this period they are advected 600–1200 km. The year-class strength is largely determined during this period, and we suggest that the transport processes influence recruitment both directly (advectional loss of larvae) and indirectly through temperature and predator–prey interactions. A three-dimensional baroclinic hydrodynamic model is implemented for parts of the Norwegian and Barents seas. Currents from this model are fed into a Lagrangian particle tracking model to simulate the transport of eggs/larvae/juveniles of Arcto-Norwegian cod. Sensitivity studies have been carried out to determine the parameters that are important to this model transport. The model results are then validated against observed distributions of early juvenile and 0-group cod; in particular, the interannual variations in distribution and abundance are compared with interannual variations in wind-induced transport processes.

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Introduction

Compared with other Atlantic cod stocks the Arcto-Norwegian cod has a long route of pelagic drift of 600–1200 km from the spawning area to the area where the juveniles settle to the bottom. Spawning occurs in March and April along the coast off mid and North Norway, and mainly in Lofoten (Ellertsen *et al.*, 1989). The eggs and larvae are carried towards the northeast by the Norwegian Coastal Current. Lateral spreading takes parts of the population into the Atlantic Current, which flows parallel to the Coastal Current. Three months after spawning, the early juveniles are found in the southwestern Barents Sea, and particularly in high concentrations above the bank Tromsøflaket (Bjørke and Sundby, 1987). Five months after spawning they are surveyed pelagically by the international 0-group survey. They are then spread out in the entire Atlantic watermasses of the Barents Sea and partly above the narrow shelf region off the coast of West Spitsbergen (ICES, 1977–1986). After this stage they settle to the bottom and become more stationary.

It is during this period of life, and particularly during the first three months (Sundby *et al.*, 1989) that the year classes of cod are generally determined, although changes in the ecosystem conditions in some years may alter this general feature because of anomalous mortality at ages 1 and 2 (Mehl, 1989; Ulltang, 1993). Consequently, pelagic drift along the coast of Norway is a critical temporal/spatial window for cod recruitment. How does advection and spreading influence recruitment directly? How does the transport interact with biological and biophysical processes? Larval loss by advection out of the natural habitat, which is considered an important process for Northwest Atlantic cod stocks (Werner *et al.*, 1993), could also influence recruitment of the Arcto-Norwegian cod. Occasionally, cohorts of juveniles have been observed far off the shelf into the Norwegian Sea in regions where retroflection back to the shelf areas is unlikely. There is also interannual variation in the distribution of the pelagic juveniles within the Barents Sea. Some years have a typical western distribution while others have an eastern distribution. It is not known at present how these distributional features are influenced by transport directly and how they are influenced by spatially dependent growth and mortality. It has been shown that the pelagic juveniles are generally larger in the western area of distribution (Bjørke and Sundby, 1987; Helle, 1994) although they are approximately the same age (Suthers and Sundby, 1993).

During the last few years numerical models have been introduced as a tool in the study of fish larvae transport. In the North Sea, this has been done for herring (Bartsch *et al.*, 1989), sprat (Bartsch and Knust, 1994), and sandeel (Berntsen *et al.*, 1994). For cod it has been studied by Werner *et al.* (1993) at Georges Bank. The present paper is a first approach to the use of such

techniques for studying the recruitment problems in the Arcto-Norwegian cod stock.

The model system

The hydrodynamic model

The hydrodynamic model used is the well-known Princeton Ocean Model developed by Blumberg and Mellor (1987). It applies the primitive equations and is discretised by finite differences. A bottom-following "σ-coordinate" system is used in the vertical. Horizontally, the numerics are done by central time and space differences ("leapfrog"). For the vertical mixing, a level $2\frac{1}{2}$ Mellor–Yamada turbulence closure scheme is used. Some modifications to the model have been done at the Norwegian Meteorological Institute and at the Institute of Marine Research. Most important is the use of the Flow Relaxation Scheme (FRS) as an open boundary condition. This technique has been described by Martinsen and Engedahl (1987).

In this study the model is driven by density gradients and wind forcing. Tidal forcing is not included. The model is run in a *diagnostic mode*, which means that the initial salinity and temperature fields are kept constant in time. The model domain with bottom topography is shown in Figure 1. The rectangular frame surrounds the subarea used in most of the plots. Horizontally, the grid consists of 80 × 60 cells with a grid size of 20 km. In the vertical, 9 σ-levels have been used.

The transport model

The transport processes are modelled by a simple Lagrangian particle tracking model. A more comprehensive description of this model will be given in Ådlandsvik (1994). It is driven by the stored current velocity fields from the hydrodynamic model. These fields are interpolated in time to the internal time step of the transport model, and used to move the particles to their next position in a "Euler forward" way. Spatial variability in the current field leads to a spreading of the particles. Smaller-scale current variability is not resolved by the hydrodynamic model. The spreading on this scale is parameterized by random walk diffusion, where each particle is given an individual axi-symmetric Gaussian random velocity every time step. Cod larvae can adjust their vertical position by swimming. No biological assumptions about this vertical behaviour are used, instead the particles are simply kept at a fixed depth.

The presence of land complicates these kinds of transport model. The coast is very crudely represented. The Norwegian coast has a lot of islands and narrow fjords, not resolved by the model grid, where particles may be trapped and perhaps released to the open sea at a later time. In the model this is parameterized in a very simple way; the velocity on land is zero. Thus particles may be advected or diffused in and out of land cells, but the advection is zero if the particle is more than half a grid cell from the sea. Particles on land are considered

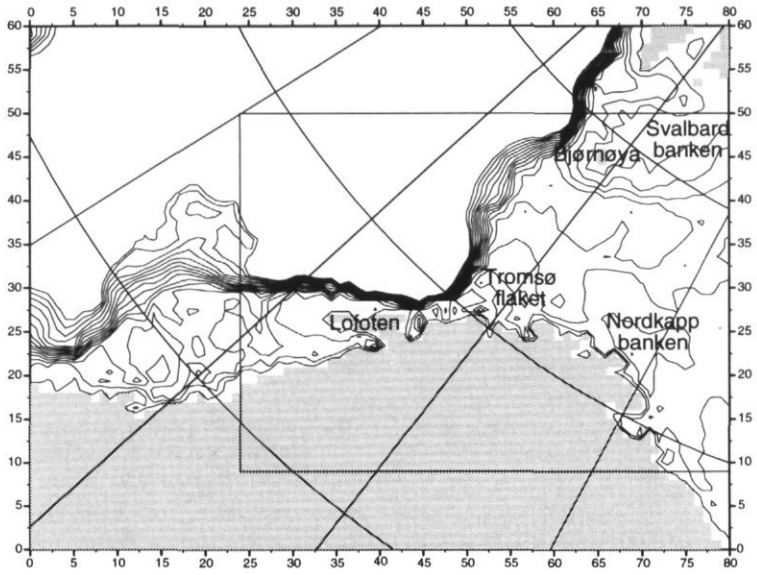


Figure 1. The model domain. Isobaths are drawn every 100 m down to 1500 m. Also indicated is the subdomain used to display the model results.

(temporarily) lost and are excluded from most subsequent calculations.

Some postprocessing of the particle data is performed. The moments of the particle are easily calculated. The zeroth moment N_s is just the number of sea particles. The first moment $\vec{\mu}$ is the position of centre of gravity of the sea particles. This position is given in grid coordinates. The second moment is really a second-order tensor, but here only its trace

$$\sigma^2 = \frac{1}{N_s} \sum |\vec{x}_i - \vec{\mu}|^2, \quad (1)$$

is used. The number σ^2 is the mean squared distance from the sea particles to their centre of gravity or simply the *variance*. The unit is m^2. For a pure Fickian diffusion with (eddy) diffusivity K, $\partial\phi/\partial t = K\nabla^2\phi$, we have

$$\frac{d\sigma^2}{dt} = 4K \quad (2)$$

This is explained in Csanady (1973), but see also Ådlandsvik (1994).

At a particular time the set of particle positions may be depicted as a particle cloud (see, e.g., Fig. 3). It is often more useful to have a concentration field instead. Here the concentration fields are computed by summing axi-symmetric bell-shaped functions around each particle. The width of the bell functions is a length scale, the influence radius. For more details see Ådlandsvik (1994). In this paper an influence radius of 4 grid units (80 km) is used. The concentration field in Figure 5 (10 m) is computed in this way from the particle cloud in Figure 3 (90 days). In all concentration plots each contour level is $\sqrt{10}$ times the level below, starting with the outermost level at 0.01 particles per grid square.

Input data

A monthly gridded salinity and temperature climatology for a large area covering the Nordic seas has been compiled from the global climatology of Levitus (1982) and the North Sea climatology of Damm (1989). Along the Norwegian coast for the months of April and May these fields were enhanced by incorporating CTD station data from IMR. This work is described in Martinsen *et al.* (1992) and more detailed in Ottersen and Ådlandsvik (1993).

The initial current and surface elevation are obtained by running the hydrographic model diagnostically for 30 days with no wind forcing on a large model domain covering the Norwegian, Greenland, Iceland, Barents, and North seas. Details of this procedure are given in Martinsen *et al.* (1992). Figure 2 shows this initial current field in 10 m. These fields are also used at the lateral boundaries of the model domain.

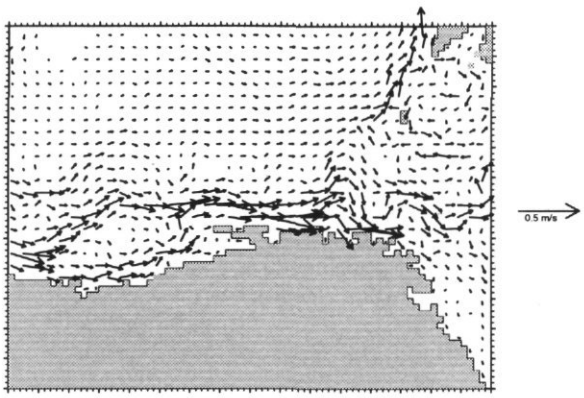


Figure 2. The initial current field at 10 m depth.

The variations in the input come from the meteorological data. Air pressure and wind stress are taken from the Hindcast Archive of DNMI (Eide *et al.*, 1985). These data are given in a 75 km grid every sixth hour.

The standard run

The hydrodynamic model is run throughout the months of April, May, and June, and the current results are stored every sixth hour.

The particles were released in the Lofoten area, as shown in Figure 3. The release grid cells are numbered (34–37, 26), (33–34, 27), and (34–36, 28). The initial particle distribution is given by subdividing each release grid cell into 10 by 10 subsquares with a particle in the centre of each subsquare. This gives 100 particles per release cell, in total 900 particles. The particles were released on 1 April and were transported for 90 days.

Eggs, larvae, and juveniles are found mainly above 50 m depth. At mean wind speeds, 80% of the eggs are found above 20 m (Sundby, 1983). The larvae are concentrated between 5 and 30 m depths (Ellertsen *et al.*, 1984). Here, in the standard run, the particles are kept at a fixed depth of 10 m. The parameters for the standard run are summarized in Table 1.

The time evolution of the particle distribution is shown in Figure 3 and Table 2. The particles are moving northwards from Lofoten and spread out over the southern Barents Sea. They are confined to the shelf, very few penetrate into the deep Norwegian Sea. After 30 days the particles are distributed from Lofoten and northwards. They are slowed down at Tromsøflaket but have penetrated further east close to the coast and northwards along the shelf break. After 60 days the particles are spread over a larger area with highest

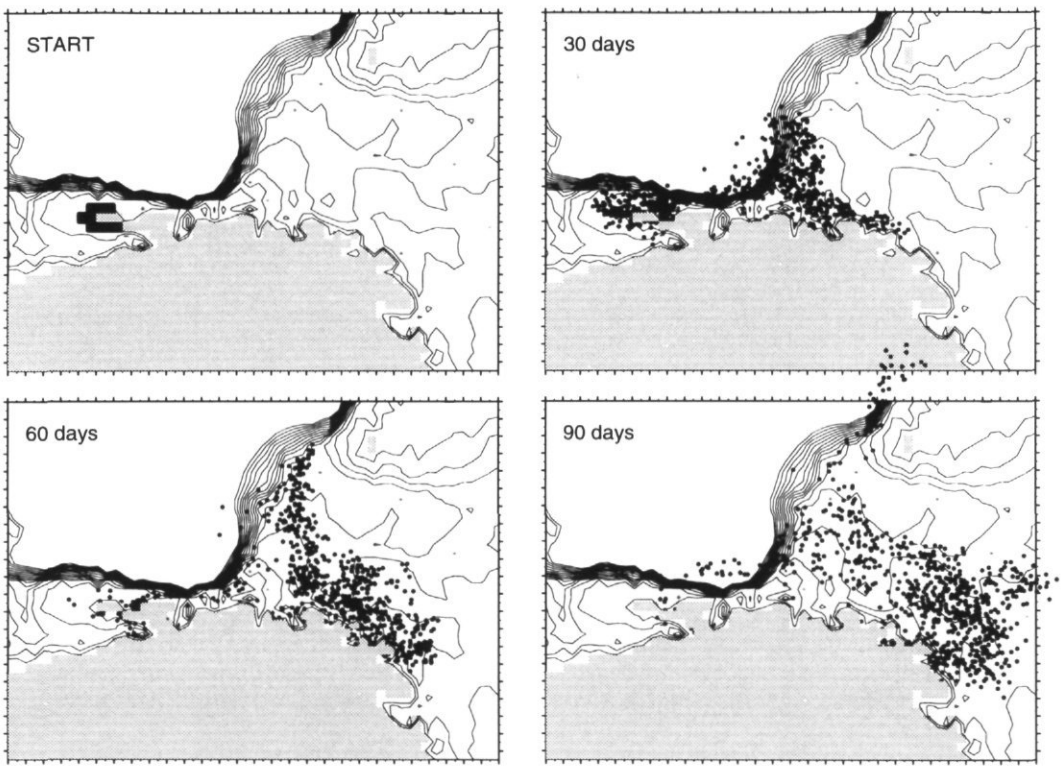


Figure 3. The positions of the particles in the standard run after 0, 30, 60, and 90 days.

concentrations at Nordkappbanken and northeast of Tromsøflaket. After 90 days they are dispersed further and cover a large area of the southern Barents Sea, limited in the north more or less by the 400 m isobath.

Table 1. The parameters used in the standard run.

Start time	1 April 1985
Transport time	90 days
Particle depth	10 m
Internal time step	1 hour
Random walk diffusion coefficient	100 $m^2 s^{-1}$

Table 2. Particle statistics of the standard run. The columns are: time in days, the number of particles at sea, grid coordinates of the centre of gravity, and the variance σ^2.

	N_s	μ_x	μ_y	σ^2 ($10^9 m^2$)
0 days	900	34.4	26.4	1.0
30 days	830	46.0	29.2	36.2
60 days	766	59.8	28.8	43.2
90 days	796	66.9	28.7	48.6

The highest concentration is still over Nordkappbanken. Some particles at the shelf break northwest of Bjørnøya are heading for the west coast of Spitsbergen.

The time series of σ^2 is given in Figure 4. During the first 25 days the variance increases rapidly. After this period the variance increases more slowly. This happens because the fastest moving particles are slowed down at Tromsøflaket and the slower ones are catching up.

Sensitivity studies

Before drawing conclusions from model results it is important to examine the sensitivity of these results to changes in various model parameters. In this section some results from such sensitivity studies of the transport model are presented. Further studies and more details will be presented in a technical report (Ådlandsvik, 1994).

Particle depth

To study the effect of different depths along the Norwegian coast, particles were released at 10, 20, 30, and 50 m depths with the other parameters at their standard rate.

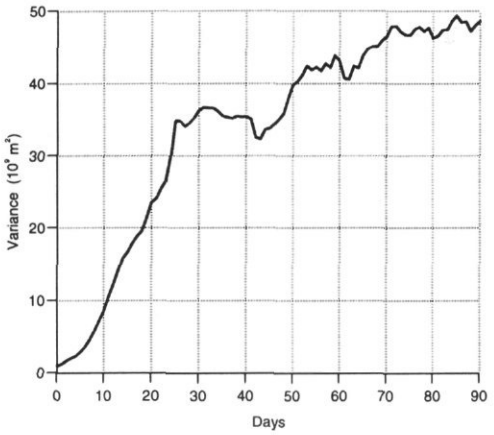


Figure 4. The time evolution of variance (σ^2) in the standard run.

The results after 90 days are shown in Figure 5. The main features are similar, with the largest concentration at Nordkappbanken. The position of the centre of gravity is nearly fixed, as shown in Table 3.

From Figure 5 and also from Table 3 it can be seen that the 10 m distribution is the most dispersed. The 10 m field, in particular, has a larger component west of Bjørnøya. The 30 m distribution is unique in that very few sea particles are left in the Lofoten area. This shows up in Table 3 as the low value of σ^2. The 20 and 50 m distributions are very similar, the exception is that the particles west of Bjørnøya are missing in the 50-m field.

Table 3. Particle statistics after 90 days with particles at different depths.

	N_s	μ_x	μ_y	σ^2 (10^9m^2)
10 m	796	66.9	28.7	48.6
20 m	822	69.8	26.1	25.5
30 m	856	70.3	26.1	19.1
50 m	838	68.4	26.5	26.7

Experience gained from modelling larval drift in the North Sea (Bartsch and Backhaus, 1987; Berntsen *et al.*, 1994) and early stages of cod and haddock at the Georges Bank (Werner *et al.*, 1993) indicates that depth and vertical behaviour are very important. The results from this test indicate that the depth is less important along the North Norwegian coast. This may be explained by differences in the current conditions. Our

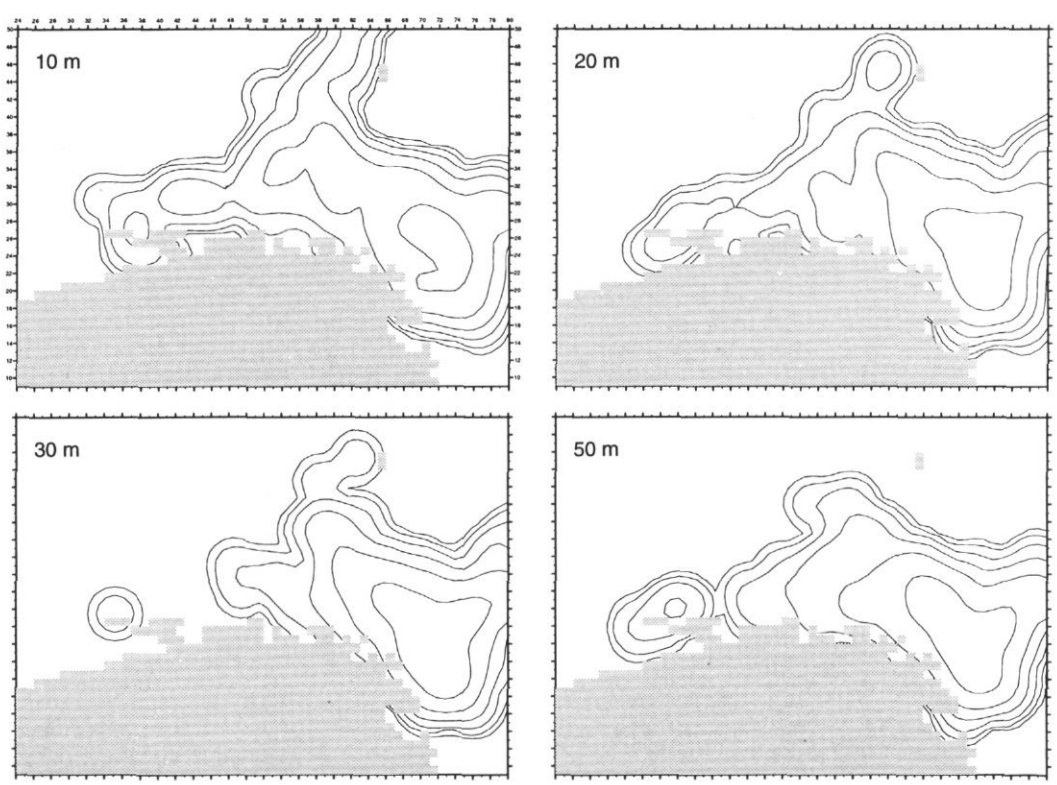


Figure 5. Concentrations derived from the particle distribution after 90 days with the particles at 10, 20, 30, and 50 m depth.

area is dominated by the throughflow of the rather strong and deep Norwegian Atlantic Current. At a time scale of months the main contribution of the vertical variation in the wind-driven current component is to increase dispersion near the surface.

Horizontal diffusion

The random walk is performed by giving the particles an axi-symmetric normally distributed velocity with standard deviation u_σ and moving them a time step Δt. This corresponds to a Fickian diffusion coefficient $K = \frac{1}{2}u_\sigma^2 \Delta t$ (Csanady, 1973; Ådlandsvik, 1994).

Figure 6 and Table 4 show the particle distributions with varying diffusion coefficient K. The other parameters are kept from the standard run. The pictures without friction, $K = 0$, and with friction, $K = 10\ m^2\ s^{-1}$, are similar. With $K = 100\ m^2\ s^{-1}$, the standard run, the particles are clearly more spread out, but the area covered is more or less the same. With $K = 1000\ m^2\ s^{-1}$ the diffusion dominates the picture. The particles are spread out over the southern Barents Sea, but also out in the deep Norwegian Sea. However, even in this case the transport direction is northwards.

Table 4. Particle statistics after 90 days with varying diffusivity.

K ($m^2\ s^{-1}$)	N_s	μ_x	μ_y	σ^2 ($10^9 m^2$)
0	791	70.0	25.7	21.4
10	797	69.4	26.2	31.0
100	796	66.9	28.7	48.6
1000	695	60.8	34.0	86.6

The time series of σ^2 is shown in Figure 7. We can see that diffusion takes time to work. During the first 25 days all the curves are similar. The $K = 0$ and the $K = 10\ m^2\ s^{-1}$ series are very similar also after this time, both showing a concentration of the particles. The higher diffusion in the standard run causes the particles to disperse slightly during the last 60 days. The $K = 1000\ m^2\ s^{-1}$ case does not show any concentrating effects and continues a near linear dispersion.

This shows that the level of diffusivity applied is very important for the distribution. The total dispersion

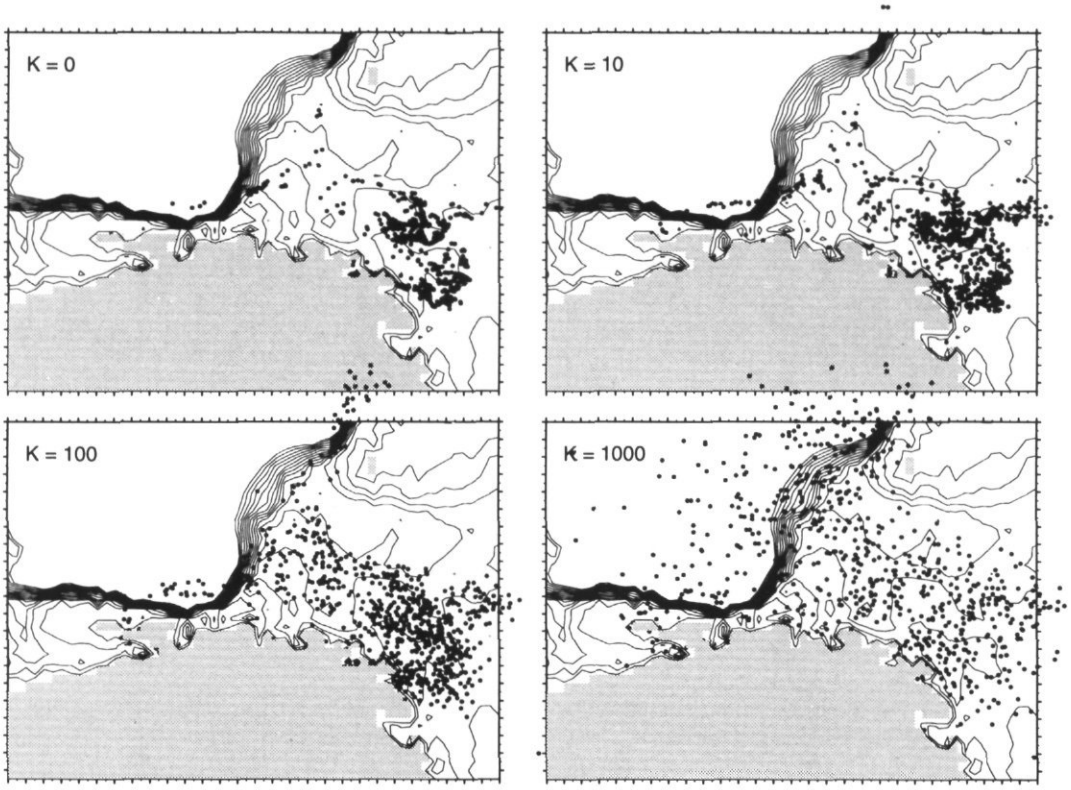


Figure 6. Particle distributions after 90 days simulation with horizontal eddy diffusivity coefficient, K = 0, 10, 100, and 1000 $m^2\ s^{-1}$.

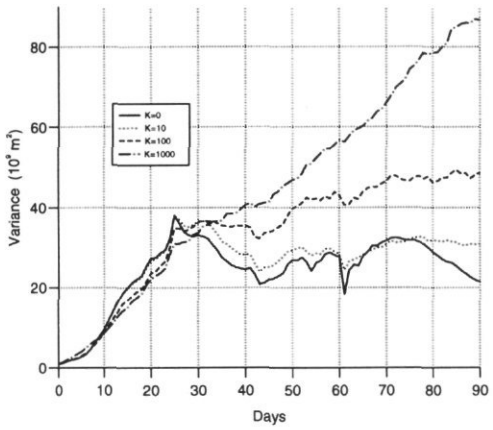


Figure 7. Time evolution of variance with different horizontal eddy diffusivity.

depends on both the spatial variability of the current field and on the constant random walk diffusion. In our case, the extra diffusion from $K = 10\ m^2\ s^{-1}$ is negligible. With $K = 1000\ m^2\ s^{-1}$ there is too much dispersion compared with the real distributions of early juvenile and 0-group cod (Figs. 11, 12).

Dependence on spawning time and area

The particle distribution depends on the release time and area. The purpose here is to examine the strength of this dependence for small disturbances. Case (a) is the standard run. In case (b) the simulations starts on 27 March 1985, 5 days earlier than the standard run. For case (c) the particles outside Lofoten were moved inside. More precisely, the 900 particles were released with 100 in grid cell (33, 27) and 200 in each of the grid cells (34–37, 26). In test (d) the subdivision of the release grid cells was turned off, and all particles were released in the centre of their grid cell using the same grid cells as the standard run.

The results after 90 days are shown in Figure 8. These concentrations are similar. This is also confirmed by the particle statistics in Table 5. The time series of σ^2 (Fig. 9) shows that the results differ more at an earlier stage. In case (b), after about 20 days the curve is close to the standard series (a), but with a time shift of 5 days. In case (c), with simulated spawning confined to inside Lofoten, the curve levels off at the same time (25 days), but at a lower level than the standard run. From 45 days the variance starts to increase rapidly and catches up with the standard run. The smallest perturbation (d) remains close to the standard run all the time.

It seems that finer details of spawning location and time are not important at our time and space scale in this area. This may be caused by the concentrating effects of the bank Tromsøflaket.

Table 5. Particle statistics after 90 days with various release time (b) and locations (c), (d).

Case	N_s	μ_x	μ_y	σ^2 (10^9m^2)
(a)	796	66.9	28.7	48.6
(b)	751	64.9	28.7	50.2
(c)	776	64.8	28.7	46.0
(d)	788	67.3	28.5	48.9

A test run was also performed with simulated spawning further south, off the Møre coast. Because of poor simulation of the Norwegian Coastal Current in this part of the domain and artifacts of the land treatment, the particles became stranded and did not participate in the large-scale transport process.

Interannual variations

As shown below, there are large interannual variations in the early juvenile and 0-group distributions. One possible explanation is the different meteorological conditions from year to year. A preliminary study with a simple wind-driven model (Ådlandsvik, 1989) gave some indications that easterly distributions are more common in years when low air pressure caused increased Atlantic inflow to the Barents Sea.

To study the effect of different windfields, the model was run for 10 years from 1977 to 1986. The only difference between the model runs is the windfield, the other parameters were taken from the standard run. Figure 10 shows the results after 90 days and the statistics of the distributions are given in Table 6.

Some main features are similar for all these years. The particles are transported northwards and spread out in the southern Barents Sea. Peak concentrations are

Table 6. Particle statistics after 90 days simulation for the years 1977–1986.

	N_s	μ_x	μ_y	σ^2 (10^9m^2)
1977	534	64.3	24.0	61.8
1978	709	66.2	25.8	65.7
1979	775	67.6	27.5	97.7
1980	651	54.7	26.7	75.8
1981	814	58.1	28.9	37.8
1982	704	55.7	28.5	57.0
1983	615	62.8	25.5	137.1
1984	457	50.6	26.2	66.7
1985	796	66.9	28.7	48.6
1986	736	69.2	26.6	76.5

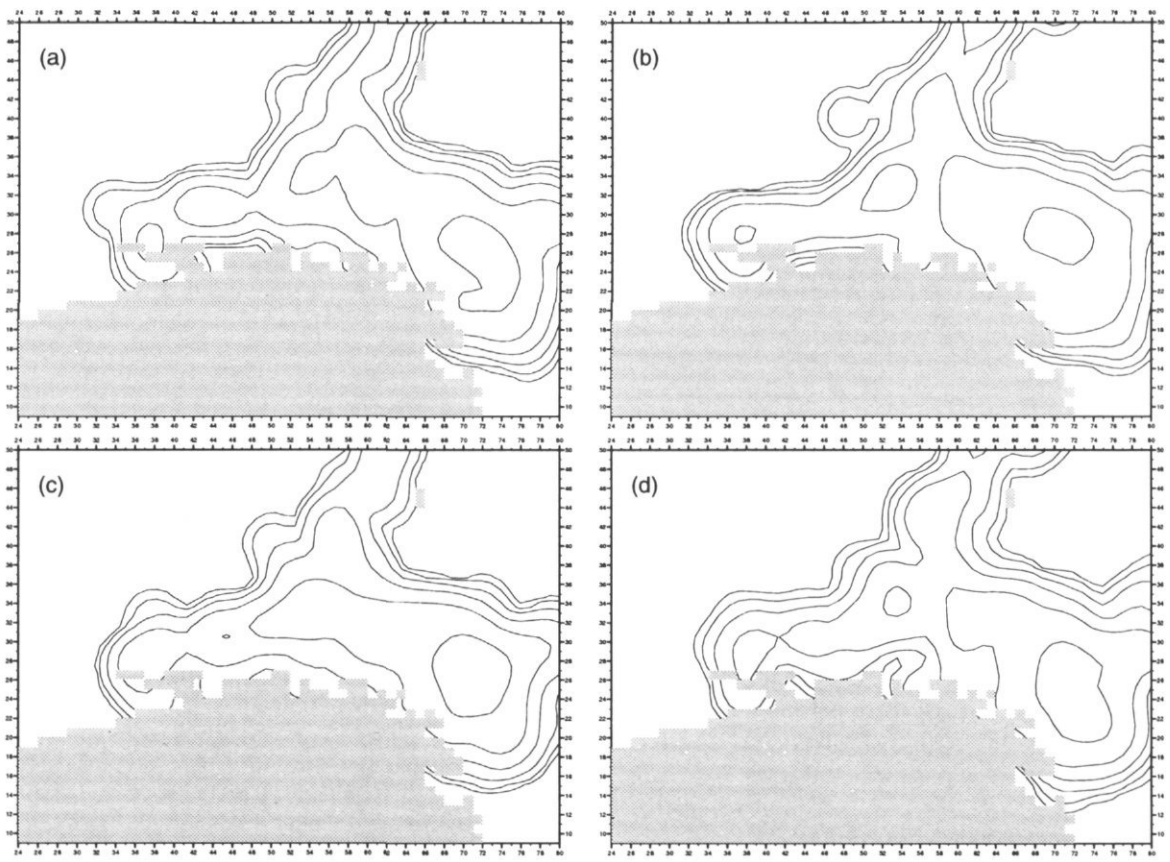


Figure 8. Derived concentrations after 90 days' simulation. Case (a) is the standard run; in case (b) the particles were released 5 days earlier; in case (c) all particles were released inside Lofoten; and in case (d) all particles were released in the centre of their grid cell.

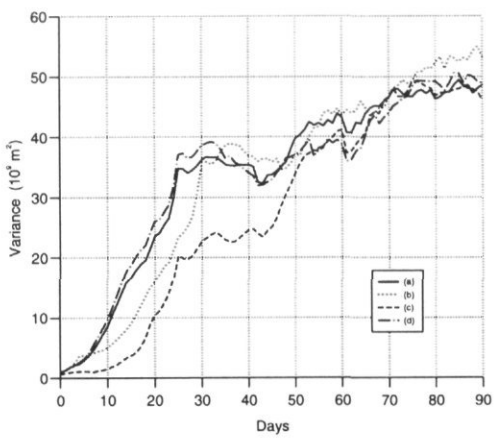


Figure 9. Time evolution of variance with various release time (b) and area (c), (d).

found at Nordkappbanken. In most of the years there is a local maximum at Tromsøflaket. During all these years no particles were found at Svalbardbanken. A third maximum is in the Lofoten area, possibly an artifact of the land treatment in the model. None of the years gave high concentrations in the Norwegian Sea.

The interannual differences are quite pronounced, however. They cannot be read directly from Table 6 because these numbers are greatly affected by the Lofoten component. Some of the years (1980, 1981, 1982, 1984) have a westerly distribution, others (1977, 1979, 1982, 1985) have a large component west of Bjørnøya, in some years (1978, 1980, 1981, 1984) the distribution was more concentrated.

Comparison with early juveniles and 0-group survey data

Distribution and abundance based on survey data exist for both early juvenile cod (about 3 months after spawn-

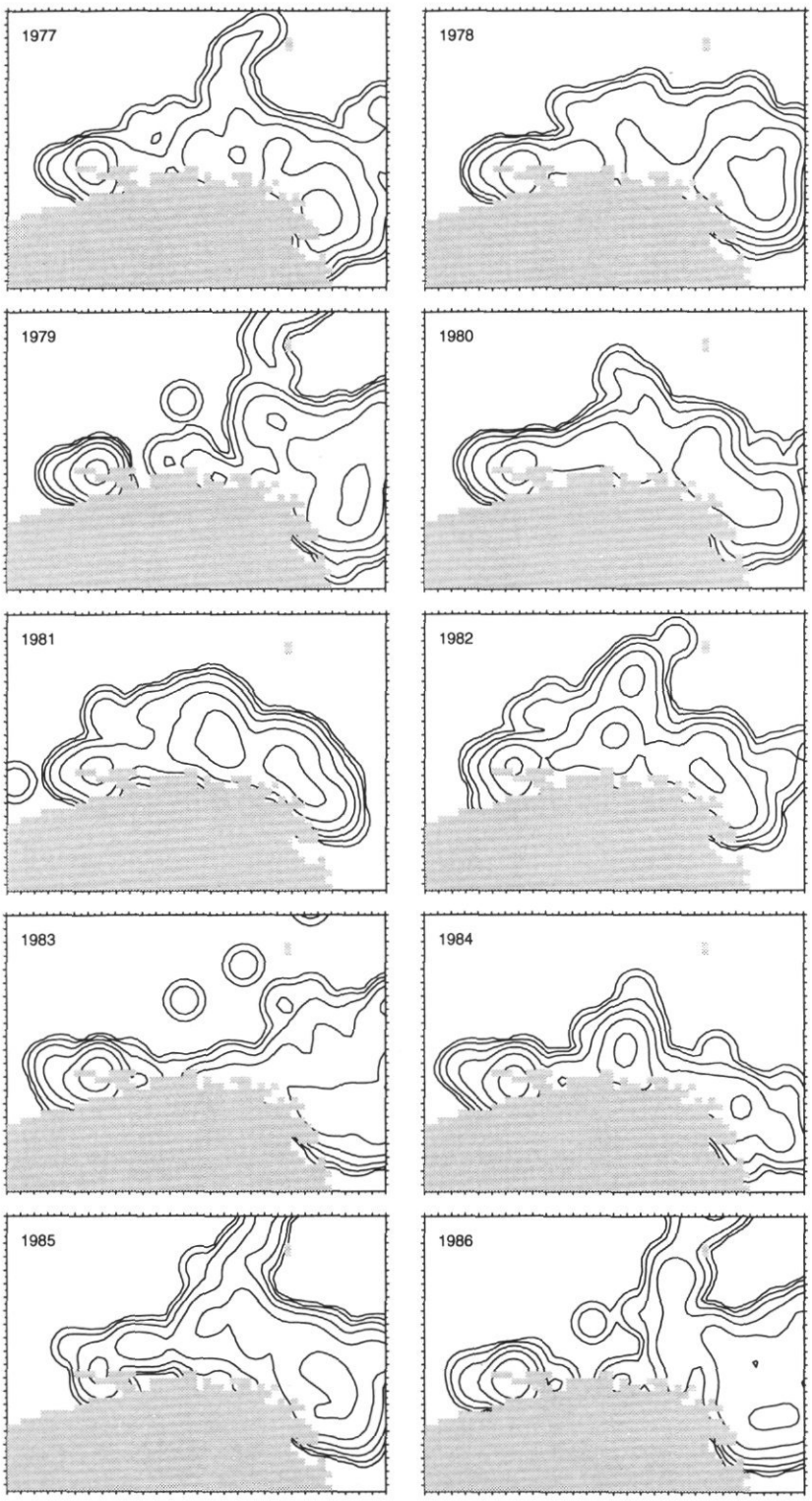


Figure 10. The computed concentrations after 90 days' simulation for the years 1977–1986.

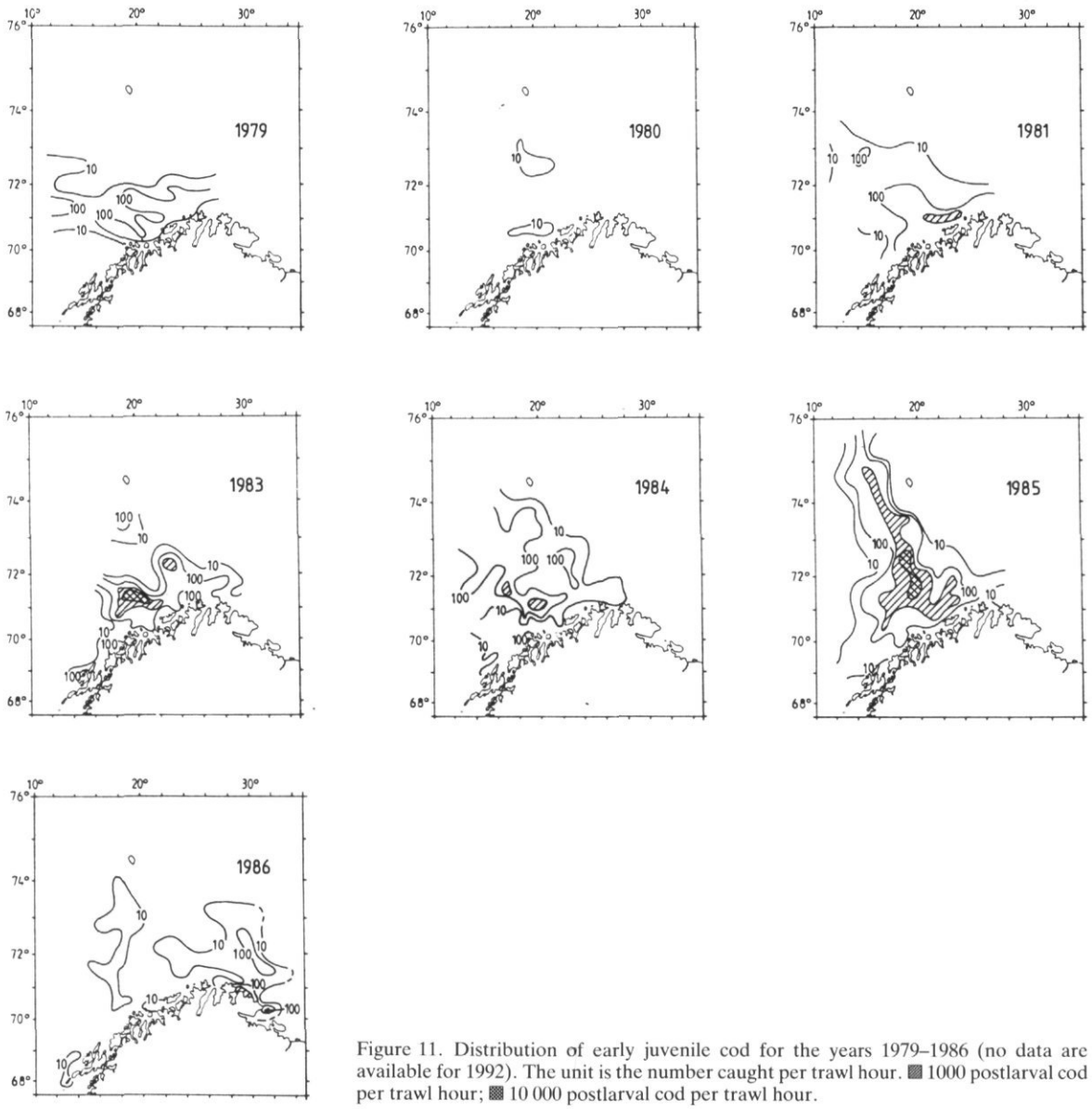


Figure 11. Distribution of early juvenile cod for the years 1979–1986 (no data are available for 1992). The unit is the number caught per trawl hour. ▩ 1000 postlarval cod per trawl hour; ▩ 10 000 postlarval cod per trawl hour.

Table 7. Abundance indices of early juveniles and 0-group.

	Early juv.	0-group
1977	—	0.49
1978	—	0.22
1979	7.2	0.40
1980	0.4	0.13
1981	15.4	0.10
1982	—	0.59
1983	74.7	1.69
1984	23.5	1.55
1985	56.5	2.46
1986	—	1.37

ing) and 0-group cod (about 5 months after spawning) for the present test period. Both surveys are based on sampling with a midwater trawl with 29 × 29 m opening hauled at three depths covering the upper 60 m (see Bjørke and Sundby (1987) for further details).

Table 7 gives abundance indices for the two surveys. The early juveniles index is a linear index, while the 0-group index is logarithmic. The early juveniles indices are taken from Sundby *et al.* (1989). The 0-group indices are taken from ICES (1989).

Figure 11 shows the distributions of early juveniles as taken from Bjørke and Sundby (1987) and Bjørke *et al.*

(1987) (for the year 1986), and Figure 12 shows the distributions of 0-group cod from the 0-group reports (ICES, 1977–1986); the 0-group abundance and distribution exists for all years, while survey data for early juveniles are not available for 1977, 1978, and 1982. In addition, the abundance index for 1986 was not calculated because the eastern boundary was not covered owing to an extreme distribution.

Since the survey data of the early juveniles and the 0-group cod are only available on maps, the comparison with the model results is limited to qualitative considerations. The aim is to follow up with a more quantitative comparison when the survey results become available in a digitized form.

The four first year classes (1977, 1978, 1979, and 1980) were all weak, while the last four were strong (1983, 1984, 1985, and 1986). The distribution of the early juveniles has a good resolution with isolines at 10, 30, 100, 300, 1000 (and in some years 3000 and 10 000) fish per trawl hour, while the 0-group distributions only have isolines of 1 and 85 fish per nautical mile.

The most predominant general feature of the early juvenile distribution is the high concentrations most years above Tromsøflaket. This occurred for all years except 1986, when the main part of the distribution was extremely easterly. The second most predominant feature is high concentration above Nordkappbanken, an equally large bank to the east of Tromsøflaket.

The various years show features of typical easterly or westerly distribution. Westerly distributions of early juveniles are shown by high concentrations to the west and northwest of Tromsøflaket. During the 0-group survey, such distributions will subsequently give a high fraction of the year class to the west of Spitsbergen, as in 1979, 1984, 1985, and 1986. The model runs do indeed show this feature in 1979, 1985, and 1986, but not in 1984. In 1978 and 1982 the early juveniles surveys are missing, but the 0-group surveys these years both show a westerly distribution. The model distribution corresponds with the 0-group distribution in 1982, but in 1978 the model and 0-group distributions are dissimilar.

In 1979, 1985, and 1986 the survey distributions were easterly as well as westerly. The model runs show this feature in all three years. However, the model runs also show a typical easterly distribution in 1983 that did not show up in the surveys. The 1983 early juveniles survey had the most concentrated distribution of all. More than 90% of the juveniles were found at Tromsøflaket. Considering the high abundance, also the 0-group distribution was fairly concentrated. Of all years, 1986 had the most extreme distribution, clearly split up in an extreme westerly and extreme easterly distribution. The model runs also indicated 1986 as the most extreme regarding easterly and westerly distribution.

Summarizing discussion

The modelled particle distributions are quite robust. Minor fluctuations in depth, release time, and locations do not have significant impact on the distribution. On the other hand, the interannual variations are much larger. This suggests that the *integrated wind history* is more important than the precise timing of smaller-scale events for the model distribution.

Comparison with survey data shows that the model reproduces main features of survey distribution in most of the 10 years. In particular, the model reproduces the extreme distribution in 1986. On the other hand, the 1983 model distribution is entirely different from the survey distributions. While the survey distributions are central to westerly and fairly concentrated, the model run gives an extreme easterly and wide distribution.

From comparison with survey data it is clear that the model transport is too fast in the initial phase along the coast of Northern Norway. The early juveniles survey indicates that it takes at least 80 days for the major part of the population to reach Tromsøflaket, but the model runs indicate about 50 days. The flow features of the Coastal Current along the coast of Northern Norway are dominated by the irregular coastline and a number of troughs and banks. It has been shown that bank-topographic steering of the current concentrates eggs and larvae (Sundby, 1984), and consequently the banks will contribute to a reduction in the transport speed towards the Barents Sea. The model does not resolve these topographic features. Finer resolution in the hydrodynamic model along this part of the coast might be the most important factor for improving the model results.

There is large variation in the extent of the modelled distributions, as indicated in Table 6, but the model runs show that extended distributions occurred in years of both bad (1977, 1979) and good year classes (1985, 1986). A characteristic spatial feature of the Barents Sea juvenile cod is the splitting of the distribution along the two main branches of the Atlantic Current, i.e. along the North Cape Current into the Barents Sea and along the West Spitsbergen Current. The years of extended distributions (1977, 1979, 1985, 1986) are all associated with a branched distribution. This is clear from Table 6 and Figure 10.

The effects of bottom topographic steering on the distribution of eggs, larvae, and early juveniles have been demonstrated in earlier investigations. The smaller coastal banks off Northern Norway are important during the initial advection and spreading of the eggs and larval stages (Sundby, 1984). The larger banks, Tromsøflaket and Nordkappbanken, in the southwestern Barents Sea influence the subsequent transport of the early juveniles

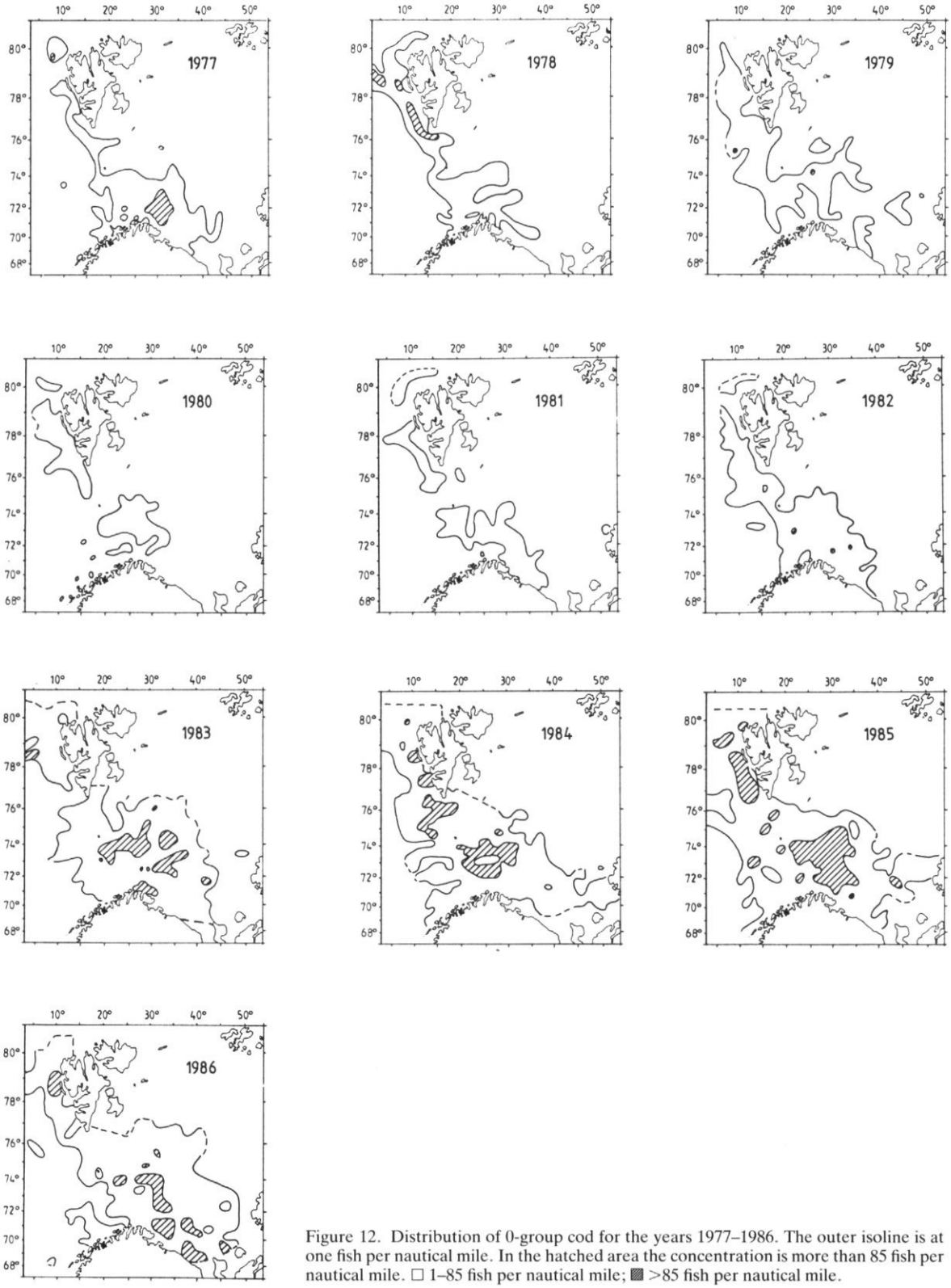


Figure 12. Distribution of 0-group cod for the years 1977–1986. The outer isoline is at one fish per nautical mile. In the hatched area the concentration is more than 85 fish per nautical mile. □ 1–85 fish per nautical mile; ▨ >85 fish per nautical mile.

in July (Bjørke and Sundby, 1984, 1987). The model clearly resolved the bank topographic steering of Tromsøflaket and Nordkappbanken, and the influence on the spreading of the particles was evident: the first arriving particles were retained and the later particles caught up with the first. This gives high concentrations above Tromsøflaket. Bjørke and Sundby (1987) found that 40–90% of the year class was concentrated above Tromsøflaket during the early juveniles survey in July in the period 1979–1985.

During the 0-group survey in August/September there is apparently no sign of the influence of bottom topography. The same is found in the model results, the topographic signal in the distribution decreases with time. With a smaller value of diffusivity the topographic effects are present for a longer time. For both survey and model distributions this is a matter of length scale. The horizontal extent of the distribution increases continuously because of dispersion effects. When the extent exceeds the length scale of the topographic feature, the effects of topographic steering are lost.

Distribution of both early juveniles and 0-group fish indicates that only a small fraction of the year class is lost westwards off the shelf into the Norwegian Sea, but since this area is only occasionally covered by the surveys, this loss cannot be quantified. The model runs also indicate that the loss to the Norwegian Sea is fairly small. However, in the model runs particles are released only at the main spawning area, Lofoten, where about 50–60% of the spawning occurs. Spawning also occurs to the south and to the north of Lofoten. Releases at the southernmost spawning areas along the coast of Møre could give a more westerly distribution, and a larger fraction of the year class into the Norwegian Sea. It should also be mentioned that the model runs to the beginning of July, while the 0-group distributions are surveyed in August/September.

For 1978, 1983, and 1984 the model and survey distributions were dissimilar. There are several possible causes for this discrepancy. As mentioned earlier, the model transport is too fast along the coast from Lofoten to Tromsøflaket. The subsequent transport and spreading from Tromsøflaket therefore starts about a month earlier in the model, under the influence of a possibly quite different wind history.

The present simulations are based on identical egg releases in Lofoten each year. We know that the spawning period is very constant from year to year (Ellertsen *et al.*, 1989), but interannual variations in the spawning pattern, with more spawning remote from Lofoten, could give larger misfits in some years. For example, the importance of the Møre region in mid-Norway as a spawning area has varied throughout this century (Sætersdal and Hylen, 1964). Finally, site-specific survival of the juveniles could completely change the distributional features caused by transport alone. However, the good qualitative agreement between modelled and real distributions in most of these 10 years indicates that the processes that govern survival of the juveniles are quite large-scaled.

Acknowledgments

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Encounter rates between first-feeding cod larvae and their prey during moderate to strong turbulent mixing

Svein Sundby, Bjørnar Ellertsen, and Petter Fossum

Sundby, S., Ellertsen, B., and Fossum, P. 1994. Encounter rates between first-feeding cod larvae and their prey during moderate to strong turbulent mixing. – ICES mar. Sci. Symp., 198: 393–405.

New data on cod larval feeding and prey concentrations were analysed to study the influence of small-scale turbulence on the encounter rate between larvae and their prey. The data were sampled in Lofoten, northern Norway, during the first-feeding period in late April and early May, with plankton pumps sampling over a larger range of wind velocities than for data presented earlier. In addition, the feeding rate of the larvae was investigated in an area of high turbulent energy dissipation rate induced by tidal mixing. The analysis shows that the feeding rate of the cod larvae increases by a factor of about 7 as the wind speed increases from 2 to 10 m s^{-1}. In addition, in the area of strong tidal mixing, with a turbulent energy dissipation rate corresponding to higher levels than induced by a 10 m s^{-1} wind speed, the feeding rate continued to increase. It has been suggested that there could exist an optimal level of turbulence above which a decrease of feeding success will override the increasing contact rate. The present data indicate that such a possible optimal level must be found at higher wind speeds than 10 m s^{-1}.

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Introduction

The influence of turbulence on plankton encounter rates is a biophysical process which substantially alters traditional consideration about energy demands and behaviour of larval fish, and consequently the recruitment processes. Sundby and Fossum (1990) used a combination of "historical" field and laboratory data on larval cod in Lofoten to evaluate the theory by Rothschild and Osborn (1988). The few data available represented a limited range of turbulent conditions, but indicated good agreement with the theory. The encounter rate increased by a factor of 2–3 as the turbulence of the mixed layer increased from conditions corresponding to wind speeds of 2 m s^{-1} to 6 m s^{-1}. Recently, also laboratory experiments support these findings: MacKenzie and Kiørboe (1993) have shown that turbulence corresponding to moderate wind conditions does increase the attack rate for larval cod and herring.

Three major questions arise from the discussion of Sundby and Fossum (1990): (1) The cod larvae were sampled using a plankton net vertically hauled from 50 m to the surface, thus averaging out possible depth-dependent feeding rate. How could depth-dependent turbulence, as outlined by MacKenzie and Leggett (1993), influence the feeding of larvae at different depths? (2) All data were sampled at low wind speeds, below 6 m s^{-1}. Is there an optimum level of turbulence at some higher wind speed above which capture of food declines because the relative motion between predator and prey becomes so great that the predator does not get time enough to attack? Simulations by MacKenzie *et al.* (1994) indicate that optimal turbulence may be found at wind speeds between 10 and 20 m s^{-1}, depending on the parameterization of the reaction time of the cod larvae. (3) The analysis was made on a fairly limited number of larvae from "historical" material. It was felt that more data were needed as supportive evidence.

In order to address these questions a field project was conducted in each of the four years 1989, 1990, 1991, and 1992, during peak abundance of first-feeding cod larvae in Lofoten, northern Norway. The data from 1989, 1991, and 1992 are considered in this paper. The larval concentrations in 1990 were too low for taking out large enough samples for gut content analysis.

Material and methods

Sampling sites

All together, 73 stations at 4 sites in the area of first-feeding cod larvae in Lofoten were sampled and ana-

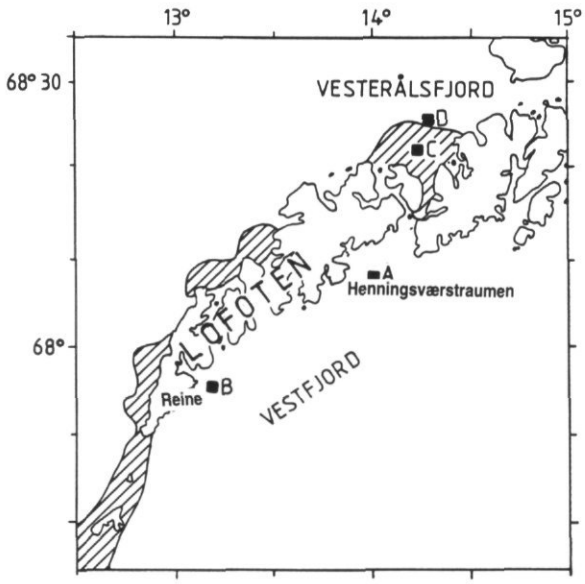


Figure 1. Overview of sampling sites A, B. C, and D (Table 1). Regions of high tidal mixing where the water column is mixed to the bottom are shaded.

lysed (Fig. 1). Most of the stations, 49, were taken within a quasi-stationary gyre at Henningsværstraumen (site A in Fig. 1), a well-known first-feeding area where cod larvae are found at high concentrations (Ellertsen *et al.*, 1990) and the water masses and their biological properties show limited fluctuations. Site B off Reine in Lofoten is located downstream of the core region of first-feeding larvae. The water mass and biological properties are similar to those of site A, but the fluctuations are larger because of the occasional influx of offshore water (Furnes and Sundby, 1981). The environmental properties at sites C and D in Vesterålsfjorden to the north of Lofoten were different from those at sites A and B. In this region cod larvae of older stages usually dominate (Ellertsen *et al.*, 1984). Site C is located in a shallow region of strong tidal mixing. Site D is located to the north of the front outside the tidally mixed shelf water. During sampling at site D the water masses were characterized by low naupliar concentrations and high concentrations of phytoplankton. Table 1 gives the characteristics of the sampling sites.

The ship was always anchored during sampling, and cod larvae, zooplankton, and hydrographical parameters were sampled simultaneously. The stations were taken every third hour throughout the day.

Cod larvae sampling

The larvae were sampled with a modified version of the submersible pump described by Solemdal and Ellertsen (1984). The equipment was made smaller so that it would be handled in rougher weather. Consequently, the pump capacity was also lower: 0.6 $m^3 s^{-1}$ in 1989 and 1991, and 0.7 $m^3 s^{-1}$ in 1992. Sampling depths were 5, 10, 15, 20, 30, and 40 m, occasionally also 2 m and 50 m when larval concentrations were high enough. Mesh size of the net was 375 μm. Sampling time at each depth was generally 60 s. In 1992, when larval concentrations were extremely high, sampling times for some stations were reduced to 30 and 15 s. Sampling time never exceeded 120 s, because the larval quality became too poor for staging and gut content analysis. The larvae were preserved in a 4% formaldehyde–seawater solution. A full station profile was made in about 1.5 h.

Zooplankton sampling

Zooplankton was sampled with a plankton pump with a capacity of 260 l min^{-1}. Sea water was pumped on deck, and a sample volume of 25 l was filtered through a net

Table 1. Overview of the data sampled at the four sites (A, B, C, and D in Fig. 1) during the period of maximum abundance of first-feeding cod larvae in Lofoten in 1989, 1991, and 1992.

Site	Bottom depth	No. stations	No. samples	No. larvae analysed	Time	Remark
A Henningsværstraumen	90–102	49	160	1 625	1–2 May 1989 1–9 May 1991 4–5 May 1992	Gyre region with retention
B Reine	72	7	31	269	26–27 April 1992	Moderate advection
C Vesterålsfjorden I	24	5	6	44	7–8 May 1989	Strong tidal mixing
D Vesterålsfjorden II	68	12	62	915	30 April–1 May 1992	Green gut

with 90 μm mesh size. The nauplii in each sample were manually counted. Sampling depths were 0, 5, 10, 15, 20, 30, and 40 m, occasionally also 2.5 m, 7.5 m, and 25 m.

Sampling of physical parameters

A Neil Brown CTD was used to measure temperature and salinity. In 1989, wind was measured on the ship on a provisionally installed Aanderaa weather station. A 10 min wind speed average was recorded every 30 min. In 1991 and 1992 meteorological parameters were recorded on a permanently installed Thies ship weather station. Wind speed and direction were recorded every 10 min based on five 2 min averages. The Aanderaa weather station was mounted on a small island nearby sampling site A so that continuous wind data would be obtained when the ship moved to other stations. Current profiles were recorded using a hull-mounted Acoustic Doppler Current Profiler (ADCP). In 1991 and 1992 a waverider and a current-meter mooring were deployed at site A. The waverider recorded statistics on wave height and frequency every 30 min, measured over a 10 min period. The current-meter mooring had five Aanderaa current meters. The current-meter rig was also deployed at site D.

Data analysis

The stage 7 (8–10 days old; Fossum (1986)) cod larvae were picked out, their gut content determined, and also the number of nauplii in the gut (feeding ratio; Tilseth and Ellertsen (1984)). Larvae sampled during the dark period (sample times 0100 h and 0400 h) of the day have not been analysed, since the feeding activity is reduced around midnight.

The feeding ratio was compared with the naupliar concentration in the sea at the depth at which the cod larvae were sampled. Also the depth-averaged feeding ratio at each station was compared with the depth-averaged naupliar concentration. The relationship between feeding ratio and naupliar concentration was established using the model of Sundby and Fossum (1990).

$$A(c) = A_{max}[1 - \exp(-b\,c)] \quad (1)$$

where c is the naupliar concentration in the sea, A(c) is the feeding ratio, A_{max} is the maximum possible feeding ratio (full gut), and b is the coefficient representing the velocity component of the contact rate. Sundby and Fossum (1990) used $A_{max} = 5.1$ in accordance with laboratory experiments on stage 7 larvae by Solberg and Tilseth (1984). The present data indicated a lower value of A_{max}. The rougher treatment of the cod larvae in the fish larvae pump may have caused regurgitation (see discussion) and consequently a lower feeding ratio. With the exception of one anomalous feeding ratio value of 5.5, the maximum average feeding ratio of the present data was 3.8 (Fig. 2). A non-linear two-parameter regression analysis, using the Gauss–Newton method (SAS, 1988), was made to estimate b and A_{max}. However, since A_{max} is the asymptotic value of the feeding ratio (at very high concentrations of nauplii, c), and all the present nauplii concentrations measured were below 50 nauplii l^{-1}, the upper range of the naupliar concentration was not sufficiently covered to obtain reliable estimates of A_{max}. This resulted in very low estimates of A_{max} at low wind speeds, because the feeding ratio, A(c), was then low even at high nauplii concentrations. Therefore, a one-parameter non-linear regression (SAS, 1988) estimating only parameter b was subsequently applied to the data, keeping A_{max} fixed at values ranging from 2.5 to 5.1. The relative change in parameter b was similar for any chosen A_{max} value above 3.0. In this article, the regressions for $A_{max} = 3.5$ are presented.

Since the spin-up and decay time of wind-induced turbulence is not well understood and the measured feeding ratio of the larvae is established during a period of about 2 h prior to sampling (Solberg and Tilseth, 1984), only groups of samples with a relatively stable wind history were selected for analysis. The selection was made based on the wind records prior to analysis of the gut content of the cod larvae. With this procedure, 15 of the 88 stations were not included in the present analysis. The feeding ratio was compared with the mean wind speed of the 8 h period prior to sampling. The data were also analysed for changes in feeding ratio with depth and changes throughout the day. All in all, 73 stations with 259 samples were analysed during the three years (Table 1). The average sample size was 11 cod larvae.

Results

All the samples are pooled in Figure 2 to show the average number of nauplii in the cod larval gut (feeding ratio) versus the nauplii concentration in the sea for each sample. The scattered relation between food concentration and gut content appearing in the figure corresponds with many other larval investigations, and may lead to the erroneous conclusion that there is a poor functional relation between food concentration and larval feeding.

Wind-dependent feeding rates

In Figure 3 the pooled samples are split up into 15 different events of distinct environmental conditions

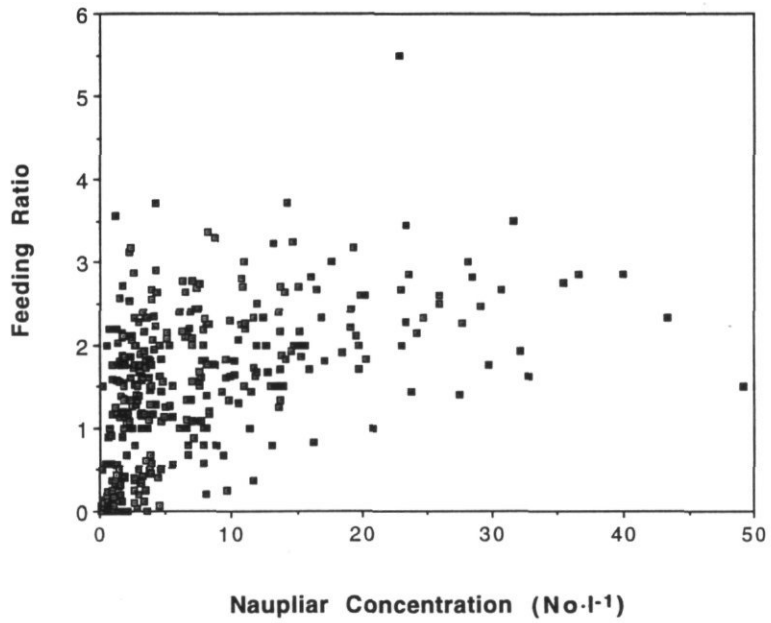


Figure 2. Feeding ratio of cod larvae versus naupliar concentration in the sea for the entire data set (259 points). One point represents one sample depth.

(Table 2). Panels 1–13 of Figure 3 show groups of samples under wind speeds (8 h average prior to sampling) increasing from 2.0 m s^{-1} to 10.5 m s^{-1}. The event of Panel 4 is from site B. All the others are from site A, located at the quasi-stationary gyre at Hennings-værstraumen. Each event was fitted by one-parameter non-linear regression to Equation 1 with $A_{max} = 3.5$.

The regression line is drawn in each panel. Although the data in each panel are scattered and do not cover the entire range of naupliar concentrations and feeding

Table 2. Estimates of b in Equation (1), including the 95% confidence intervals for b, for 13 various wind events from 2 m s^{-1} to 10.5 m s^{-1} (sites A and B), for an event of strong tidal mixing (site C), and for an event of high concentrations of phytoplankton (site D).

						Based on each sample		Based on each station	
Site	Time	No. of stations	No. of samples	No. of larvae analysed	8 h mean windspeed (m/s)	Estimated mean value of b	95% confidence int. (±)	Estimated mean value of b	95% confidence int. (±)
A	8–9 May 1991	4	8	78	2	0.023	0.013	0.023	0.020
A	6 May 1991	4	14	147	3.2	0.057	0.015	0.055	0.022
A	7 May 1991	3	6	63	3.5	0.067	0.016	0.039	0.023
B	26–27 April 1992	7	31	269	3.5	0.051	0.006	0.072	0.033
A	1–2 May 1991	9	37	360	4	0.062	0.014	0.056	0.012
A	4 May 1992	6	26	321	5.4	0.159	0.051	0.124	0.182
A	6–7 May 1991	3	8	62	6.2	0.137	0.065	0.129	0.098
A	7–8 May 1991	3	10	83	6.2	0.097	0.050	0.108	0.135
A	5 May 1991	4	12	86	6.5	0.111	0.067	0.073	0.041
A	1 May 1989	3	6	76	6.9	0.267	0.482	0.186	0.582
A	4 May 1991	4	10	89	7.5	0.108	0.045	0.101	0.069
A	2 May 1989	3	10	131	8.6	0.195	0.153	0.169	0.056
A	5 May 1992	3	13	129	10.5	0.218	0.061	0.225	0.123
C	7–8 May 1989	5	6	44	4.5	0.360	0.404	0.581	0.505
D	30 Apr–1 May 1992	12	62	915	4.7	0.020	0.005	0.035	0.011

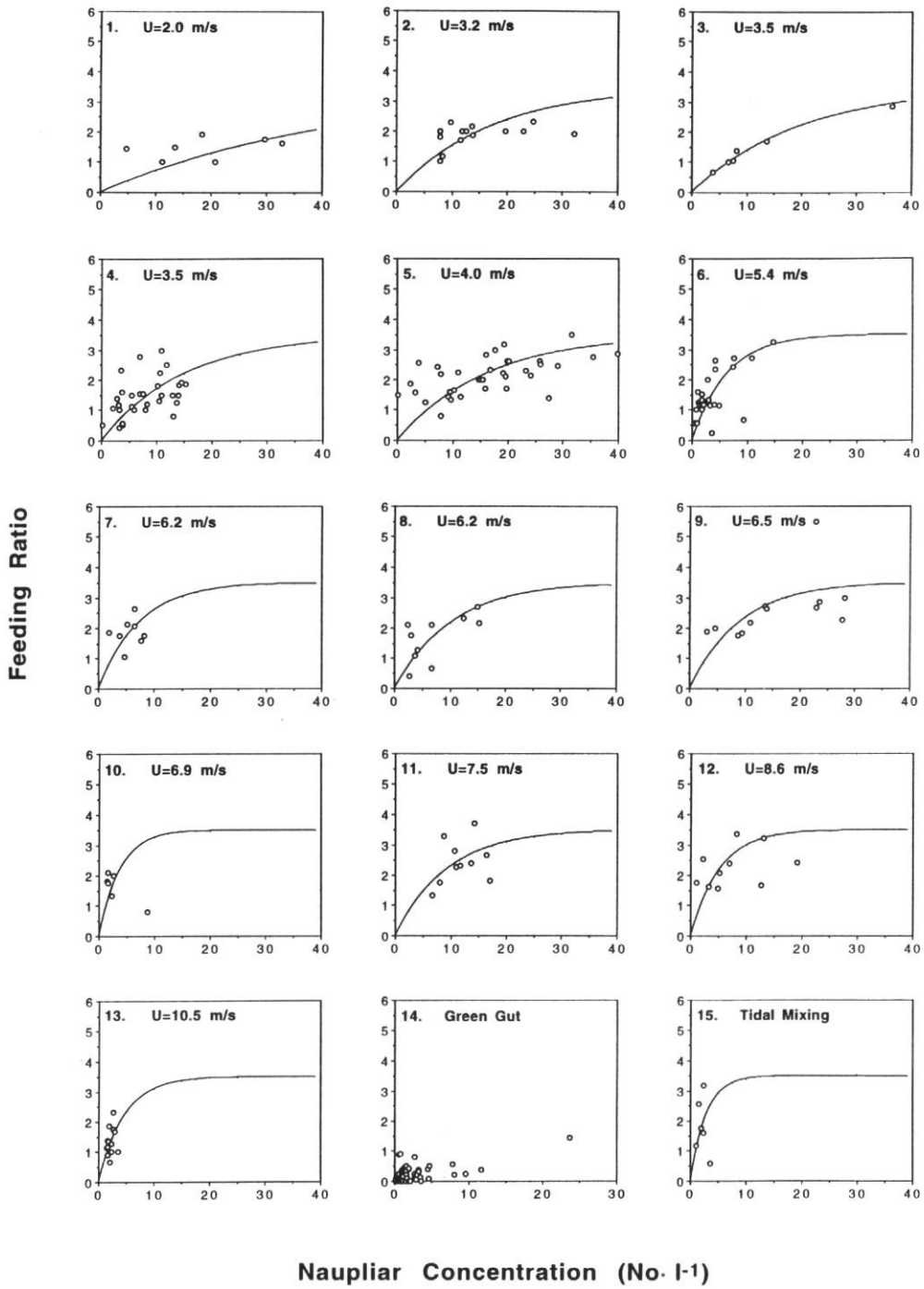


Figure 3. Feeding ratio of cod larvae versus naupliar concentration in the sea for the data in Figure 2 split into 15 different events. Panels 1–13 show increasing wind situations from 2.0 m s^{-1} to 10.5 m s^{-1}. Panel 14 shows an event where larval feeding is dominated by phytoplankton, and Panel 15 where larval feeding is dominated by strong turbulence due to tidal mixing.

ratios, there is a clear increase in the velocity component of the contract rate as wind speed increases. This is seen from the regression lines which approach A_{max} at lower nauplii concentrations as wind speed increases. In Figure 5 the estimated b coefficients from each of the panels in Figure 3 are plotted versus wind speed. The left panel of Figure 5 shows the estimates of b based on values from each sample and the right panel the depth averaged estimate, b_D, for each station (based on depth-averaged feeding ratios and nauplii concentrations).

When the contribution to the encounter rate from the larvae's own motion is small compared to the contribution from turbulence, there is an approximately linear functional relationship between the contact rate and wind speed. For the present cod larvae, this is valid for wind speeds above 4 m s^{-1} (Sundby and Fossum, 1990). Linear regressions for the data in the two panels of Figure 5 give:

$$b = 0.02439 \cdot U - 0.01945; \quad R^2 = 0.652 \qquad (2)$$

$$b_D = 0.02244 \cdot U - 0.02329; \quad R^2 = 0.793 \qquad (3)$$

where U is the wind speed in m s^{-1}.

Based on these equations, an increase in wind speed from 2 m s^{-1} to 10 m s^{-1} gives an increase of contact rate by factors of 7.6 and 9.3 respectively, while the theoretically calculated increase of contact rate according to the Rothschild and Osborn (1988) theory gives in the order of 4.0 when an average swimming speed of 0.17 cm s^{-1} is applied in the calculations.

In Figure 4 the data are pooled in four separated wind groups (group I: 2 m s^{-1}; group II: 3.2–4.0 m s^{-1}; group III: 5.4–6.9 m s^{-1}; group IV: 7.5–10.5 m s^{-1}), and it is very evident that feeding ratio increases as wind increases, since there are more data along the entire span of nauplii concentrations. Nevertheless, there is a general tendency for the nauplii concentration to decrease as wind speed increases. This is not primarily because peak concentrations are broken down within the mixed layer. The same reduction is found in the depth-

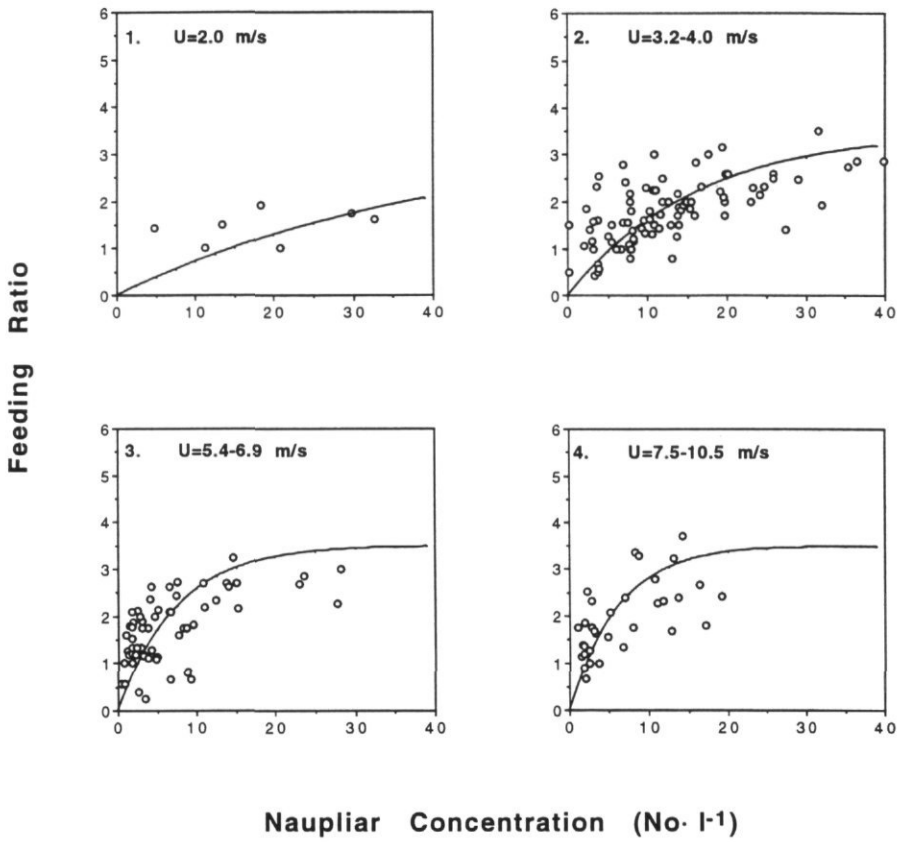


Figure 4. Feeding ratio of cod larvae versus naupliar concentration in the sea. Panels 1–13 of Figure 3 pooled into four wind groups. Panel 1: 2.0 m s^{-1} (identical to Panel 1 of Figure 3); Panel 2: 3.2–4.0 m s^{-1}; Panel 3: 5.4–6.9 m s^{-1}; Panel 4: 7.5–10.5 m s^{-1}.

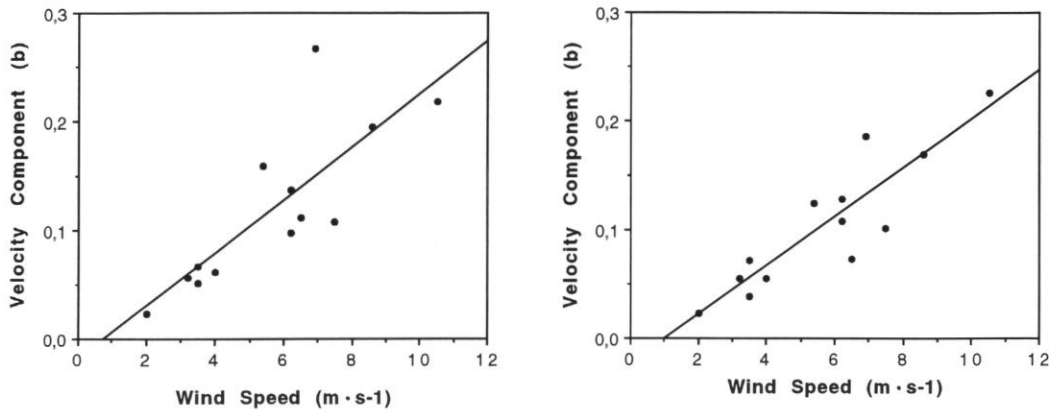


Figure 5. (Left) Estimated values of b in Eq. (1) versus windspeed for the 13 wind events, Panels 1–13 of Figure 3. Based on each sample depth. (Right) Estimated values of b in Eq. (1) versus windspeed for the 13 wind events, Panels 1–13 of Figure 3. Based on depth average of each station.

averaged nauplii concentration, indicating that some of the nauplii drop out of the entire upper layer (0–40 m depth) as wind speed increases.

Figure 6 shows the analogue plots of Figure 5 for the four wind groups, and the values are tabulated in Table 3. The linear regression lines are:

$$b = 0.02091 \cdot U - 0.01247; \quad R^2 = 0.967 \qquad (4)$$

$$b_D = 0.01841 \cdot U - 0.01053; \quad R^2 = 0.991 \qquad (5)$$

These relations give increases of contact rate as the wind speed increases from 2 m s^{-1} to 10 m s^{-1} by factors of 6.7 and 6.6, respectively.

Feeding rates enhanced by tidal mixing

Panel 15 in Figure 3 shows the result from site C, located at a shallow plateau at an average depth of 25 m. The 8 h mean wind speed prior to sampling was only 4 m s^{-1}. However, the tidal current is high compared to that of the surrounding deeper water. The density was homogeneous, indicating strong tidal mixing. An approximate estimate of the turbulent energy dissipation rate, ε, induced by tidal mixing can be acquired by applying the Greenberg (1983) relation:

$$\varepsilon = \rho\, c_D\, [(u^2 + v^2)^{3/2}]/H \qquad (6)$$

where ρ is the density of sea water c_D is the drag coefficient, H is water depth, and the terms in brackets the cubed time average of the current velocity over the tidal period.

Table 4 gives the calculated tidally induced rate of turbulent energy dissipation in W m^{-3} for the sites A, B, C, and D. At sites A, B, and D, water depth is too great to allow the turbulent energy induced by the tide to propagate to the surface layers. At site C, bottom depth is only 25 m and the water column completely mixed. The value of $\varepsilon = 3 \times 10^{-3}$ W m^{-3} is considerably higher than the ε-value induced by a 10 m s^{-1} wind speed ($\varepsilon = 1.3 \times 10^{-3}$ W m^3), and this corresponds well with the calculated b-coefficient of 0.360.

Table 3. Estimates of b in Equation (1), including the 95% confidence intervals for b, for the wind events (sites A and B) pooled in four wind groups: I. 2 m s^{-1}; II. 3.2–4.0 m s^{-1}; III. 5.4–6.9 m s^{-1}; IV. 7.5–10.5 m s^{-1}.

8 h mean windspeed (m/s)	No. of stations	No. of samples	No. of larvae analysed	Based on each sample: Estimated mean value of b	Based on each sample: 95% confidence int. (±)	Based on each station: Estimated mean value of b	Based on each station: 95% confidence int. (±)
2	4	8	78	0.023	0.013	0.023	0.020
3.2–4.0	23	88	839	0.062	0.008	0.056	0.009
5.4–6.9	19	62	628	0.134	0.031	0.112	0.048
7.5–10.5	10	33	349	0.163	0.052	0.148	0.057

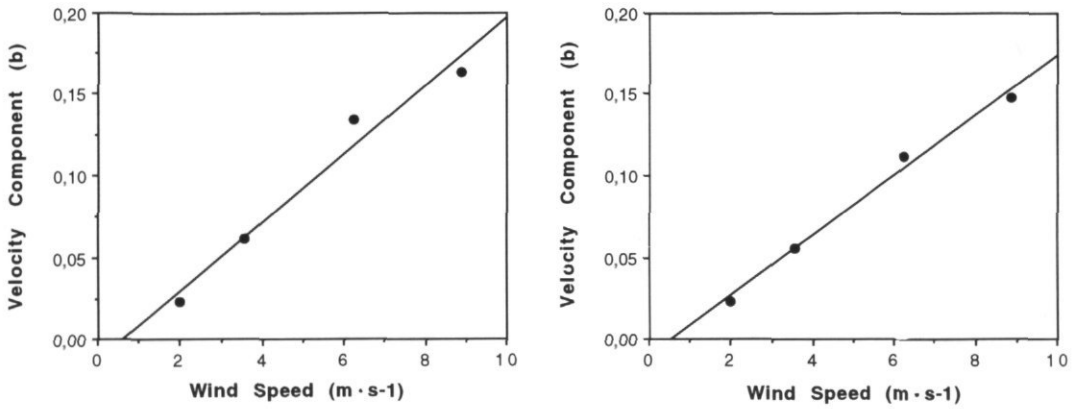


Figure 6. (Left) Estimated values of b in Eq. (1) versus windspeed for the four wind groups, Panels 1–4 of Figure 4. Based on each sample depth. (Right) Estimated values of b in Eq. (1) versus windspeed for the four wind groups, Panels 1–4 of Figure 4. Based on depth average of each station.

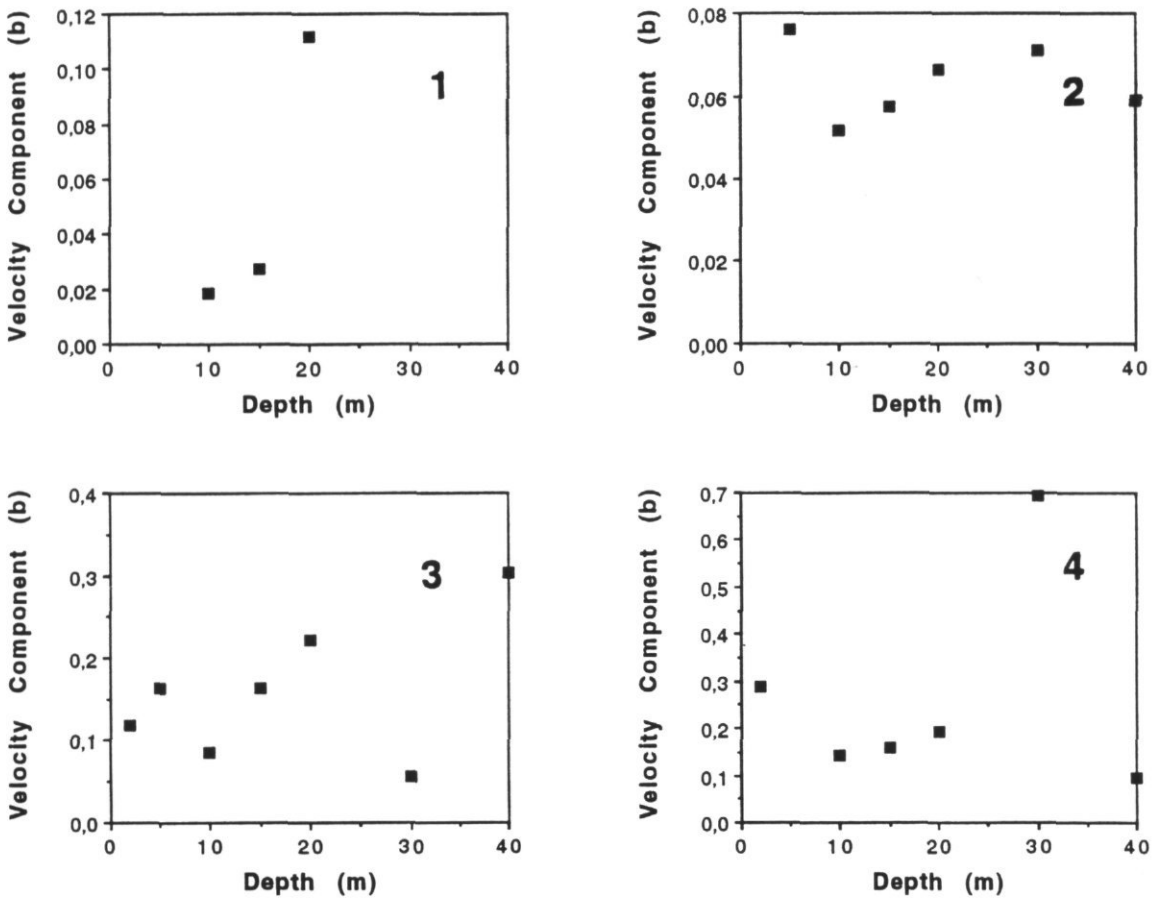


Figure 7. Estimated values of b in Eq. (1) versus depth for the four wind groups. Panel 1: Wind group I; Panel 2: Wind group II; Panel 3: Wind group III; Panel 4: Wind group IV.

Table 4. Bottom depth (m), mean tidal current (m s^{-1}), and calculated turbulent energy dissipation rate (W · m^{-3}) according to equation (6) for the sampling sites.

Site (see Fig. 1)	Bottom depth (m)	Mean tidal current (m s^{-1})	Calculated ε (W m^{-3})
A	100	0.10	2.80×10^{-5}
B	70	0.15	1.35×10^{-4}
C	25	0.30	3.00×10^{-3}
D	80	0.40	2.22×10^{-3}

Depth-dependent feeding rates

The wind-induced turbulence will generally decrease down through the mixing layer (e.g. Yamazaki and Kamykowski, 1991; MacKenzie and Leggett, 1993). Consequently, with the apparent strong influence of wind-induced turbulence on the feeding rate of the cod larvae, it is to be expected that there could be vertical differences in the feeding rate. Light intensity is another parameter which might contribute to vertical variations in the feeding rate of cod larvae. Figure 7 shows the values of the b-coefficient plotted versus depth for the four wind groups. Each point in the four panels represents the average of the samples in each depth. There is no tendency towards a decrease of feeding rate (represented by coefficient b) with increasing depth. On the contrary, the general trend appears to be a small increase of the feeding rate with increasing depth. Figure 9 shows the variation (in percent) with depth of coefficient b (where 100% is the depth average) together with the similar variation in naupliar concentration. For the two lowest wind groups there is a clear trend of decreasing nauplii concentrations with increasing depth below 10 m depth. For all four wind groups there is an inverse relationship between feeding rate and nauplii concentration.

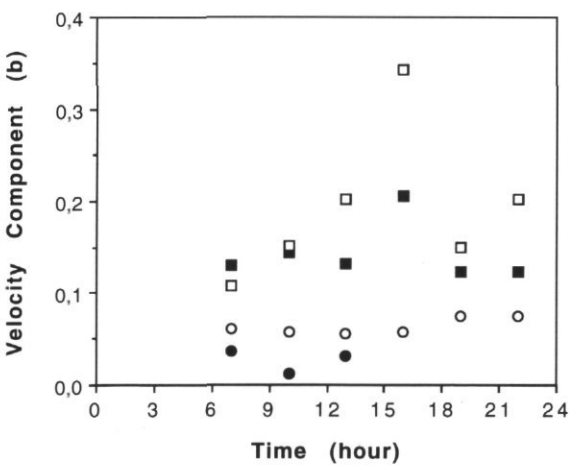


Figure 8. Estimated values of b in Eq. (1) versus time of the day from 07.00 h to 22.00 h for the four wind groups. Filled circles: Wind group I. Open circles: Wind group II. Filled squares: Wind group III. Open squares: Wind group IV.

Diel variations of feeding rate

As in the case of Sundby and Fossum's (1990) study, the feeding ratio taken at 0100 and 0400 h was not analysed, because feeding activity of the cod larvae is known to drop during the dark period of the day (Ellertsen *et al.*, 1980; Skiftesvik, 1994). For the present region at the beginning of May darkness is from about 2200 to 0200 h. As the gut clearance rate is about 2 h, the effect of darkness will be seen in the larval gut with about 2 h delay. However, the data are analysed for possible changes through the light period of the day, from 0700 to 2200 h. Figure 8 shows the b-coefficients through the day for the four wind groups. There is no clear tendency for diel variations. However, polynomial regression of 2. order of the data for all wind groups pooled together do indicate a peak in the afternoon.

The pit fall of green gut

Panel 14 of Figure 3 shows the sampling at site D. Even though there was a moderate wind speed of 4.7 m s^{-1} and fairly high nauplii concentrations, up to 20 nauplii l^{-1}, the larvae had very low feeding ratios. However, their guts were completely filled with green material. Unfortunately, no phytoplankton samples were taken. In a phytoplankton bloom the particle concentration may be about 10^6 l^{-1}, which is about 10^5 times higher than the concentration of the nauplii. Cod larvae have occasionally been observed with green guts, both in the field and in mesocosm rearing experiments (Wiborg, 1948; Nordeng and Bratland, 1971; Kvenseth and Øiestad, 1984; van der Meeren, 1991).

Discussion

The estimated increase in feeding rate related to increase in wind speed (here represented as the b coefficient) corresponds well with the estimates of Sundby and Fossum (1990), but the values of the b coefficient in the present investigation are only 50–70% of the previous values. The values of A_{max}, estimated by non-linear two-parameter regression analysis, were also lower for all wind groups in the present study. In Sundby and Fossum (1990) the larvae were sampled using a net vertically hauled from 50 m to the surface at a speed of 50 cm s^{-1}. Usually with this gear the sampled larvae are of very high quality because of their gentle treatment during sampling. The fish larvae pump used in the

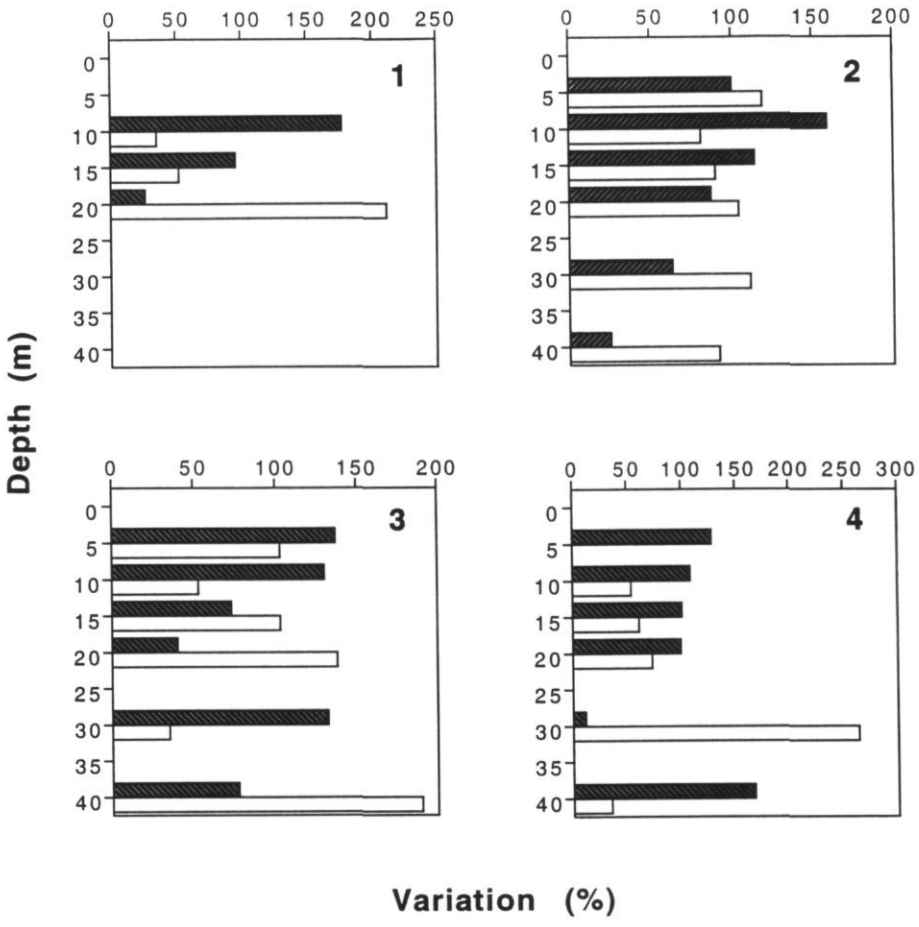


Figure 9. Relative change (in percent) with depth of naupliar concentration (dark bars) and values of the coefficient, b, (white bars) for the four wind groups. Panel 1: Wind group I; Panel 2: Wind group II; Panel 3: Wind group III; Panel 4: Wind group IV.

present investigation gives the larvae much rougher treatment. Parts of the non-uniform flow field through the tube of the pump have a velocity more than five times the flow in the vertically hauled net. For this reason the maximum sampling time had to be set at 120 s. During the tests, sampling times longer than 120 s resulted in problems in staging the larvae and analysing the gut content. The rough treatment in the fish larvae pump must have caused regurgitation by the larvae being smashed against the net at high speed, and hence reducing the measured feeding ratio.

Both in the present study and in the study by Sundby and Fossum (1990) the field measurements indicate a stronger enhancement than calculated from the theory during low turbulent conditions (i.e. wind speed <5 m s^{-1}). For example, our data in 1990 indicated an increase in feeding rate by a factor of 2.8 when wind speed increased from 2 to 6 m s^{-1}. Similarly, the present data indicate an increase by a factor of 3.8. The calculated increase of contact rate by the theory gave only 2.2. However, from moderate wind speeds (>5 m s^{-1}) the results of the field measurements coincide with the theory. The larval cruising speed applied in the theory was 0.17 cm s^{-1} according to the average cruising speed measured in the laboratory by Solberg and Tilseth (1984). Their measurements ranged from 0.08 to 0.25 cm s^{-1}. If a lower cruising speed is applied in the theory, e.g. 0.10 cm s^{-1}, the increase of encounter rate calculated from the theory equals the calculated increase of feeding rate from the field measurements. This demonstrates that the calculated encounter rate is sensitive to variations in larval swimming speed when turbulence is low. In moderate turbulent conditions the contribution from turbulent velocity dominates, and the contact rate becomes insensitive to variations in larval swimming speed. The fact that the results from the field measure-

ments coincide with the theoretical calculations, during conditions when the larval swimming speed does not influence the calculations, points to the question whether the laboratory measured cruising speed can be directly transferred to the field. Larval growth is a balance between ingestion and energy consumption. Even at wind speeds of 4 m s^{-1}, the larvae would be wasting their energy resources if cruising for food, because the turbulence would do the job anyway. From this point of view the larvae should save their energy resources for the short final attack on the prey and for rapid escape reactions from predators. Munk and Kiørboe (1985) have indeed shown that this is what occurs with herring larvae when the encounter rate increases: the swimming activity is reduced and the attack rate increases. Larval growth itself is an important factor for survival, and it is unlikely that the larvae are adapted to energy-wasting behaviour like excessive cruising. Turbulence (together with light) is the most characteristic feature of the mixed layer, the site where most of the plankton production occurs. We therefore suggest that the cruising speed in the field is lower than it is in the laboratory.

The high encounter rate derived from the field measurements could also partly be due to biased sampling. If larvae with a full gut are more vulnerable to regurgitation than larvae with a partly filled gut, then the relationship between naupliar concentration and feeding ratio (Equation 1) will become artificially more curved and the estimated coefficient, b, will become too high.

As outlined by MacKenzie and Leggett (1991) the influence of turbulence on the encounter rate between larvae and their prey should decrease downwards through the mixed layer, because the rate of turbulent dissipation energy decreases through the mixed layer. The present data failing to show this feature may be an artefact of the continuously charging vertical position of the individual larva during the previous 2 h of feeding due to large-scale vertical turbulence of the mixed layer.

Green guts have occasionally been observed in first-feeding cod larvae (e.g. Wiborg, 1948; Nordeng and Bratland, 1971). This is most likely connected with heavy phytoplankton blooms, when concentration can exceed 10^6 cells l^{-1}. During such conditions the distance between cells is less than 1 mm, and so it is likely that the larvae have problems avoiding the phytoplankton cells. For each nauplius encountered the larvae would first hit more than 1000 phytoplankton cells. High concentrations of phytoplankton can be found along frontal regions during first feeding. However, the general phytoplankton bloom occurs in the present region more than one month before the larvae start hatching.

Simulations by MacKenzie *et al.* (1994) suggest that the optimal level of turbulence for cod larvae occurs at wind speeds from 10 to 20 m s^{-1}. The present study supports this conclusion. However, there are few data on this upper interval of wind speeds. The situation with strong tidal mixing (Panel 15 of Fig. 3) indicates that the encounter rate continues to increase even at turbulent intensities corresponding to wind speeds of more than 15 m s^{-1}. The wide range of optimal wind speed suggested by MacKenzie *et al.* (1994) was due to the uncertainty of the time assessed for the cod larvae to respond with an attack. This emphasizes the need for more data on the behavioural characteristics of cod larvae

The question of a possible optimal level of turbulence with respect to fish recruitment and plankton production above which the enhancement of production is exceeded by opposing effects has been considered by many authors from different starting points. For example, Cury and Roy (1989) have demonstrated that there is an optimal window for recruitment to pelagic fishes in an upwelling region, and have explained this by the balance between wind-induced upwelling which enhances production and the opposing effect by wind mixing, which breaks down prey patches. Peterman and Bradford (1987) supported Lasker's (1975) stable ocean hypothesis on the Southern California anchovy, indicating that wind and, hence, turbulence would be negative for recruitment. These examples indicate the need for addressing the questions of basic biological processes, since a wide range of processes could be hidden behind a correlation between recruitment and any physical parameter, e.g. wind. Any particular wind situation can change (1) advection/retention, (2) vertical mixing, (3) entrainment, (4) upwelling, (5) frontal structures, (6) plankton contact rates, (7) buoyancy, (8) temperature, and (9) light conditions. These processes will in turn cascade into the biological processes of both predator and prey. Recruitment response to such a variety of changes could take very different directions depending on species, species interaction, and habitat.

The stable ocean hypothesis, which assumes that successful larval feeding depends on patches of high food concentrations, has often been held up against the theory of turbulence and plankton contact rates. Davies *et al.* (1991) amalgamated these two processes in a series of models coming to the conclusion that turbulence at intermediate levels reduces growth due to patch dissipation, while growth is higher at low turbulence levels due to high patch concentrations and at high turbulence level due to enhanced contact rate. This demonstrates that changing wind can be quite complicated even when considering just two of the aforementioned physical processes.

However, the physical conditions for the Arcto-Norwegian cod larvae are very different from those described in the stable ocean hypothesis. Their first feeding occurs about one month after the temperature

minimum of the year during well-mixed conditions, and the patchy distribution of the prey is caused by the behaviour of the prey itself. The maximum prey concentration is usually found at about 10 m depth (Fig. 9), while the peak concentration of cod larvae is usually at 10–20 m depth. Consequently, the peak concentrations of predator and prey generally do not coincide but there is an overlap.

As discussed above, the apparent increase of encounter rate towards increasing depth (Fig. 9) is probably an artefact, because the gut content of the larvae represents a record of feeding during the previous couple of hours. During this period the larvae have also been feeding at depth other than the depth at which they were sampled. The vertical distribution of the larvae is a "frozen" image of a dynamic process. Even if the vertical distribution is stationary, the vertical position of the individual larva changes continuously owing to large-scale vertical mixing, vertical behaviour and change in buoyancy of the larvae when they feed (e.g. Sclafani *et al.*, 1993). This dynamic behaviour also renders the present data from Lofoten difficult to relate to a depth-dependent turbulence model such as the one developed by MacKenzie and Leggett (1993), and we assume that depth-averaged data best describes the relation between larvae and their prey for the present data. However, improved studies of the gut content could make it possible to discriminate between newly eaten and more digested nauplii, and in this way relate the gut content to the actual depth at which they were sampled and to the actual turbulence at the sampling depth.

Acknowledgments

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Patterns of distribution, spawning, and growth in North Atlantic cod: the utility of inter-regional comparisons

K. M. Brander

Brander, K. M. 1994. Patterns of distribution, spawning, and growth in North Atlantic cod: the utility of inter-regional comparisons. – ICES mar. Sci. Symp., 198: 406–413.

Cod populations throughout the North Atlantic follow a common life history pattern, but with considerable regional variations in their growth rate, age of maturity, migration patterns, and timing of spawning. The comparative method is a powerful tool both for identifying factors which shape life history patterns and for investigating them quantitatively. Most studies of cod population dynamics are carried out for stock assessment and management purposes and are confined to interpreting only changes within stocks. There is a strong case for undertaking comparative studies and for treating cod as a species rather than as a collection of discrete units. Two studies which make comparisons between stocks are presented in order to bring out the benefits of a comparative approach. The first concerns processes governing recruitment and in particular the hypothesis that differences in timing of cod spawning throughout the range are due to variability in the timing of plankton production. The second investigates the effect of temperature on growth in different stocks. The results suggest that temperature is responsible for most of the observed differences in growth and that the effect is big enough to have significant consequences for assessment of the impact of climate change and also for short-term catch forecasts.

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Introduction

In addition to the effects of fishing, North Atlantic cod stocks are affected directly and indirectly by many physical and biological factors which act in complex, often non-linear, ways. It is therefore difficult to determine which factors have shaped distribution and life history patterns and caused population changes. The separate and joint effects of temperature, oxygen, and specific gravity on survival of eggs, larvae, and later life history stages have been demonstrated experimentally and these results can be used to interpret population changes which are under way in areas like the Baltic and the Labrador Shelf. However, experiments are limited to studying the response of individuals or small groups of fish in simplified artificial environments and they complement, but do not replace field investigations of the behaviour and dynamics of stocks.

Routine stock assessments, carried out for fisheries management purposes, provide most of our information on changes in North Atlantic cod populations. Four characteristics of this body of work are that the primary cause of observed changes is presumed to be fishing, that it is rare for any other factors to be taken into consideration, that stocks are assessed independently of each other, and that most of the information appears only in the "grey" literature and is not fully analysed and interpreted as it would be for a scientific publication. It is timely to widen the perspective of stock assessment work to consider factors other than fishing and to consider cod as a species rather than as a collection of isolated stocks. In particular, I wish to make a case for comparative studies on the lines advocated by Bakun (1985), who comments that "it seems surprising that the (comparative) method has not found wider use in the fishery-environmental field, which appears to be preoccupied with diversity rather than synthesis, and prone to view each local situation as unique". There is a danger that in concentrating on local phenomena we neglect wider issues and miss simple general patterns.

Two examples will be used to demonstrate the utility of the comparative approach. The first looks for patterns of distribution and spawning among stocks, which may reflect important causal mechanisms. The second ana-

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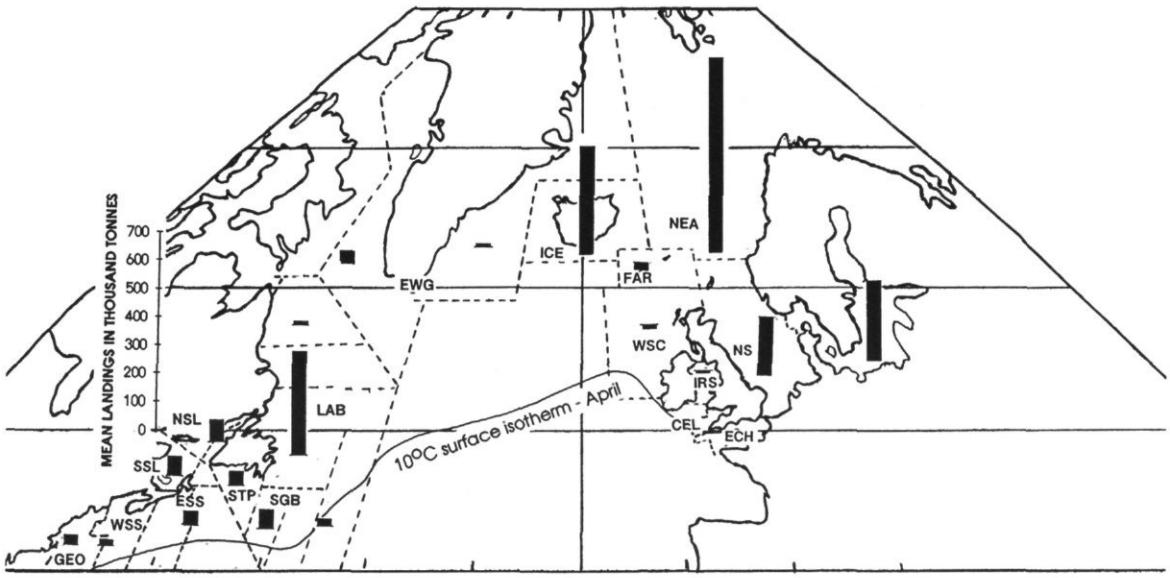


Figure 1. Distribution and average landings of cod stocks throughout the North Atlantic. The southern boundary of cod distribution follows roughly the 10°C surface isotherm in April. Surface temperature follows the same pattern throughout the year and the 10°C isotherm indicates the probable location, but not the actual level of the thermal limit of the cod distribution. The area codes correspond to stocks included in the growth analysis in Table 1.

lyses data on weight-at-age and average temperature for different stocks in order to see whether a simple general relationship can be established, which may help to interpret observed changes in growth rates.

Patterns of distribution and spawning

Juvenile and adult cod are widely distributed on continental shelves of the North Atlantic and sometimes in deeper water. Average annual landings, shown in Figure 1, give an indication of relative stock sizes.

Some of the factors which limit distributions (e.g. temperature, depth, salinity) have been studied in detail and their effect on individuals and on populations can be shown. For example, the levels of plasma antifreeze glycoproteins in juvenile cod at Newfoundland helps them to survive low temperatures, which adults of the same stock or cod from other stocks cannot tolerate (Goddard *et al.*, 1992). Population levels of cod stocks at the cold end of the range react negatively to periods of low temperature and the direct and indirect processes which bring this about are slowly becoming apparent (e.g., Ellertsen *et al.*, 1988; Ellertsen and Solemdal, 1993).

The effects of low salinity on cod distribution are rather clear and well studied in the Baltic, where in combination with reduced oxygen levels in the deep basins they restrict the volume in which cod eggs can maintain their buoyancy and survive (Nissling, 1994; Lablaika and Kalejs, 1993). A natural experiment on the effect of changes in this "volume of survival" may be underway, owing to recent flushing leading to salinification and reoxygenation of the deep basins. The large average catches of cod from the Baltic (Fig. 1) suggest that cod production per unit area is not limited by salinity until very low levels are reached and the eggs lose buoyancy. Catches in the Gulf of St Lawrence, where salinity is slightly reduced, are also high.

Although juvenile and adult cod are widely distributed, spawning is concentrated at certain regular, restricted locations and times of year. For example, juvenile and adult Arcto-Norwegian cod are distributed over a huge sea area, but spawning is restricted to a few coastal locations, of which the Vestfjord is the main one (Fig. 2). The timing of spawning is very regular in that area, with 90% of the eggs laid within a three-week period in late March and early April (Fig. 3). Spawning off Iceland is also restricted in space and time, but in other stocks in the North Sea, Baltic, and Northwest Atlantic it is more widespread and occurs over several months.

Regular patterns of cod spawning have evolved in response to regular seasonal and spatial patterns in the environment and the questions we need to address are:

1. How restricted and regular are the spawning patterns in space and time?
2. What are the factors shaping the present patterns of spawning and how strongly do they act on survival?

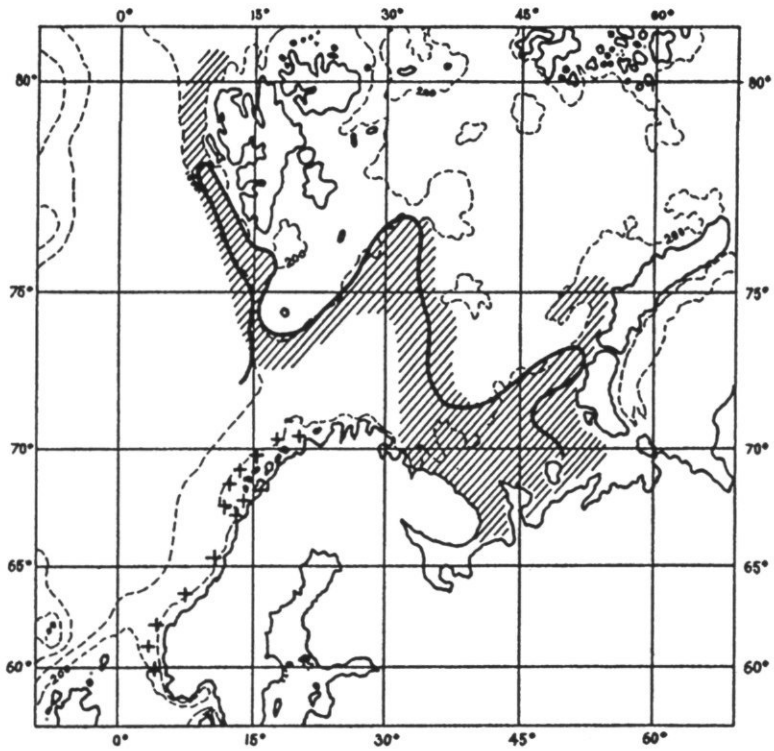


Figure 2. Distribution of Arcto-Norwegian cod as fingerlings (shading), spawning areas (crosses), and limit of distribution of adults (heavy line) (from Marty, 1965; after Maslov and Barenenkova).

3. How are patterns likely to respond to future environmental changes?

Brander (1994) estimated the time of spawning for five cod stocks around the British Isles and related it to the timing of plankton production, which varies in a regular way due to differences in depth and tidal mixing (Fig. 4). For example, spawning in the Bristol Channel, where the spring bloom is late (Joint and Pomeroy, 1981), occurred mainly in March and April, but in the English Channel at the same latitude it occurred mainly in February in areas where production begins much earlier (Pingree *et al.*, 1986). The hypothesis that timing of spawning is coupled to timing of plankton production is also supported by information on Georges Bank (Sherman *et al.*, 1984), the Scotian Shelf (Brander and Hurley, 1992), East and West Greenland, Labrador and the Grand Banks (Myers *et al.*, 1993), although for the latter areas the coupling appears to be so loose that the authors conclude that "recruitment will not be strongly influenced by changes in the timing of the plankton peak".

Economou (1991) considered a number of hypotheses concerning the adaptive significance of concentrated spawning and subsequent dispersal of fish eggs and larvae and proposed that larval starvation was a major factor. The risk of starvation is alleviated by locating spawning so that larvae remain in a suitable feeding environment, but at the same time are dispersed, so that they do not compete for food as they develop. A review of data on a number of fish species, including cod by MacKenzie *et al.* (1990), found that food rarely limited larval growth in field studies, and they concluded that "much of the potential variability in larval feeding rates that might be expected to occur in the sea because of natural variation in food densities has probably already been dampened by spawning behaviour".

The evidence to date suggests that the timing and location of cod spawning is coupled to plankton production, but there is some doubt about how close the coupling is and what the consequences are for larval survival. The power of a hypothesis depends on how specific it is and I think it is worth continuing to specify and assemble the data for more rigorous testing of the coupling hypothesis and of the "match–mismatch" hypothesis of which it forms a part. The data used so far suffer from many limitations and the exact form of the expected relationship between spawning time and plankton production is not clear.

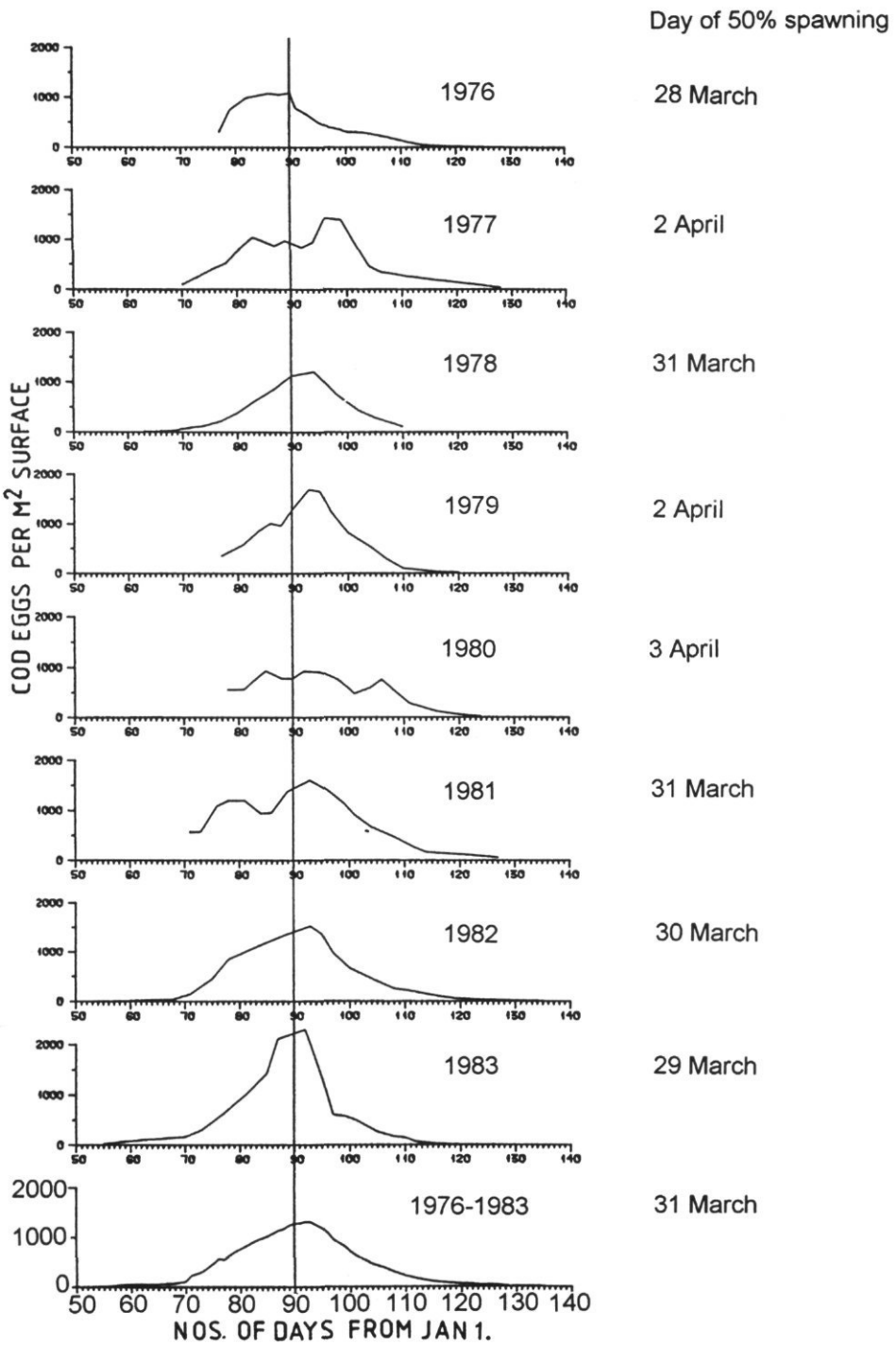


Figure 3. Mean numbers of cod eggs less than three days old at three localities in the Vestfjord and estimated median spawning dates (from Ellertsen *et al.*, 1988).

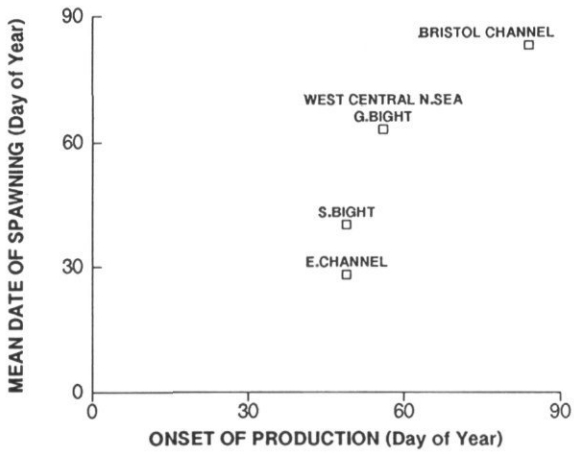


Figure 4. Relationship between timing of cod spawning and timing of onset of plankton production for areas around the British Isles (from Brander, 1994).

Spawning time and duration can be estimated quite precisely from early stage egg abundance curves (e.g., Fig. 3) or from proportions of maturing and spent fish (Myers *et al.*, 1993). The timing of late egg and larval stages can be calculated using temperature data. Defining and estimating "plankton production" and timing poses much greater problems, since survival (and hence reproductive success) depends on larvae encountering sufficient quantities of the right size and kind of food throughout their development. Encounter frequency is a function of relative motion of predator and prey and not simply of prey abundance (MacKenzie and Kiørboe, 1994). Furthermore, since cod spawn several weeks before their larvae start to feed, the successful reproductive strategy must anticipate feeding conditions which may vary from year to year, depending on weather patterns.

We should not be discouraged by the difficulties of defining and measuring the food environment of larvae. If a regular seasonal and area pattern of spawning has evolved, which minimizes larval starvation, then there must be regularities in the physical environment (particularly topography, tidal mixing, freshwater runoff, and advection) which affect production of food particles, contact rates, retention of larvae in areas of adequate food and dispersal to avoid competition. Physical and biological process models are being developed, with assimilation of field observations, to generate patterns of plankton production (e.g., Tett *et al.*, 1993), encounter probability (MacKenzie *et al.*, 1994) and transport (Thompson *et al.*, 1993; Lough *et al.*, 1994). These are being used to explain the regularities in cod spawning and to link physical and biological processes at all scales.

Effects of temperature on growth rate

Growth is the integration of a series of processes (feeding, assimilation, metabolism, transformation, and excretion) whose rates are all controlled by temperature; indeed Brett (1979) identifies it as the only Controlling Factor. Since cod stocks experience very different temperature regimes it is not surprising that growth rate varies between and also within stocks. Some within-stock studies are mentioned below, but in general the effect of temperature on growth of cod is surprisingly poorly documented. One reason for this is that it is difficult to quantify between-year or between-area temperature differences within a stock sufficiently precisely, because the dynamic range in temperature may be quite small, and concurrent information on stock distribution and temperature are scarce. Comparisons between stocks give a much wider dynamic range of temperature, so that the precision of individual temperature estimates is less critical, but the results cannot necessarily be applied to explain within-stock differences.

Material and methods

Recent weight-at-age data for 17 cod stocks from throughout the North Atlantic are given in Table 1, with their sources. The mean weight of four-year-old cod was chosen as the index of growth rate for each stock, because estimates of mean weight of younger ages from commercial fisheries are affected by selectivity of the fishing gear (in slow growing stocks) and the growth rate of older fish slows down following maturity. The mean weight of four-year-old cod ranges from 0.61 kg in the Northern Gulf of St Lawrence to 7.3 kg in the Celtic Sea.

Data on ambient temperature experienced by fish are not routinely available. Heessen and Daan (1994) examined the relationship between the average ambient temperature experienced by different age groups in the North Sea (i.e., bottom temperature weighted by observed fish distribution) and the average bottom temperature. Distribution patterns change with age and may be related to depth preferences as much as to temperature, but the resultant ambient temperature experienced up to age 4 is very close to the average temperature (Fig. 5). Data on average bottom temperature for all areas have been obtained from a number of sources and are given in Table 1.

Results

The relationship between average annual bottom temperature and growth rate, as represented by the mean weight of four-year-old fish, is very close (Fig. 6), accounting for 95% of the variance:

Table 1. Recent weight-at-age data for 17 cod stocks from the North Atlantic.

Stock	East+West Greenland	NE Arctic	Iceland	Faroe	West Scotland	North Sea	Celtic Sea	Irish Sea	Eastern Channel	Labrador/ Grand Bank	Southern Grand Bank	N Gulf of St Lawrence	St Pierre Bank	S Gulf of St Lawrence	Eastern Scotian shelf	Western Scotian shelf	Georges Bank
Code	EWG	NEA	ICE	FAR	WSC	NS	CEL	IRS	ECH	LAB	SGB	NSL	STP	SSL	ESS	WSS	GEO
Age																	
1				0.58	0.67	0.63	0.64	0.80								0.88	1.05
2				0.99	1.26	0.93	1.81	1.79							0.47	0.88	1.76
3	0.78		1.31	1.35	2.74	1.93	4.27	3.52	2.82	0.36	0.55	0.43	0.60	0.54	0.77	1.36	2.78
4	**1.03**	**0.92**	**1.90**	**2.67**	**4.69**	**3.63**	**7.32**	**5.40**	**4.66**	**0.61**	**0.85**	**0.61**	**0.75**	**0.67**	**0.88**	**2.03**	**3.47**
5	1.13	1.46	2.47	3.59	6.08	5.94	9.37	7.30	6.08	0.97	1.59	0.83	1.17	0.82	1.15	2.74	4.43
6	1.34	2.16	3.16	4.52	8.21	8.10	10.99	8.63	8.50	1.41	2.30	1.09	1.74	0.98	1.46	3.86	5.59
7	2.46	2.94	3.78	5.57		9.92	15.26	11.53		1.88	3.83	1.38	2.37	1.15	1.56	5.47	7.12
8	3.33	4.03	5.67	6.62						2.27	5.56	1.59	2.91	1.30	1.94	7.58	9.60
9	5.41	6.46	7.32	8.00						2.63	7.53	1.83	3.69	1.37	2.35	9.77	8.46
10	7.48	8.03	9.78	10.18						3.14	9.04	2.01	4.23	1.48	2.25	13.25	15.00
11	8.34									3.80	11.98	2.29	6.34	1.71	2.87	13.63	
12										4.96	13.98	2.40	7.68	1.93	3.41	15.66	
13										5.49	13.60		8.64	2.47	4.16	16.90	
14										7.61			9.72	3.66	11.29	21.20	
15										11.58					9.34	15.73	
Temperature	**3**	**4**	**5.8**	**7.4**	**10**	**8.6**	**11**	**10**	**11**	**2**	**2.5**	**2.5**	**2**	**2.5**	**5**	**6**	**8**
Weight Refs	1	2	1	3	4	4	5	5	4	6	7	8	9	10	11	12	13
Temp Refs	14	15	16	17	18	19	18	18	18	14	14	14	14	14	14	14	14

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9 CAFSAC Res Doc 92/111 An Assessment of the cod stock in NAFO subdivision 3PS.
10 CAFSAC Res Doc 92/105 Examination of the status of the Gulf of St Lawrence cod stock following the 1992 fall Groundfish survey.
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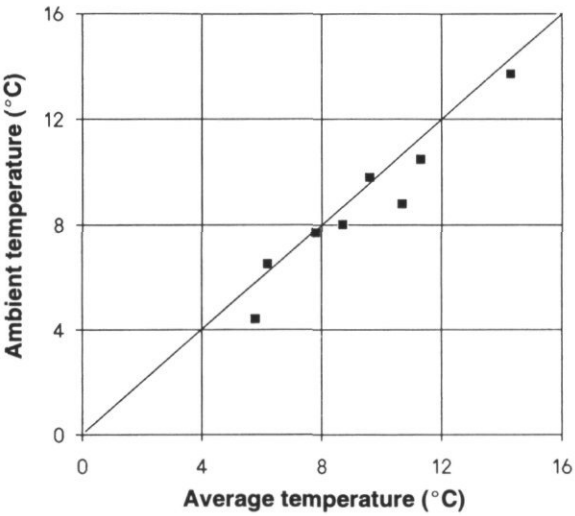


Figure 5. Average ambient temperature for cod ages 0–4 in relation to average North Sea bottom temperature during different quarters of the year. 45°line shown. Redrawn from Heessen and Daan (1994).

$$\ln(\text{wt in kg}) \text{ at } 4 = 0.2542 \times \text{temp } (°C) - 0.9499$$

$r = 0.98$ for 15 degrees of freedom; $p < 0.01$. Thus each degree increase in temperature results in a 29% increase in growth rate between stocks (averaged up to age 4). A more detailed review of previous studies of the between- and within-stock effects of temperature on cod growth has been submitted for publication and growth models incorporating temperature have been fitted to the data in Table 1 (Brander, submitted). There is evidence for both year-to-year (Hermann and Hansen, 1965) and area-to-area (Jónsson, 1965) effects, which are of similar magnitude to the relationship described here.

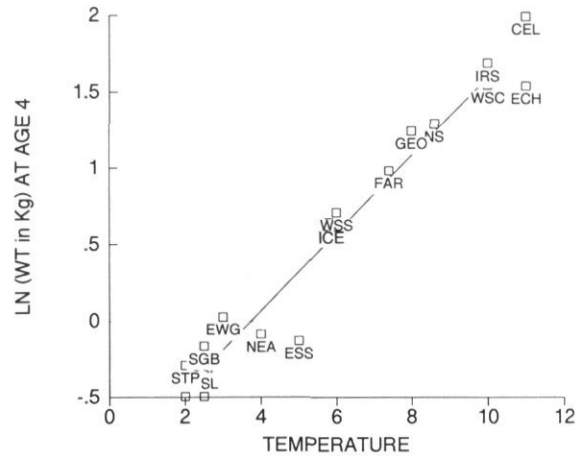


Figure 6. Relationship between average bottom temperature (°C) and ln (weight of four-year-old cod in kg) for seventeen North Atlantic stocks.

Discussion

Fish production is governed by the processes of recruitment and growth, but most of the interannual and long-term variability in production is ascribed to recruitment. The nature of the coupling between early feeding cod larvae and plankton production is at the heart of much recent research into recruitment variability. Comparisons of distribution and timing of spawning between areas help to identify common factors and to refine the models linking plankton production and successful spawning strategies; however, there is still some way to go, both in developing models of larval food production and in carrying out related field studies.

Most of the evidence to date supports the hypothesis that timing and location of spawning in cod (but not in all fish species) are closely coupled to plankton production, but there are apparent exceptions. At Flemish Cap, for example, the peak of *Calanus* abundance occurs almost two months later than the peak of cod larvae abundance and Myers *et al.* (1993) conclude that there is only a general, rather than a precise, match between larval production and planktonic food, which implies that recruitment will not be strongly influenced by changes in the timing of the plankton peak. The mismatch in this case may be due to inadequate data, but the main point in the context of the present paper is that the comparative approach can be seen to be useful in highlighting instances like this, which may lead to rejection or reformulation of the match–mismatch hypothesis.

Some substantial issues are also raised by the comparison of size-at-age for different stocks with different temperature regimes. The regression of ln(weight-at-age 4) on temperature indicates that 95% of the variability between stocks can be explained by the temperature and that there is a very big effect of temperature on growth (29% per C°). Growth rate of juvenile sockeye salmon was also found by Brett and Higgs (1970) to increase very rapidly with increasing temperature. Clearly, it is much easier to establish such a relationship between stocks with widely differing average temperatures than it is to quantify the effects within a stock. Since the rates of all the constituent processes involved in growth (feeding, assimilation, metabolism, transformation, and excretion) are controlled by temperature, it is worth investigating whether a similar relationship applies within stocks. Equally, there is little point in investigating the effects of density dependence, food, or other factors on

growth until the temperature effects have been removed.

Finally, if the slope of the between-stock regression is a guide to the magnitude of the temperature effect, then one of the major, predictable climate-induced changes in cod production will be via the growth rate. Growth may also be affected by other, less predictable factors, such as food, and of course the overall production of cod also depends on recruitment and natural mortality, but, other things being equal, increasing temperatures can be expected to have a marked effect on growth rates. Short-term catch forecasts should also incorporate temperature effects in order to predict future weight-at-age.

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Age-specific paternal influences on reproductive success of Atlantic cod (*Gadus morhua* L.) of the Grand Banks, Newfoundland

Edward A. Trippel and M. Joanne Morgan

Trippel, E. A., and Morgan, M. J. 1994. Age-specific paternal influences on reproductive success of Atlantic cod (*Gadus morhua* L.) of the Grand Banks, Newfoundland. – ICES mar. Sci. Symp., 198: 414–422.

Declining numbers of old fish and some possible effects that this may have on a stock's spawning period and on the production of viable progeny were examined for Atlantic cod (*Gadus morhua* L.) of the Grand Banks, Newfoundland. Investigations utilized 18 years of spring research-vessel survey data spanning April to June and sampling of offshore spawning assemblages in the years 1991–1993. Analyses concentrated on paternal attributes and demonstrated that young mature males (ages 5–6 years) usually completed their spawning season before older males. Spermatocrit was highly variable (0.13–0.96) within and across twelve age groups and was not correlated with age or gonadosomatic index. The paternal influence on hatching success varied by up to 2.25-fold. However, with respect to all paternal parameters examined, i.e., age, body length, gonadosomatic index, and spermatocrit, there occurred no significant correlate with hatching success. In light of the abrupt decline of age 7+ fish in 1991 on the Grand Banks, and the faster depletion of the testes in young, relative to old fish, this stock may experience a shortening of the spawning season in future years relative to the historical average. Findings also indicate that spermatogenesis proceeded under the cold-water conditions of 1990–1992.

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Introduction

Assessment of spawning-stock biomass in relation to recruitment potential and stock rebuilding is currently an important issue for fisheries managers of Canadian Northwest Atlantic groundfish stocks. Elsewhere, the identification and recommendation of spawning-stock biomass levels to safeguard against stock collapse have made the assumption that gamete quality is not a function of the reproductive experience of the individual, be they virgin, repeat spawner, or potentially senescent (Goodyear and Christensen, 1984; Gabriel *et al.*, 1989; Serebryakov, 1990; Mace and Sissenwine, 1993, and others). If gamete quality and related fertilization and hatching success change with reproductive experience, then the stock component of a stock–recruitment relationship should also be adjusted for gamete quality in relation to the relative abundance of different mature age groups in the population. The abrupt decline in 1991 of age 7+ Atlantic cod (*Gadus morhua* L.) of the Grand Banks, Newfoundland, to a level of about 10% of the long-term average (Baird *et al.*, 1992) and the concurrent decline in age and size at sexual maturity (Morgan *et al.*, 1993) suggest that evaluation of gamete quality in relation to parent reproductive history may be an important prerequisite to the development of a sound management strategy designed to enhance stock recovery. Improving our understanding of the male's role in progeny production in this commercially exploited species is critical to this process.

The reproductive biology of cod in relation to age and body size has been studied much more for females (Sorokin, 1957; Shapiro, 1988. Kjesbu, 1989; Kjesbu *et al.*, 1991) than for males. Those aspects of male cod reproduction that have been reported on, e.g., testes weight, gonadosomatic index, and sperm motility (Sor-

okin, 1960; Krivobok and Tokareva, 1972; Westin and Nissling, 1991), were measured for cod occurring in the Northeast Atlantic, the Baltic, and the Barents Sea. Only recently have some of these characteristics been evaluated for Northwest Atlantic cod, and these analyses have been restricted to captive cod of Scotian Shelf origin (Trippel and Neilson, 1992). Furthermore, compared to other fishes (Trippel and Harvey, 1990; Ridgway *et al.*, 1991), very little is known about the relative importance of different age groups of male cod with respect to overall female spawning success.

The purpose of this study was to document the influence of age on several reproductive attributes of male cod collected from Grand Banks, Newfoundland, and to discuss the implications of these results with respect to future recruitment in this currently depressed stock. Specifically, we examined (i) temporal synchrony in testes depletion as a function of age, (ii) spermatocrit in relation to age and gonadosomatic index, and (iii) sperm potency and associated hatching success in relation to age and body size.

Methods

Cod were collected from spawning aggregations on 28–30 May 1991, 27–30 May 1992, and 5–6 June 1993 from NAFO Subdivision 3L of the Grand Banks. In 1991, collections focused on the Virgin rocks area (46°00′N 50°00′W), whereas in 1992 and 1993 cod were collected closer to the edge of the continental shelf (48°50′N 50°00′W) (Fig. 1). Cod were captured by otter trawl in 15–30 min tows at bottom depths ranging from 75 to 85 m in 1991 and from 340 to 380 m in 1992 and 1993. Bottom temperatures ranged from −0.6 to 0.9°C in 1991, from 2.2 to 2.7°C in 1992, and from 3.0 to 3.4°C in 1993.

Fork length, body weight (W), gonadal stage of development (Templeman *et al.*, 1978; Morrison, 1990), testes weight (T), and gonadosomatic index (GSI = (T/W) × 100)) were determined for 168 males in 1991 and 157 males in 1992. Otoliths were extracted from these fish and ages assessed. Spermatocrit is a measure of the proportion of semen occupied by sperm cells and has implications for fertilization success in the wild (Bouck and Jacobson, 1976). Spermatocrit was estimated by spinning two samples of semen from each male in non-heparinized tubes in a centrifuge for 10 min at 7500 rpm and measuring the proportion of semen occupied by packed sperm cells in each sample. Mean values were used to represent spermatocrit of a male; the two samples from the same individual were commonly within 2–3% of each other. We evaluated the temporal synchrony of gonadal depletion across age classes using two methods. First, the gonadosomatic indices of different age classes were compared. Presumably, those fish closer to the completion of spawning would have lower values than fish just starting spawning. Employment of GSI for this purpose seemed justified as the GSI of spent males has been reported to be unrelated to body size (i.e., <2%) in the Pacific cod (*Gadus macrocephalus*)

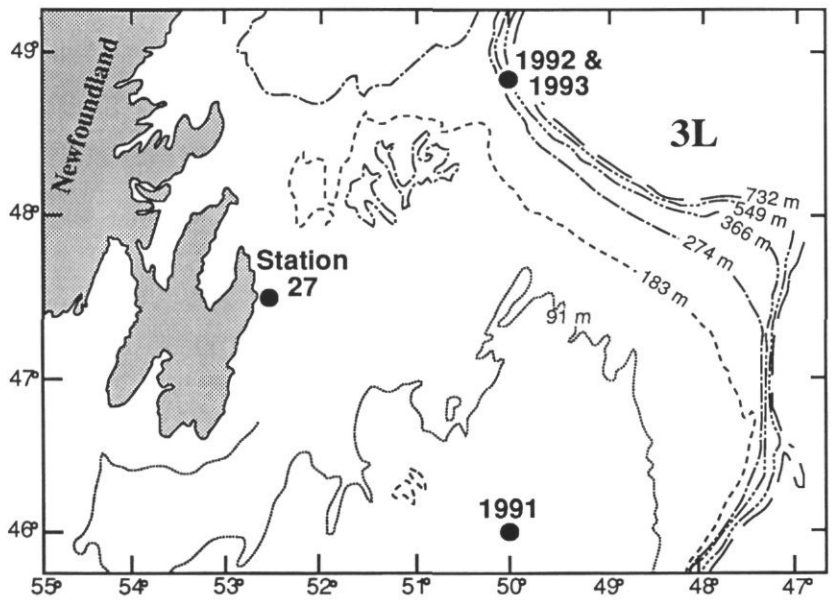


Figure 1. Study area showing the collection sites and location of Station 27.

(Teshima, 1985). Second, the percentage occurrence of unspent mature males of each age class from spring groundfish research vessel survey data spanning April to June, 1973–1992, was calculated. The main spawning period of cod in Division 3L generally ranges from 1 May to 1 July (Myers *et al.*, 1993). From the April to June samples, the description of the maturity stages comprising unspent males are those pertaining to be maturing to spawn in the year of capture (ripening or ripe) as well as those having some milt extruded, though with residual milt remaining in the testes and vas deferentia (partially spent). Spent males were characterized as having completed spawning in the year of capture, with recovery not sufficiently advanced for the outer edges of testes to be pinkish or greyish in colour (Templeman *et al.*, 1978).

On 26 May 1992 and on 5–6 June 1993, sperm and eggs were stripped from several cod to examine fertilization and hatching success of eggs sired by different sizes and ages of males in a manner similar to that reported in Trippel and Neilson (1992). In 1992, ten males 40–67 cm in length were used in crosses with eggs of a six-year-old, 51 cm and 1185 g female. In 1993, six males 45–66 cm were crossed with a seven-year-old, 48 cm, 1030 g female and four males 51–65 cm were crossed with a six-year-old, 48 cm and 845 g female (crosses in 1993 were conducted in triplicate, whereas in 1992 no replicates were performed). For each cross, 100–200 eggs were placed in a beaker containing a 1:100 semen:seawater suspension of 250 ml; each sperm mixture was prepared immediately before the addition of eggs. Eggs and sperm were left in the beaker for 1 min, during which time they were stirred six times and then poured onto a 300 μm mesh screen to remove excess sperm. Eggs were returned to the beaker and 250 ml of sea water was added. Crosses were conducted in beakers kept on crushed ice. They were incubated at 2°C for 8–12 h, which ensured that any zygotes formed could be identified by the presence of 2–4 blastomeres. A light microscope (magnification ×40) was used to estimate percentage fertilization of each cross. Because of conditions at sea, accurate estimates of fertilization success were not obtained in 1993, though a qualitative examination revealed high fertilization rates and good egg quality (Kjørsvik *et al.*, 1990). After assessment of fertilization, eggs were returned, maintained at 2°C and water was exchanged daily. Three days after initiation of the crosses, eggs were transferred from the research vessel "Alfred Needler" to the Northwest Atlantic Fisheries Centre, where they were maintained at 4°C. Hatching occurred from 13 to 14 June 1992 and from 21 to 25 June 1993 (17–18 and 15–20 d post-fertilization, respectively). Hatching success was evaluated by recording the number of larvae in each incubator two days after the completion of hatching. Pearson product-moment correlation coefficients were computed among the various reproductive attributes. Student's *t*-test and Duncan's multiple range test were used to examine for statistically significant differences in fertilization rate and hatching rate among males (SPSS, 1990).

Results

Although high variability was evident within age classes, young males more frequently exhibited gonadal conditions indicative of ending their spawning season sooner than old males. This was noticeable from the gonadosomatic index values in 1991 and 1992 (Fig. 2A) and from the spring research vessel survey data (Table 1; Fig. 3). Specifically, the mean GSIs of mature cod increased with age from 6% for age 4 to 13% for age 12 fish in 1991. Mean GSIs through ages 5–10 increased from 5 to 11% in 1992 (calculated from individual values in Fig. 2A). GSI was positively correlated with both age ($r = 0.48$, $p < 0.01$ in 1991; $r = 0.58$, $p < 0.01$ in 1992) and fork length ($r = 0.40$, $p < 0.01$ in 1991; $r = 0.52$, $p < 0.01$ in 1992). Analysis of spring research survey data spanning 1973–1992 indicated that the incidence of mature males still retaining sperm (i.e., unspent) was highest among age 9+ fish, whereas there were higher occurrences of spent gonads among young cod (ages 5–8) (Fig. 3). Interestingly, in 9 of the 14 years of sampling since 1976 the very young males (age 4) exhibited a higher incidence of the unspent condition as opposed to those that were slightly older (ages 5–8). Moreover, in 9 years all age 4 males captured had not initiated spawning (i.e., gonad ripe).

Table 1. Spring groundfish research vessel surveys for Division 3L indicating the number of captured mature male cod that were aged.

		Number of mature males in age sample
1973	7 Apr–6 May	138
1974	7–21 May	38
1975	9–25 May	233
1976	23 Apr–3 May	292
1977	4–18 May	314
1978	6–17 May	472
1979	17 May–4 Jun	663
1980	10 May–2 Jun	567
1981	6 Apr–7 May	646
1982	6–17 May	954
1985	17 Apr–26 May	943
1986	7–25 May	1068
1987	14 May–1 Jun	930
1988	5–24 May	718
1989	6–28 May	843
1990	18 May–4 Jun	823
1991	11–29 May	371
1992	13 May–6 Jun	230

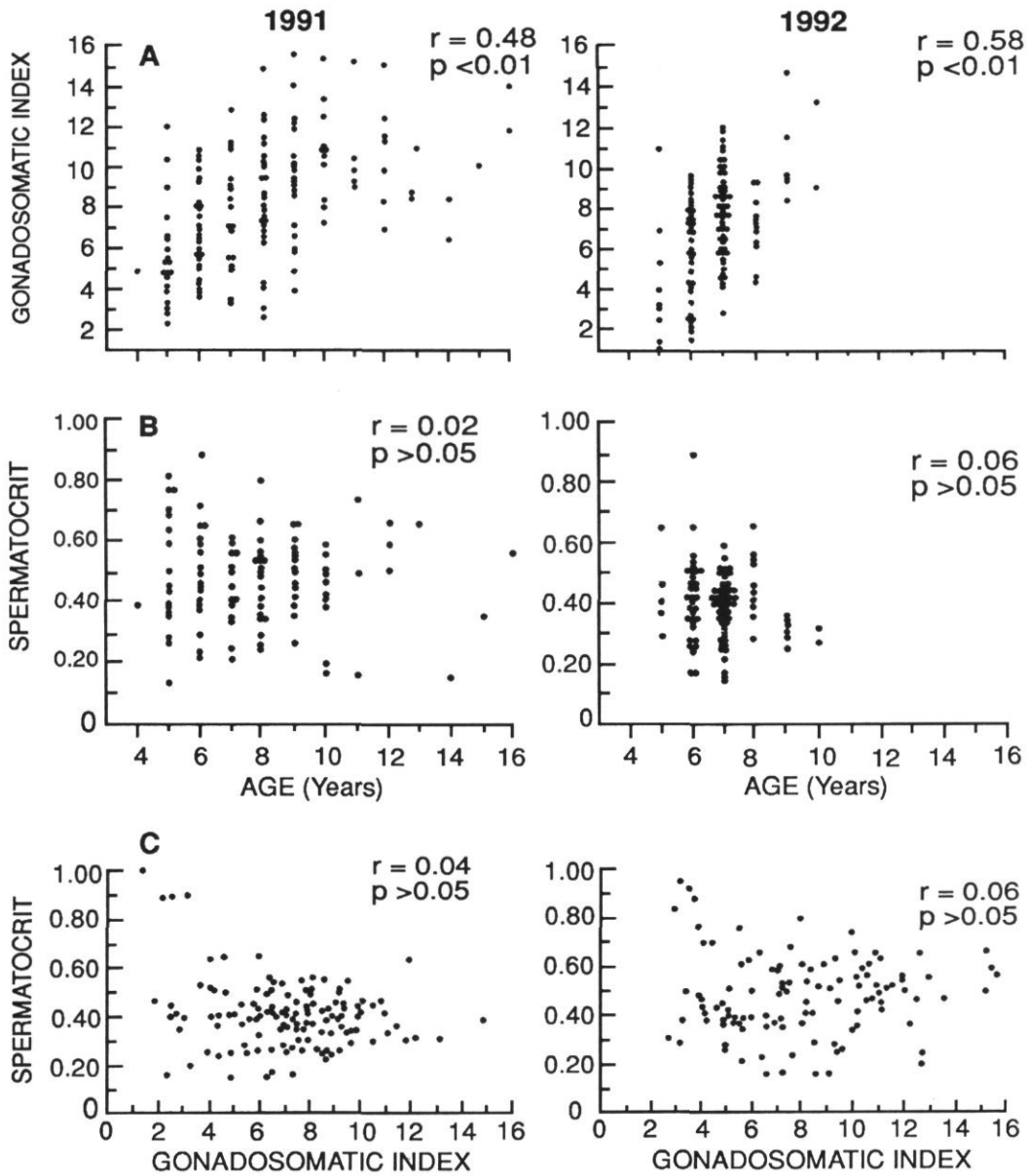


Figure 2. Relationships between gonadosomatic index and age (A), spermatocrit and age (B), and spermatocrit and gonadosomatic index (C) for male cod collected from the Grand Banks from 28 to 30 May 1991 and 27 to 30 May 1992.

Spermatocrits were highly variable within and across age groups in both 1991 and 1992, ranging from 0.13 to 0.96 (Fig. 2B). Age and spermatocrit were not significantly correlated ($r = 0.02$, $p > 0.05$ in 1991; $r = 0.06$, $p > 0.05$ in 1992). In both years, mean spermatocrits ranged from 0.35 to 0.50 for ages 4–16 (Fig. 2B). Spermatocrit and GSI were not correlated ($r = 0.04$, $p > 0.05$ in 1991; $r = 0.06$, $p > 0.05$ in 1992; Fig. 2C), although spermatocrit was high (>0.85) for several males having nearly depleted testes (GSI < 3%).

Fertilization rates in 1992 for small cod (40–50 cm, 520–940 g, age 5–6) and medium-size cod (61–67 cm, 1910–2435 g, age 7–10) were on average 80% (range 70–86%) and 87% (range 85–93%), respectively (differ-

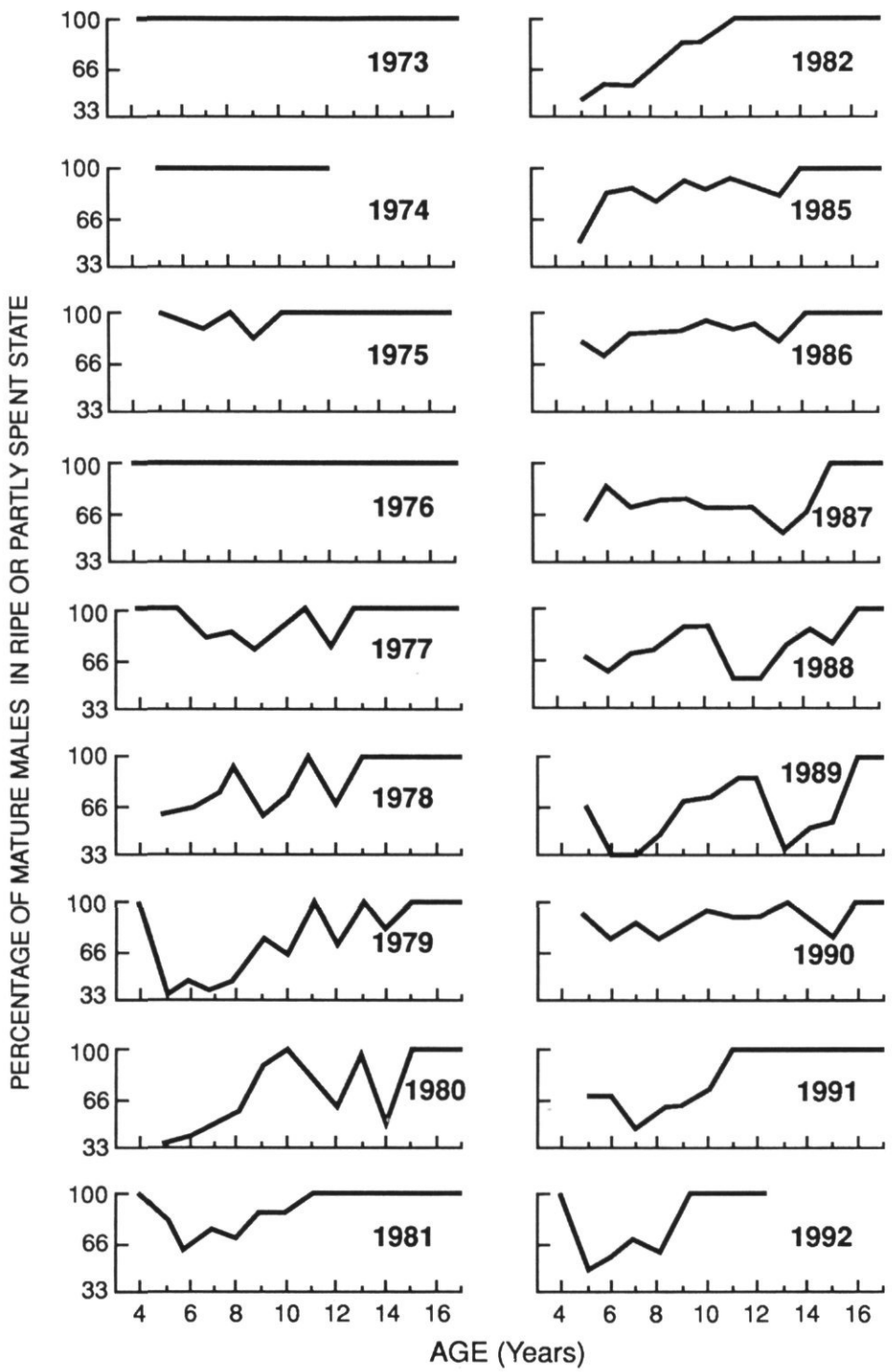


Figure 3. Percentage occurrence of ripe and partly spent mature male Atlantic cod (i.e., unspent males) of the Grand Banks in relation to age from data collected during research vessel spring groundfish surveys of April to June, 1973–1992. Refer to Table 1 for dates and sample size of each survey.

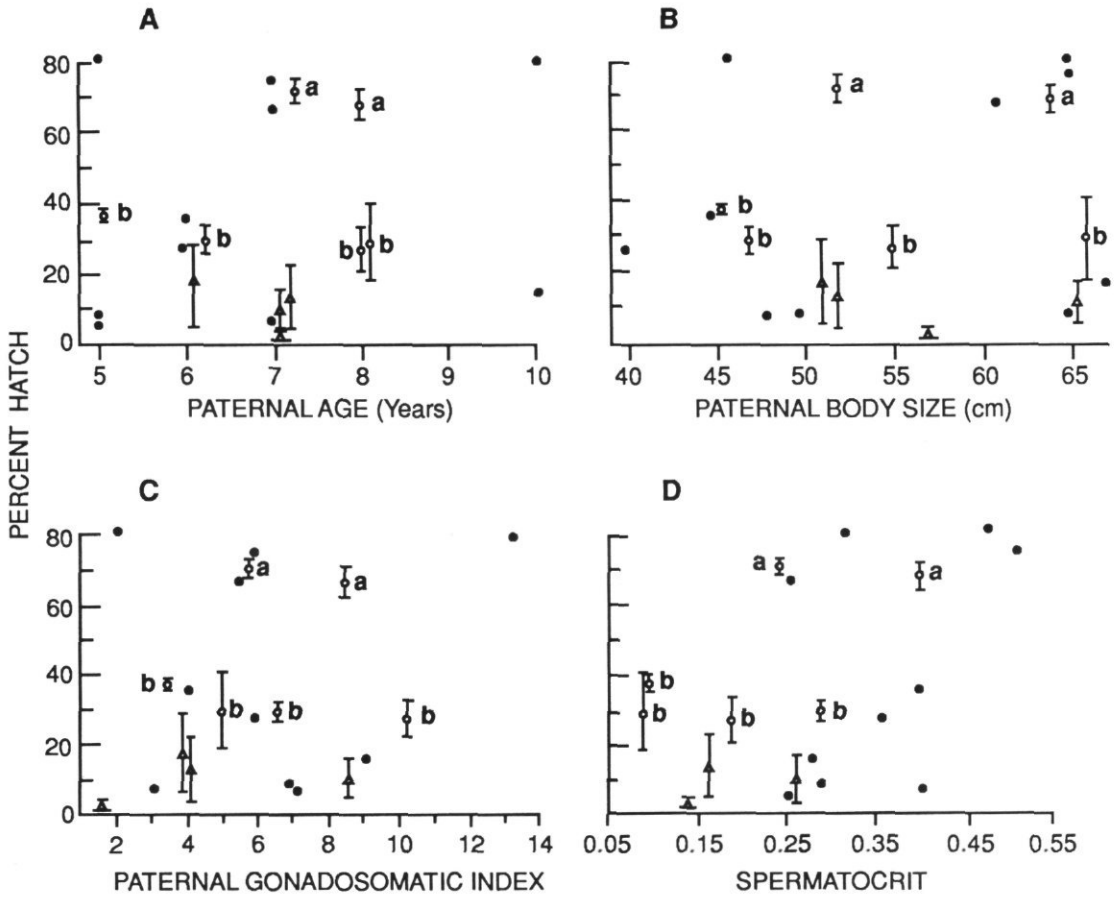


Figure 4. Relationships between hatching success of Grand Banks cod eggs and paternal age (A), paternal fork length (B), paternal gonadosomatic index (C) and, spermatocrit (D). Solid circle (1992): female age 6, 51 cm, and 1185 g; open circle (1993): female age 7, 48 cm, and 1030 g; and open triangle (1993): female age 6, 48 cm, and 845 g. Bars represent one standard error. Comparison of hatching success should be confined to crosses using eggs of the same female (i.e., having the same symbol). For each symbol, values not having a common letter differ significantly (Duncan's multiple range test, $p < 0.05$).

ences in fertilization success were not statistically significant; t-test, $p > 0.05$). Hatching success for eggs of an age 6 female fertilized by ten different males ranged from 5 to 81% in 1992 (Fig. 4; solid circles). Hatching success did not correlate significantly with age, body length, GSI and spermatocrit (all correlation coefficients were less than 0.10, $p > 0.05$).

Males tested in 1993 varied significantly in their capacity to sire young to the hatching stage (Duncan's multiple range test, $p < 0.05$) (Fig. 4). Specifically, two males achieved a mean hatching success of 68 and 72%, whereas four males achieved a mean hatching success of 30–37% when crossed with eggs of an age 7 female (Fig. 4; i.e., the open circles marked by the letter "a" were significantly greater than open circles marked by the letter "b"; Duncan's multiple range test, $p > 0.05$). Mean hatching rates spanned 2 to 18% for the other males used in 1993 and were not significantly different from one another (Duncan's multiple range test, $p > 0.05$, represented by open triangles in Fig. 4). The paternal parameters examined in 1993, as in 1992, did not correlate with hatching success ($r < 0.10$, $p > 0.05$; Fig. 4).

Discussion

The influence of parent age on spawning times may have important implications for recruitment. Cod spawning activity in Division 3L of the Grand Bank occurs predominantly from 1 May to 1 July with peak activity occurring from mid-May to early June (Myers *et al.*,

1993). In light of these spawning times, results from the present study indicate that a greater degree of spawning by young males occurs in early May, whereas older fish continue to spawn into June. The differential success of gametes spawned at different times of the spawning period is of significance to understanding annual variations in recruitment (e.g. the match–mismatch hypothesis; Sinclair and Tremblay, 1984; Lambert and Ware, 1984), especially in consideration of the recent reduction in numbers of old fish from this stock. That is, in the near future, a higher concentration of spawning and the stock's overall zygote production may occur by young fish during the early part of this stock's historical spawning period (all other factors such as environmental influences being equal). The change of a parent stock from one consisting of many to one consisting of few age classes may negatively affect recruitment. Presumably, an extensive multi-age spawning stock would spread its egg production over a longer time period than a spawning stock comprised of few young age classes, hence improving the chances that at least some portion of the stock's egg production is matched with environmental and feeding conditions favourable to larval survival. This situation may be widespread over the Grand Banks, as our evaluation of asynchronous spawning with respect to age has been confirmed for cod in other regions of the Northwest Atlantic (Hutchings and Myers, 1993).

A large proportion of the age 4 mature males had failed to commence spawning by the time of the spring surveys of April–early June. These findings have implications for the estimation of spawning-stock biomass in that the inclusion of these young fish may lead to overestimated values of spawning potential. In white sucker (*Catostomus commersoni*), 60% of young, small precocious males failed to spawn and underwent gonadal atresia in a small Ontario lake (Trippel, 1984), whereas in another lake, gonadal atresia was widespread among all ages of females and was associated with a low abundance of males (Trippel and Harvey, 1990). Sampling Grand Banks cod during July and August would be required to substantiate whether these age 4 males failed to spawn (and underwent gonadal atresia) or whether they started their spawning season much later than older cod. These younger males may comprise a greater portion of the spawning stock than in earlier years, as the age at 50% maturity of males in Division 3L from 1981 to 1992 has declined significantly from 5.2 to 4.3 years over this period (Morgan *et al.*, 1993).

Grand Banks cod declined abruptly in abundance during 1991 (Baird *et al.*, 1992; Parsons, 1993) and their principal prey, capelin (*Mallotus villosus*), declined from 7 million tonnes in 1990 to 0.1 million tonnes in 1991 and was 0.2 million tonnes in 1992 (Miller, 1992). In our trawl samples, the relative abundance of age 7 and older male cod declined from 53 to 16% between 1991 and 1992. At Station 27 (Fig. 1), water temperatures have been below normal throughout the water column since 1983 (Drinkwater, 1993) and were especially cold during the period of gametogenesis prior to the 1991

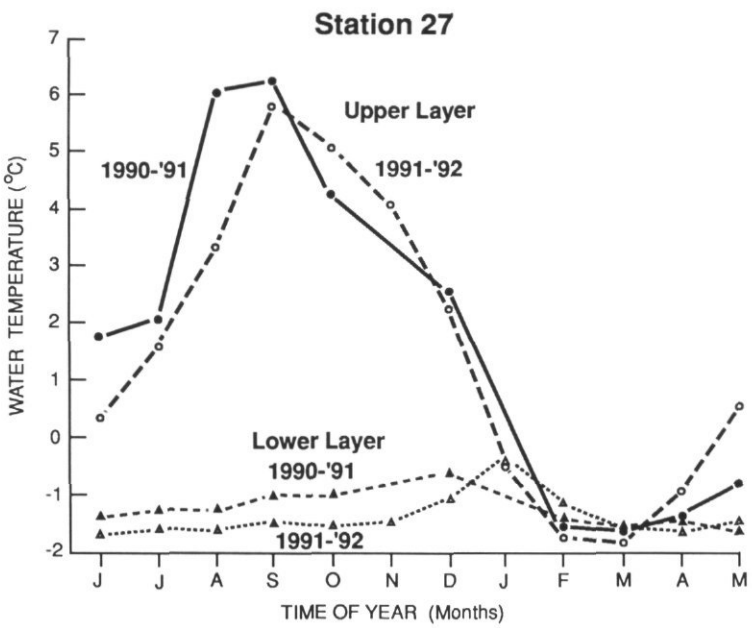


Figure 5. Water temperature of the lower and upper layers at Station 27 from April 1990 to May 1992.

spawning season (Fig. 5). The findings of this study indicate that spermatogenesis did proceed and was not seriously impeded under these cold water conditions.

High variability in spermatocrit across all ages was observed. We found no connection between the relative amount of sperm remaining in the testes and spermatocrit; except in some instances when the testes comprised <3% of total body weight and the semen was thick (spermatocrit >0.85). The range of spermatocrit in Atlantic cod is similar to that of the related freshwater burbot (*Lota lota*) (mean = 0.67, range 0.36–0.91) and was higher than values reported for salmonids and coregonids (means 0.18–0.34) (Piironen and Hyvarinen, 1983).

Spermatocrit as a measure of sperm density has implications for fertilization success, as a higher density of sperm would theoretically result in higher sperm:egg micropyle encounter rates. A review of the literature on spermatocrit in teleost fishes has shown spermatocrit, or its close correlate, sperm density, not to be correlated with fertilization success in concentrated sperm mixtures in two of three studies; however, in diluted suspensions, sperm density correlated positively with fertilization success in all instances (Trippel and Neilson, 1992). In captive cod of Scotian Shelf origin, spermatocrit (range = 0.18–0.99) failed to correlate significantly with egg fertilization success ($r < 0.30$) (Trippel and Neilson, 1992). In the present study, the spermatocrit of individual cod, ranging from 0.26 to 0.51, also failed to correlate with fertilization rates ranging from 70 to 93% in a semen dilution of 1:100. Experiments involving more diluted suspensions of semen would be useful to further evaluate sperm potency of wild fish.

In summary, empirical evidence agrees with previous work done on captive cod and does not support the hypothesis that spermatocrit and sperm potency vary as a function of male age and that weighting of different age groups on these aspects is unnecessary to fine-tune estimates of spawning-stock biomass. Apparently, a pertinent finding from the study is the faster depletion of testes in young, relative to old fish, which may have serious implications for spawning times and future recruitment success in this age-truncated stock. We have also shown that the paternal influence on hatching success can be quite high, which to our knowledge has not been previously documented in wild Atlantic cod.

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ICES mar. Sci. Symp., 198: 423–429. 1994

Phytoplankton, *Calanus finmarchicus*, and fish eggs southwest of Iceland, 1990–1992

Astthor Gislason, Olafur S. Astthorsson, and Hafsteinn Gudfinnsson

Gislason, A., Astthorsson, O. S., and Gudfinnsson, H. 1994. Phytoplankton, *Calanus finmarchicus*, and fish eggs southwest of Iceland, 1990–1992. – ICES mar. Sci. Symp., 198: 423–429.

Year-to-year changes in phytoplankton biomass and the abundance of *Calanus finmarchicus* and gadoid eggs were monitored during the spawning season of cod in 1990, 1991, and 1992, near the main spawning grounds of the cod stock southwest of Iceland. In order to study annual variations, a seasonal study was also undertaken in 1991. The spring growth of the phytoplankton peaked earlier in 1991 (early May) than in both 1990 and 1992 (late May to early June), because of an earlier stratification observed in that year. During 1991 the abundance of *C. finmarchicus* showed two maxima, in May–June (ca. 50 000 individuals 100 m^{-3}) and in early August (ca. 210 000 individuals 100 m^{-3}), reflecting the two generations of *C. finmarchicus* produced during the year. Although data for the summer months of 1990 and 1992 are lacking, it seems probable that there were also two generations of *C. finmarchicus* in those years. The first spawning of *C. finmarchicus* probably peaked around one month earlier in 1991 (April) than in both the preceding and succeeding years (May). The second spawning of *C. finmarchicus* probably also occurred somewhat earlier in 1991 (May and June) than during both 1990 and 1992 (June and July). In all three years the spawning of *C. finmarchicus* began before the observed phytoplankton spring bloom, while the peak spawning in spring appeared to be closely linked to the phytoplankton growth. It is suggested that the early development of the plankton community in 1991 may have been unfavourable for the recruitment of the Icelandic cod stock.

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Introduction

In spite of the importance of *Calanus finmarchicus* as food for cod larvae (e.g., Ellertsen *et al.*, 1984; Turner, 1984; Jónsson and Fridgeirsson, 1986; Thorisson, 1989) little information is available on its life cycle on the main spawning grounds of cod southwest of Iceland. With the exception of Hallgrímsson's (1954) study, which did not cover the main spawning area, all studies on *C. finmarchicus* on the banks southwest of Iceland have been based on material collected during spring (Paulsen, 1906; Fridgeirsson *et al.*, 1979, 1981; Astthorsson *et al.*, 1983; Gislason and Astthorsson, 1991) and therefore there has been limited opportunity to interpret the seasonal dynamics of *C. finmarchicus* on the main spawning grounds.

The aim of the present paper is to examine the seasonal abundance of *C. finmarchicus* in relation to phytoplankton biomass within the main spawning area of the Icelandic cod off the southwest coast of Iceland. Also the match in the time of spawning of *C. finmarchicus* in spring and the abundance of first-feeding cod larvae, as judged by the numbers of cod eggs, is considered. The study covered the whole year of 1991, while material from the springs of 1990 and 1992 has also been analysed and therefore the question of interannual variability is also addressed.

Material and methods

The sampling was undertaken during 1990–1992 at two stations located south of Reykjanes near the main spawning grounds of the Icelandic cod stock (Fig. 1). There, the water mass is mainly Atlantic water derived from the Irminger Current but mixed with variable quantities of fresh water from the land (Stefánsson, 1961, 1981).

The stations were located 1.5 and 6.5 nm from the coast, where the bottom depth is 80 and 136 m, respectively (Fig. 1). Samples were collected at approximately monthly intervals. During 1991 the stations were occu-

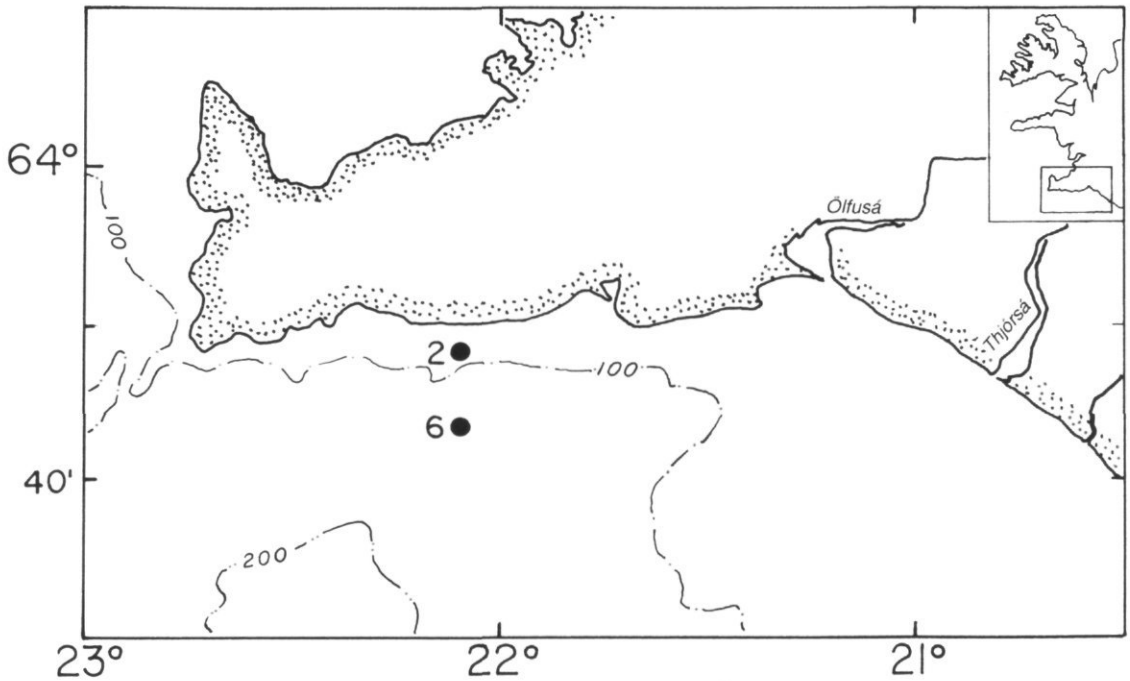


Figure 1. Location of sampling stations southwest of Iceland.

pied ten times from February to November, while in 1990 and 1992 the stations were taken respectively four and three times from the end of March to early June. An overview of the sampling is presented in Table 1. In order to emphasize annual and interannual differences we present the data as means from the two stations.

Hydrography. Temperature was recorded with a Sea Bird Electronics SBE-9 CTD. On one occasion (26 June 1991), however, temperature measurements were carried out using reversing thermometers.

Phytoplankton. Seawater samples (1 or 2 l) for the measurement of chlorophyll *a* were collected from depths of 0, 5, 10, 15, 20, and 30 m and filtered through GF/C glass-fibre filters. The filters were homogenized in 90% aqueous acetone and the extract measured in a spectrophotometer according to the method described by Strickland and Parsons (1968).

Zooplankton. The zooplankton was collected with a 60 cm diameter Bongo net with 335 μm mesh. The Bongo net was towed obliquely from the surface to ca. 10 m above the bottom (Station 2) or to 100 m depth (Station 6) and back to the surface, while the ship cruised at 2.5 knots. Payout and retrieval rates were ca. 10 m min^{-1}. The volume of water filtered by the net was measured with a HydroBios flowmeter mounted in the mouth of one of the nets and the depth was monitored with a Scanmar acoustic depth recorder fitted on the wire just above the Bongo frame. The zooplankton samples were preserved in 4% neutralized formalin after collection. Except on a few occasions, when the samples were very small, they were split with a Motoda splitter (Motoda, 1959) and a subsample analysed for species composition. For the present analysis we present abundance data only on *C. finmarchicus*, which was the most numerous zooplankter in the samples, and fish eggs. When possible, at least 200 individuals of *C. finmarchicus* and 200 fish eggs were counted. Also, all the *C. finmarchicus* counted from the samples were determined to developmental stages. The diameter of fish eggs was measured under a stereomicroscope with a

Table 1. Sampling dates in 1990, 1991, and 1992.

	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
1990	—	31	—	3, 22	6	—	—	—	—	—
1991	20	—	6	4, 31	6, 26	13	7	11	—	30
1992	—	30	—	7	3	—	—	—	—	—

micrometer eyepiece. When possible, at least 30 eggs selected randomly from the samples were measured.

Results

Hydrography

Seasonal changes in temperature in the upper part of the water column are presented in Figure 2. Minimum temperatures were recorded during March–April (5–6°C), while maximum temperatures were measured in August (11–12°C). Temperature differences in the springs of 1990, 1991, and 1992 were very small with warming of the surface waters beginning in late April during all three years (Fig. 2).

The main rivers discharging fresh water into the sea area at the southwest coast are the rivers Ölfusá and Thjórsá (Fig. 1), and the freshwater efflux plays a major role in the establishment of stratification nearshore in early spring (Thórdardóttir and Stefánsson, 1977; Stefánsson and Gudmundsson, 1978; Ólafsson, 1985; Thórdardóttir, 1986; Ólafsson *et al.*, 1993). The transition from winter conditions, with vertical isolines for temperature and salinity, to spring conditions, with the beginning of stratification during the years of investigation, can be summarized as follows (Kristmannsson, 1994; and unpubl.). Stratification of the water masses was established earliest in 1991 or in early April, reflecting an increase in the flow from the rivers Ölfusá and Thjórsá (unpubl. data from the National Energy Authority). In 1990, stratification was established one month later (early May) and in 1992 a remarkable two months later (early June) than in 1991. Similar to 1991, the beginning of stratification in both 1990 and 1992 followed increases in the flows from the rivers Ölfusá and Thjórsá (unpubl. data from the National Energy Authority).

Phytoplankton

During the three years of the investigations the phytoplankton standing stock was very low in February and March (Fig. 3). In 1991 the chlorophyll *a* concentration increased sharply in April and culminated at the beginning of May (ca. 12 mg chl *a* m^{-3}). After that, the biomass of phytoplankton decreased sharply and lower values were recorded throughout the summer and early winter.

The phytoplankton spring bloom probably started earlier in 1991 than in both the preceding and succeeding years (Fig. 3). Thus, in early May, when the maximum spring bloom was observed in 1991, the concentration of chlorophyll *a* was still very low in both 1990 and 1992. In 1990, the phytoplankton biomass reached a maximum during the latter part of May, which was approximately two weeks later than in 1991, and in 1992 the maximum may have been as late as early June or even later (Fig. 3). It must be mentioned in this context, however, that because of the relatively long time interval between sampling (ca. one month), temporary maxima in the chlorophyll *a* levels may have gone undetected. This might for example have happened during May 1990 and 1992 (Fig. 3). Nevertheless, the available data do clearly indicate an earlier spring growth of the phytoplankton south of Iceland in the year 1991 than in both the preceding and succeeding years, and, further, that this difference was on the order of two to three weeks. These findings of an earlier development of phytoplankton in 1991 compared to the years 1990 and 1992 are also supported by data from stations in the vicinity of those dealt with here (H. Gudfinnsson, unpubl.).

Calanus finmarchicus

Calanus finmarchicus was the most numerous zooplankter in the samples and it usually made up 40–80%

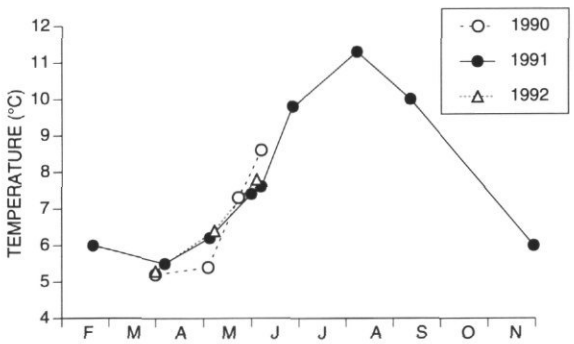


Figure 2. Seasonal changes in temperature southwest of Iceland from February to November 1991, and from March to June in 1990 and 1992. The values are means of measurements from 0, 5, 10, 15, 20, 30, 40 and 50 m from two stations.

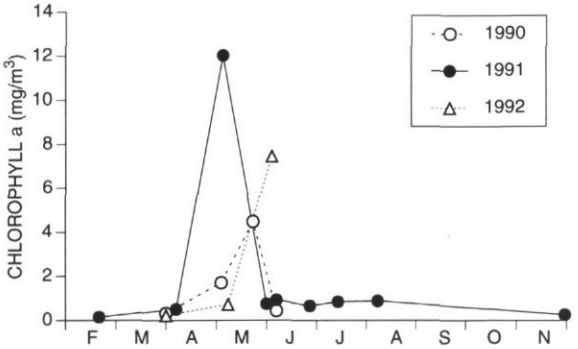


Figure 3. Seasonal variation in the concentration of chlorophyll *a* (means from 0, 5, 10, 15, 20 and 30 m) southwest of Iceland from February to November 1991, and from March to June in 1990 and 1992. The values are means from two stations.

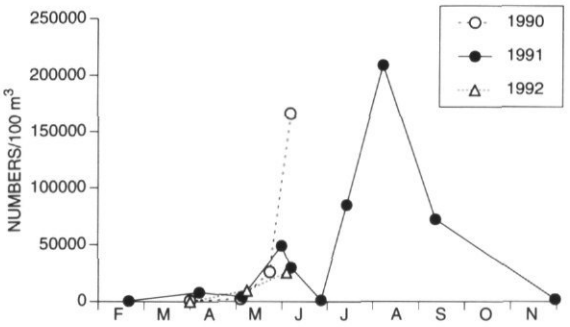


Figure 4. The abundance of *Calanus finmarchicus* southwest of Iceland from February to November 1991, and from March to June in 1990 and 1992. The values are means from two stations.

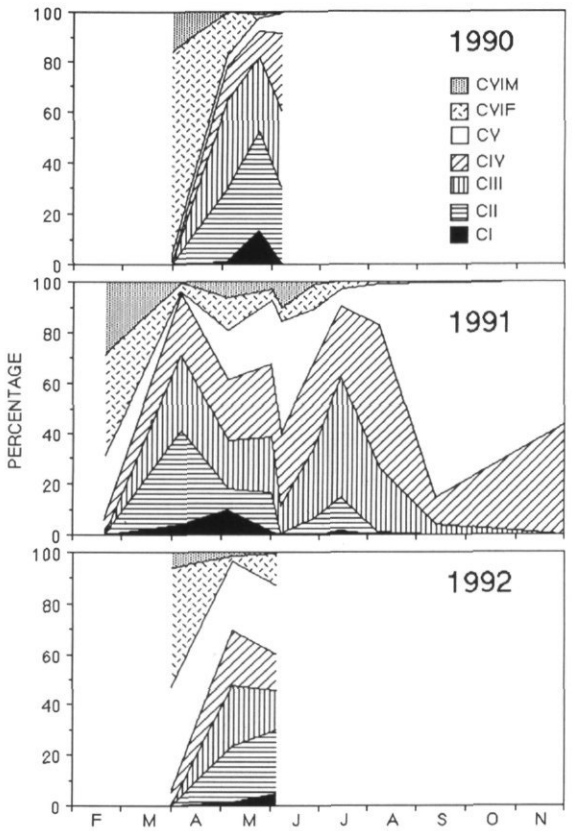


Figure 5. The relative abundance of copepodite stages of *Calanus finmarchicus* from February to November 1991, and from March to June in 1990 and 1992. The values are means from two stations.

of all the animals. Few *C. finmarchicus* were observed in the winter samples (Fig. 4), but during all three years the abundance began to increase in May. During 1991 two maxima in numbers were recorded, the first in May–June (ca. 50 000 individuals 100 m^{-3}) and the second and much greater one in early August (ca. 210 000 individuals 100 m^{-3}). After the second maximum, the numbers declined markedly in the autumn, and early winter samples (Fig. 4). During May–June 1990 the numbers caught were approximately three and six times greater than at the same time of the year in 1991 and 1992, respectively.

The age structure of *C. finmarchicus* during the whole year of 1991 and in the springs of 1990 and 1992 is shown in Figure 5. By the end of February 1991, mature individuals dominated in the samples (ca. 70%), indicating that at that time the spawning was about to begin. The offspring from this spring spawning were found in the samples on the next sampling date (beginning of April) and then the proportion of copepodite stages I, II, and III observed through the year was greatest (ca. 70%). The abundance of copepodite stages I, II, and III in spring was however greatest in late May indicating that peak spawning occurred during April. During May and June, high percentages of mature individuals (ca. 20%) were again observed, suggesting that the spring generation was now becoming mature to produce the second generation of the year. The offspring from this second spawning appeared in the samples by the end of June and in the middle of July when a second peak in the relative abundance of copepodite stages I, II, and III was observed (Fig. 5). The percentage of these young developmental stages declined in August, and in September most of the animals had developed to the overwintering stages (stages IV and V).

It can be seen from Figure 5 that during 1991 a higher proportion of the *C. finmarchicus* stock participated in the first spawning in March and April than in the second one in May and June. The number of offspring produced from the first spawning, however, was much smaller (Fig. 4), the reason probably being that the parent stock producing the first generation was much smaller than the one producing the second generation. Different predation pressures during the two periods may, however, also play a part.

As indicated by the maxima in the ratio of mature individuals in spring and the subsequent recruitment of copepodites (Fig. 5), the first spawning of *C. finmarchicus* south of Iceland probably peaked ca. one month earlier in 1991 (April) than in both 1990 and 1992 (May). Data for the summer months of 1990 and 1992 are unfortunately lacking, but it seems likely that, similar to 1991, there was also a second spawning of *C. finmarchicus* in those years. The data from 1992 do indeed support this, as the relative abundance of mature individuals was increasing at the end of the study period (Fig. 5). Calculations based on Belehrádek equations from

Corkett *et al.* (1986) also predict that in 1990 and 1992 the spring generation born in May was becoming mature in June (cf. Figs. 3, 5). After becoming mature, there would follow a period of egg maturation, and spawning would then follow shortly afterwards. Thus, similar to the first spawning of *C. finmarchicus*, the second spawning probably also occurred somewhat earlier in 1991 (May and June) than during both 1990 and 1992 (June and July). Further, it seems evident that in all three years the first spawning of *C. finmarchicus* appeared to begin before the observed phytoplankton spring bloom, while the main spawning in spring appeared to be linked to the phytoplankton growth (cf. Figs. 3, 5).

Fish eggs

Fish eggs were found in the samples from the end of March to early June (Fig. 6). The highest numbers were observed in 1991 when about three times more eggs were caught than during both 1990 and 1992. In 1990 the number of fish eggs peaked in late May, while in 1991 and 1992 maximum abundance was recorded in early May.

The size distribution of the fish eggs was similar in 1990, 1991, and 1992. Two distinct size classes with modes at about 1.1–1.2 mm and 1.4–1.5 mm were apparent in March and April. These corresponded to eggs from saithe (*Pollachius virens*), on one hand, and cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) on the other (Russell, 1976; Fridgeirsson, 1978). During this period the ratio of saithe eggs was 60–90%, the rest mainly being cod and haddock eggs. In May and June the peaks in the egg size distributions probably corresponded mainly with eggs from dab (*Limanda limanda*) (ca. 0.8–0.9 mm), whiting (*Merlangius merlangus*) (ca. 1.0–1.1 mm), and cod and haddock (ca. 1.4–1.5 mm). At this time the eggs of cod and haddock dominated (50–70%). Judging by the spawning-stock biomasses of the Icelandic cod and haddock stocks in 1990, 1991, and 1992 (cod respectively 332 000, 221 000, and 260 000 t, and haddock, respectively 107 000, 104 000, and 92 000 t Anon., 1993), the majority (ca. 70%) of the eggs classed as cod and haddock eggs were from cod.

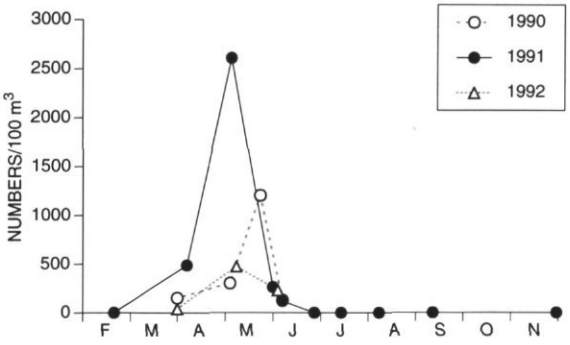


Figure 6. The abundance of fish eggs southwest of Iceland from February to November 1991, and from March to June in 1990 and 1992. The values are means from two stations.

Discussion

The earlier spring growth of phytoplankton in 1991 than in both 1990 and 1992 (Fig. 3) can probably be attributed to the earlier stratification observed in that year. Thus, our results confirm the importance of the freshwater outflow in shallow waters at the southwest coast of Iceland in initiating phytoplankton growth by stabilizing the water column (Thórdardóttir and Stefánsson, 1977; Thórdardóttir, 1986).

The first spawning of *C. finmarchicus* began before the observed phytoplankton spring bloom in all three years of the investigations (cf. Figs. 3, 5). This is consistent with findings from the Norwegian Sea (Østvedt, 1955), the Barents Sea (Skjodal *et al.*, 1987), and North Norwegian fjords (Davis, 1976; Diel and Tande, 1992). If an abiotic factor, such as change in day length during the winter–spring transition (Fransz, 1976) was alone stimulating the pre-bloom spawning of *C. finmarchicus*, then one would have expected it to occur at the same time during the three-year period. As this was not the case, some other stimulus must have been involved. Temperature is another abiotic factor possibly controlling the spawning time (Fransz, 1976; Ellertsen *et al.*, 1987); however, as the temperatures during the spring periods were very similar (Fig. 2) neither can this explain the difference in spawning time. A more likely explanation is therefore that the pre-bloom spawning was stimulated by a temporary and short-lived increase in phytoplankton, but which was not detected in our investigations, and which occurred in March 1991, and April 1990 and 1992. Thus, in early spring in the open waters south of Iceland, weak stratification may easily be broken down by winds, which means that conditions for phytoplankton growth are often unstable at that time. By the middle of March, however, radiation levels have reached the minimum necessary for plant growth (Thórdardóttir, 1986). Therefore phytoplankton increase sufficient to stimulate the spawning of *C. finmarchicus*, may have begun earlier than actually observed, and then declined owing to the breakdown of stratification.

During 1991, two generations of *C. finmarchicus* grew up southwest of Iceland, as was probably also the case in 1990 and 1992 (Fig. 5). This concurs with studies from other neritic waters at similar latitudes (e.g., Lie, 1965; Matthews *et al.*, 1978; Hallgrímsson, 1954; Astthorsson and Gislason, 1992). In all three years heavy spawning in spring seemed to be linked to the vernal blooming (cf.

Figs. 3, 5). During 1991 peak spawning probably occurred in April, while in 1990 and 1992 this probably took place in May. This is in agreement with an earlier development of the phytoplankton in 1991 compared to both 1990 and 1992. The results thus indicate a close relationship between the spring spawning of *C. finmarchicus* and the phytoplankton spring bloom on the spawning grounds of cod southwest of Iceland. Several workers have previously shown the main spawning of *C. finmarchicus* to be closely associated with the spring bloom (e.g., Marshall and Orr, 1972; Tande and Hopkins, 1981; Hopkins *et al.*, 1982; Diel and Tande, 1992; Astthorsson and Gislason, 1992).

Eggs and larval stages of copepods are considered to be the most important food for larval cod (e.g., Ellertsen *et al.*, 1984; Turner, 1984; Jónsson and Fridgeirsson, 1986; Thorisson, 1989), and the degree of match and mismatch in the time of larval fish abundance and suitable prey may explain at least a part of the variability in the recruitment of the fish stocks (Cushing, 1974, 1990). The available data do not enable an evaluation of a match or mismatch between the cod larvae and their food. However, it seems likely that the observed variability in the timing of the spring spawning of *C. finmarchicus* could have an effect on the growth and survival of first feeding larval cod, and therefore also on the recruitment of the Icelandic cod stock. Further, it is noteworthy that in spite of approximately three times higher densities of cod eggs in 1991 compared to both 1990 and 1992 (Fig. 6) the recruitment to the Icelandic cod stock was c. 45% lower in that year than in both 1990 and 1992 (Anon., 1993). This is possibly related to the early development of the plankton community in 1991, which therefore seems not to have been favourable for the recruitment.

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Gut content analysis of first-feeding cod larvae (*Gadus morhua* L.) sampled at Lofoten, Norway, 1979–1986

Petter Fossum and Bjørnar Ellertsen

Fossum, P., and Ellertsen, B. 1994. Gut content analysis of first-feeding cod larvae (*Gadus morhua* L.) sampled at Lofoten, Norway, 1979–1986. – ICES mar. Sci. Symp., 198: 430–437.

The spawning and distribution of eggs and first-feeding larvae of Northeast Arctic cod (*Gadus morhua* L.) in the Lofoten area have been monitored for several years, and a gut analysis of first-feeding cod larvae has been performed for the same time period. The larvae initiated their feeding 4 days after hatching. During the first 2–3 days of feeding the gut content was of phytoplankton origin. Small flagellates and aggregates, presumably faecal material from crustaceans, were found in connection with clusters of thin filaments. During this period the larvae also initiated feeding on nauplii of *Calanus finmarchicus*, and when the yolk sac was resorbed, 8 days after hatching, this prey organism dominated both in the gut content and in the well-mixed watermasses where the larvae were found. A relatively strong relation was found between the abundance of copepod nauplii in the watermasses and the numbers of copepod nauplii in the gut of late yolk-sac and more advanced larvae. The carapax lengths of the copepod nauplii found in the guts of the first-feeding larvae were between 120 and 400 μm, and the larvae continued to prey upon copepod nauplii in this size group until they had reached a standard length of 15 mm; the relative importance of this food item decreased after the larvae had reached a length of 10 mm. Copepod eggs, bivalve larvae, large diatoms, tintinnids, and different stages of krill are occasionally found in the guts of cod larvae. Some copepodites of *C. finmarchicus* were found in larvae with standard length down to 6 mm; however, copepodites did not become the dominant prey item until the larvae were 10 mm. When the larvae had established feeding on copepodites, the size range of the prey organisms found in the larval guts increased to 200–2000 μm.

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Introduction

Numerous studies on the gut content of marine fish larvae have been carried out (Wiborg, 1948; Bhattacharyya, 1957; Nishiyama and Hirano, 1985; Heath, 1989), showing that the minimum size of the prey is determined by the energy demand of the larvae, while the upper limit of prey size is set by the mouth opening. The general trend is that the larvae start to feed on a material of phytoplankton origin, then after 2–3 days switch over to copepod nauplii and thereafter to copepodites and copepods when the mouth opening is large enough to feed upon them. Various other prey species, such as appendicularians, mollusc veligers, tintinnids, rotifers, and different stages of krill, are occasionally found in the larval gut.

Cod (*Gadus morhua* L.) larvae, both from rearing experiments and in the sea, are often found to have an unidentifiable green mass and algae in their gut at the first-feeding stage (Wiborg 1948; Nordeng and Bratland, 1971; Bainbridge and McKay, 1968; Last, 1978; Kane, 1984; Kvenseth and Øiestad, 1984; van der Meeren, 1991). After a few days they start to feed on different stages of copepods, in the Lofoten area mainly on *C. finmarchicus*; however, an enigma is that the fatty acid content of 2–3 weeks' old larvae seems to be dominated by acids from phytoplankton origin (Klungsøyr *et al.*, 1989).

A large sampling programme for larval cod and their prey organisms was carried out in the Lofoten area during 1979–1986 (Ellertsen *et al.*, 1990) to test the critical period concept first put forward by Hjort (1914). In the present work, a gut content analysis was performed on this material to investigate the importance of "green guts" for first-feeding cod larvae, to evaluate the importance of different stages of *C. finmarchicus* in the diet, and to look for a relation between the concentration of nauplii in the sea and in the larval guts as the larvae grow.

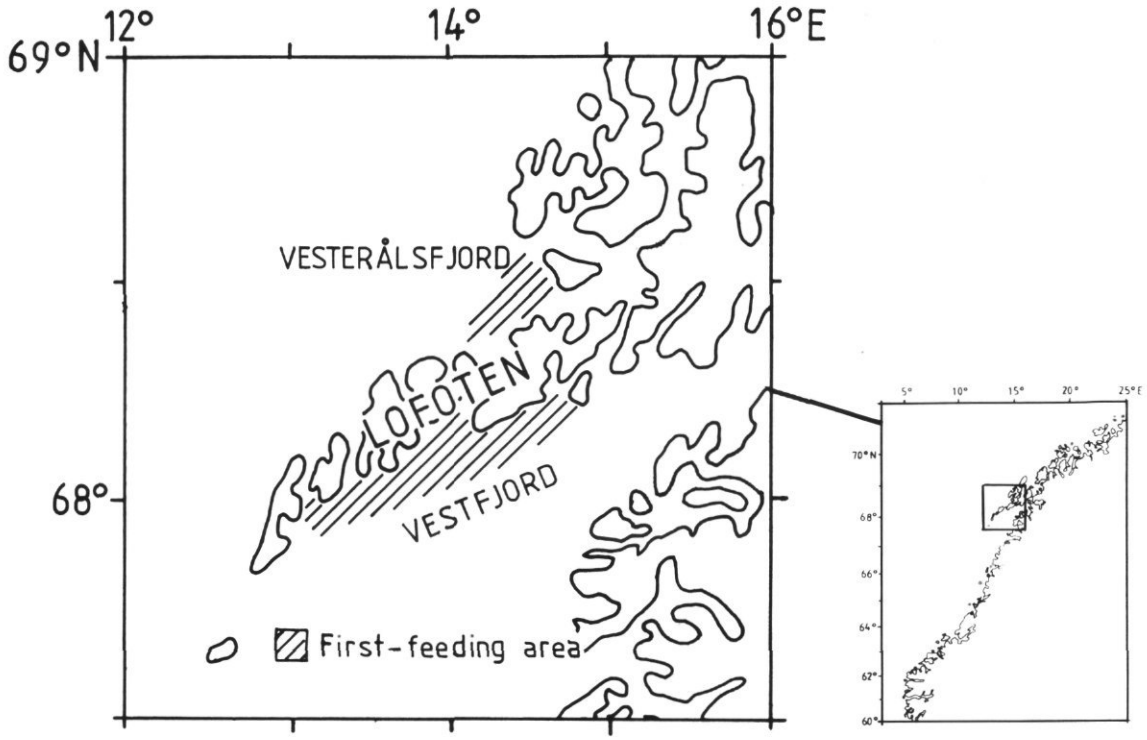


Figure 1. The Lofoten region off the coast of northern Norway where the sampling of first-feeding cod larvae took place during the period 1979–1986.

Material and methods

The data in the present paper were sampled during surveys in the Lofoten area (Fig. 1) in northern Norway during the period 1979–1986. Sampling was carried out from the end of April to the beginning of May, and in 1986 additional sampling was carried out at the beginning of June. The larvae were sampled with conical dip nets with 0.5 m^2 opening and 375 μm mesh size hauled vertically from 50 m depth to the surface. The additional sampling in June 1986 was conducted with larger dip nets with 2.0 m^2 opening and with 10 m^2 MOCNESS (Wiebe *et al.*, 1976) hauled in steps from 50 m to the surface. The nauplii were sampled at 0, 5, 10, 15, 20, 30, and 40 m with a plankton pump, and filtered out of the samples with 90 μm plankton nets. The larvae were preserved in 4% formaldehyde solution of 10‰ salinity. The numbers of nauplii from each depth were counted manually. The larvae were staged according to Fossum (1986); standard length of the larvae was measured along with dry weight. The prey organisms were identified and total length measured, except for copepod nauplii, where the carapax length was used. The feeding ratio (number of cop. nauplii $\times$ gut^{-1}) was compared with the mean naupliar concentration in the sea estimated from pump samples at the site at which the cod larvae were sampled with dip nets. The relationship between feeding ratio and naupliar concentration was established using the model of Sundby and Fossum (1990). The data were fitted to the model by the Newton method of non-linear regression (SAS, 1988).

Results

The gut contents of 2784 larvae with standard lengths between 3.6 and 18.5 mm were examined. The statistics of the larval gut examinations are given in Tables 1 and 2. The number of larvae examined varied to some extent between years, and most of the larvae examined were from 1982 and 1983. Length and weight were not significantly different between years, except from the larvae belonging to stage 9, sampled in 1986. The reason for this was that a proportion of these larvae, together with the stage 10 larvae, were sampled in early June, while all the rest of the sampling was carried out in the last part of April and within the first 14 days of May. More than 300 larvae were investigated from each stage, except from stage 10 where 43 larvae were examined. The mean length and the mean dry weight of the larvae in the

Table 1. The statistics (mean value with one standard deviation) for the larvae in the gut examinations.

	Stage	No. of larvae	Standard length (mm)	Dry weight (μg)
1979	5	19	4.6±0.2	34±5
	6	27	4.7±0.3	39±5
	7	59	4.9±0.3	50±10
	8	48	5.4±0.4	67±18
	9	18	6.0±0.4	99±24
1981	5	43	4.5±0.2	36±5
	6	32	4.8±0.3	42±6
	7	17	5.0±0.3	49±9
	8	9	5.1±0.3	51±7
	9	4	5.5±0.4	78±18
1982	5	92	4.3±0.3	36±6
	6	249	4.4±0.3	40±8
	7	260	4.6±0.4	50±13
	8	203	5.0±0.5	67±23
	9	76	5.9±0.8	130±67
1983	5	77	4.2±0.2	40±10
	6	190	4.3±0.3	42±9
	7	218	4.5±0.3	53±13
	8	209	4.9±0.4	76±27
	9	193	6.0±0.8	171±94
1984	5	23	4.3±0.2	37±8
	6	37	4.4±0.2	41±9
	7	29	4.8±0.4	53±16
	8	17	5.4±0.5	79±25
	9	14	6.2±0.7	150±83
1985	5	46	4.6±0.3	41±5
	6	89	4.5±0.3	42±6
	7	68	4.8±0.3	53±12
	8	27	5.2±0.5	80±20
	9	14	5.9±0.9	134±63
1986	5	44	4.2±0.3	40±6
	6	67	4.4±0.3	44±9
	7	104	4.7±0.4	56±13
	8	62	5.3±0.5	87±25
	9	60	7.2±1.9	376±653
	10	43	13.4±2.1	3734±1803
1979–1986	5	344	4.34±0.29	38.0±7.2
	6	691	4.40±0.31	41.2±7.9
	7	755	4.68±0.39	53.3±14.2
	8	573	5.05±0.49	73.1±24.9
	9	378	6.15±1.15	189±283
	10	43	13.4±2.1	3734±1803

different stages varied from 4.3 to 13.4 mm and 38 to 3734 μg, respectively.

Clusters of green material containing small flagellates and aggregates of presumably faecal material from crustaceans are found in stage 5–7 larvae with estimated age of 4–10 days post-hatching at the prevailing temperatures. This gut content was dominant in the youngest larvae and 75% of the gut contents were classified as this type. In all the other stages except stage 10 (age ≈ 30 days) copepod nauplii were totally dominant in the gut content. In stage 10, however, copepodites dominated, but some nauplii were still found. With the exception of the prey organisms given in Table 2 some rotifers, diatoms and different stages of krill were occasionally found. Small differences were seen between the different years. However, 1981 and 1986 had a high standing stock of nauplii, and this shows up in the larvae as a high feeding incidence and a total dominance of copepod nauplii in the gut. In 1982, on the other hand, a lower feeding incidence and a lower prevalence of nauplii were found, indicating poorer conditions in the plankton community that year.

A plot of prey size versus standard length of the cod larvae is shown in Figure 2. More than 5000 prey organisms were measured. The gut content was totally dominated by copepod nauplii until the larvae were large enough (10 mm) to feed on copepodites, mainly *C. finmarchicus*; however, some nauplii are still found in the gut content even in the large larvae. This is also exemplified by the material sampled in 1986, shown in Figure 3, when more than 99% of the gut content consisted of nauplii and copepodites, and only six other prey organisms were found out of a total of 1107.

In Figure 4, the feeding ratio of the cod larvae in different developmental stages is analysed to find a relationship between the feeding ratio and the naupliar concentration. There are some variations from the regression line because of for example turbulent mixing (Sundby and Fossum, 1990; Sundby *et al.*, 1994), but the data sets show that some relation between the gut contents and the naupliar concentration exists. In the youngest larvae (stage 5) very few nauplii are found even

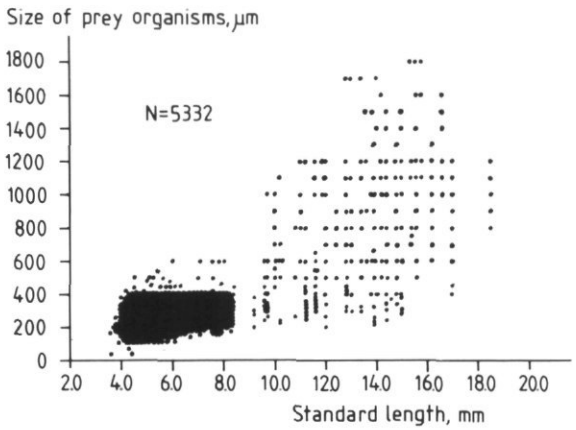


Figure 2. The size of the prey organisms found in the gut of cod larvae sampled in the Lofoten first-feeding area during the period 1979–1986.

Table 2. The frequency of different prey organisms in the gut of cod larvae sampled in the Lofoten area during 1979–1986.

Year	Stage	With gut content	Copepod			Bivalve larvae	Green gut
			Eggs	Nauplii	Cop.		
1979–1986	5	0.08	—	0.18	—	0.07	0.75
	6	0.35	0.01	0.80	—	0.08	0.11
	7	0.73	0.01	0.95	—	0.02	0.02
	8	0.85	0.01	0.98	—	0.01	+
	9	0.91	0.01	0.95	0.04	—	—
	10	1.00	—	0.16	0.84	—	—
1979	5	0.16	—	—	—	—	1.00
	6	0.52	—	0.68	—	0.18	0.14
	7	0.95	0.03	0.92	—	0.05	—
	8	0.96	0.05	0.94	—	—	0.01
	9	1.00	0.01	0.98	—	0.01	—
1981	5	0.12	—	0.20	—	—	0.80
	6	0.81	—	0.87	—	0.05	0.08
	7	0.71	0.02	0.98	—	—	—
	8	0.89	—	0.98	—	0.02	—
	9	1.00	0.06	0.88	—	0.06	—
1982	5	0.04	—	—	—	—	1.00
	6	0.26	0.02	0.68	—	0.20	0.10
	7	0.67	0.03	0.88	—	0.05	0.04
	8	0.74	0.01	0.97	—	0.02	—
	9	0.84	+	1.00	—	—	—
1983	5	0.06	—	—	—	—	1.00
	6	0.39	—	0.86	—	0.03	0.11
	7	0.78	—	0.98	—	0.01	0.01
	8	0.87	0.01	0.99	—	+	—
	9	0.90	+	0.99	0.01	—	—
1984	5	0.04	—	1.00	—	—	—
	6	0.16	—	0.50	—	0.37	0.13
	7	0.86	—	0.96	—	0.02	0.02
	8	1.00	—	1.00	—	—	—
	9	1.00	—	1.00	—	—	—
1985	5	0.13	—	—	—	0.17	0.83
	6	0.39	0.02	0.77	—	0.04	0.17
	7	0.79	0.02	0.92	—	0.02	0.04
	8	0.85	0.02	0.98	—	—	—
	9	1.00	—	1.00	—	—	—
1986	5	0.07	—	0.71	—	0.29	—
	6	0.36	—	0.98	—	—	0.02
	7	0.80	—	1.00	—	—	—
	8	0.97	—	1.00	—	—	—
	9	0.95	—	0.82	0.18	—	—
	10	1.00	—	0.16	0.84	—	—

+ Prey org. registered in small numbers.

at high naupliar concentrations. During the next stage, the ability of the cod larvae to attack nauplii improves and these larvae are often found with nauplii in their guts. The next stage, stage 7, is carefully dealt with in Sundby and Fossum (1990) and Sundby *et al.* (1994). The plots of gut content versus naupliar concentration in stages 8 and 9 larvae show that these cod larvae are often found with high feeding ratios, even at low concentrations of nauplii.

Discussion

In the present area of investigation, the first-feeding area of cod larvae in Lofoten, the composition of the zooplankton population varies considerably throughout the spring period, as it does between years too. In late winter/early spring the zooplankton is dominated by late copepodite stages or adults of *C. finmarchicus*; other organisms that may be abundant are the copepods *C.*

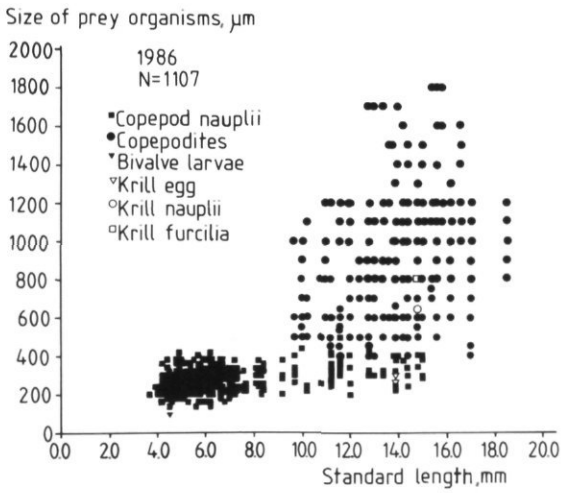


Figure 3. The size of the different prey organisms found in the cod larval guts in 1986.

hyperboreus, Oithona similis, Pseudocalanus elongatus, and krill eggs, and larvae. However, *C. finmarchicus* dominates in numbers, in February–March as copepodite stages IV, V, and adults (B. Ellertsen, unpubl. data).

In April, copepod nauplii usually predominate. At this time it is not uncommon for copepod eggs and nauplii to constitute up to 80–90% of the total number of meta zooplankton organisms. Species identification shows that the majority of copepod nauplii belong to *C. finmarchicus* (Wiborg, 1948). At times there might be a dominance of other larval forms, especially of echinoderms and cirripeds. Several benthic organisms spawn in April–May, and in an area like Lofoten the outburst of their larvae will bear evidence of such spawning. In situations with upwelling along the western side of Vestfjord, very high concentrations of krill eggs may be found, and may dominate the zooplankton community until the upwelling ceases (Ellertsen *et al.*, 1981).

With regard to size and potential food for first-feeding cod larvae, copepodite stages of most species seem to be too large. The greatest breadth of *Oithona* copepodites, however, is smaller than the mouth opening of the cod larvae (Wiborg, 1948), but still they are not observed among the stomach content. Most nauplii of the same species are below the minimum size for cod larval feeding (Ellertsen *et al.*, 1981). Small nauplii of cirripeds are within the size suitable for the larvae, but their frontal horns may make them unsuitable as food. Parallel findings for copepods with spiny appendages like *Acartia* in relation to herring (*Clupea harengus*) larvae show that these prey are less frequently found in the gut content than would be expected from their abundance in the zooplankton (Bowers and Williamson, 1951). A higher concentration of most species in the inner part of Vestfjord relative to the outer parts seems to be a normal phenomenon.

Thorough investigations of *C. finmarchicus* in 1987 revealed that there is a major flux of *C. finmarchicus* nauplii into Vestfjord owing to the watermasses drifting into the fjord along its eastern side. An overwintering stock in the inner part of the fjord also contributes to the production of nauplii in the spring, though it seems that the major stock of nauplii in April is due to the drift of nauplii itself into the fjord and the spawning of adults that have drifted into the fjord as late copepodite stages or adults. The main production of *C. finmarchicus* nauplii starts in the southernmost area of Vestfjord, reaching the central and northern parts about 1–2 weeks after the onset in the south (B. Ellertsen, unpubl. data). The nauplii are unevenly distributed in Vestfjord and outside the Lofoten archipelago. The concentrations are generally highest in sheltered areas like Austnesfjord (usually 10–20 $n \cdot 1^{-1}$), lowest at the west side of the Lofoten islands (usually 1–5 $n \cdot 1^{-1}$) (Ellertsen *et al.*, 1990). Using the *in situ* particle rate meter in combination with a plankton pump, patches with concentrations of more than 600 $n \cdot 1^{-1}$ were observed (Tilseth and Ellertsen, 1984).

Several 24-hour stations since 1975 reveal an increasing concentration of nauplii towards the surface (0–5 m) in the evening versus a more common maximum concentration at 5–15 m depth from late night throughout the day (Ellertsen *et al.*, 1979). The medium- and larger-sized nauplii show a diurnal vertical migration, whereas the smallest ones (<120 µm carapax length) do not seem to migrate (Ellertsen *et al.*, 1989). During rough weather the nauplii may be more homogeneously distributed in the upper part of the water column, and the highest concentrations may even be observed at 30 m depth. In most years our investigations on copepod nauplii and cod larvae have taken place at the same time, late April and early May. Interannual variations in concentrations of nauplii at a given date may be due to varying overall production of nauplii, or, more likely, to differences in the occurrence of the production period due to environmental factors such as the temperature.

Most fish larvae start to feed before the yolk is exhausted. In cod larvae, first-feeding is found to occur at day 4 after hatching, when the jaws are developed (Ellertsen *et al.*, 1980). At the beginning of the first-feeding period the cod larvae attack different prey organisms in the turbulent surrounding watermasses. The tendency that the cod larvae are more euryphagous during the earliest stages is also reported in first-feeding larvae of species like herring, sardine (*Sardinops sagax*), anchovy (*Engraulis mordax*), and horse mackerel (*Trachurus symmetricus*) (Arthur, 1976; Bowers and Williamson, 1951; Lebour, 1921; de Mendiola, 1974). When

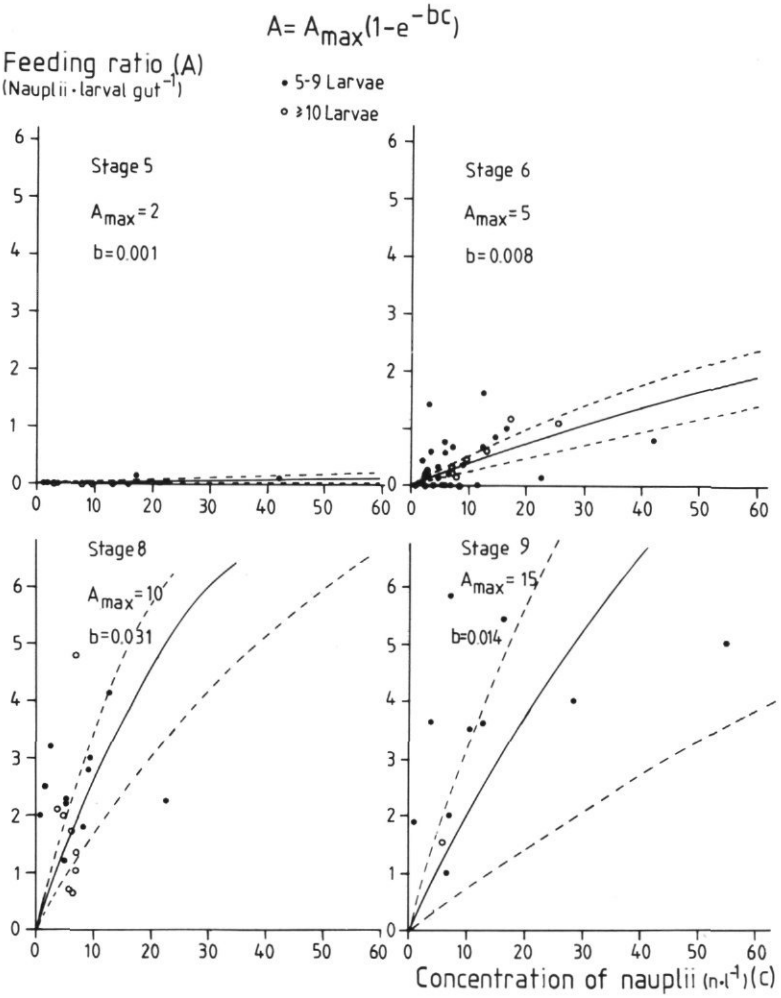


Figure 4. The feeding ratio versus naupliar concentration of different development stages of cod larvae.

the larvae start to feed, the feeding success seems to be low, as shown for other fish species, e.g. 2–6% for herring (Blaxter and Staines, 1971) and 10% in northern anchovy (Hunter, 1972). In the first 2–3 days the larvae feed mainly on immobile clusters or particles like colonies of algae, faecal pellets of copepods, large diatoms, ciliates, and rotifers. Eating faeces and aggregates has earlier been directly observed in bioassay experiments performed in the Lofoten area (Ellertsen *et al.*, 1980) and is also shown in sprat larvae (Coombs *et al.*, 1992). These food organisms are easily destroyed in the larval guts and difficult to detect with the dissecting microscope. Fixation of the cod larvae in unbuffered formaldehyde also dissolves many of the skeletons of the particles in the guts, and makes them even more difficult to identify. Consequently, the feeding incidence on such particles in the present cod larvae material must be a strong underestimate of the portion of first-feeding cod larvae in the sea with green material, ciliates, and faecal pellets in the gut.

According to van der Meeren and Næss (1993) the cod larvae are opportunists that prefer energetically favourable prey organisms like copepod nauplii if they are present in the surrounding watermasses. If not, they continue to feed on plankton from a broad range of sizes, including algae, rotifers, mollusc veligers, and protozoans. In the present material from Lofoten the switch from green material to copepod nauplii occurred within a couple of days, and already in 6–8-day-old (stage 6) larvae the gut content was dominated by copepod nauplii. However, the relative importance of green material in the gut may be difficult to investigate

when the larvae have started to feed on copepod nauplii, because the green remains in the guts in this stage may come from the nauplii as well.

Earlier investigations have shown that there seems to be a close relationship between the number of copepod nauplii in the gut of 8–10-day-old cod larvae (stage 7) and the concentration of nauplii in the sea (Sundby and Fossum, 1990; Sundby *et al.*, 1994). The present investigation indicates that this is the case also for the larvae in the last yolk-sac stage and for the more advanced larvae in stage 8 too.

At first-feeding, there is a relation between mouth size and the size of the prey organisms, as indicated by Wiborg (1948). In the present investigation, nauplii with carapax length up to 500 μm are already found in larvae at the end of the yolk-sac stage, and the larvae up to a standard length of 9 mm seem to be totally dependent on copepod nauplii with carapax length from 180 to 400 μm, even though the mouth opening should be large enough to take copepodites. When the larvae reach a standard length of 9 mm there seems to be a dramatic shift in the diet. Similar findings, with a sharp increase in food size between 8 and 12 mm exist for engraulids (Hunter, 1980). The reason for this may be that the energy demand for continuous growth cannot be fulfilled from the nauplii diet alone. The weight of the first copepodite stage is almost twice the weight of the last nauplii stage, although the widths of the two stages are nearly the same (Hunter, 1980). The energy demand of the larvae then forced them to switch over to copepodite feeding.

The feeding in cod larvae during the period of investigation seems to have occurred in three steps; first-feeding on various slow-moving prey and particles from different trophic levels. During this period the larvae have a slow growth rate (estimated from the size of the different larval stages to be in the order of 0.1 mm per day). After this period the larvae start to feed on nauplii and experience a growth rate in the size order of 0.45 mm per day (estimated from the size difference of stage 7 larvae at the beginning of May 1986 and the mean size of the stage 9 and 10 larvae found in early June 1986) and finally the larvae shift to copepodite feeding from a standard length of 9 mm. This gives good possibilities for growth and in this period the mean growth rate of the cod larvae is calculated to be in the order of 0.60 mm per day (data from larvae sampled in July, H. Bjørke, pers. comm., 1993). When the larvae move to the next phase, feeding success is probably reduced for the first couple of days, indicated by Hunter (1972), but soon increases to the former level.

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ICES mar. Sci. Symp., 198: 438–439. 1994

Distribution of cod and haddock eggs in the North Sea in 1992 in relation to oceanographic features and compared with distributions in 1952–1957 (Abstract)

M. Heath, P. Rankine, and L. Cargill

Widespread depth-stratified zooplankton sampling with concurrent hydrographic and chlorophyll fluorescence measurement was carried out at 151 stations over the northern North Sea and northwest shelf during spring 1992. Cod and haddock eggs were identified, staged, and removed from the samples. At the same time, trawl sampling was carried out over the area to determine the spawning state of adult cod and haddock.

Hydrographic conditions on the outer shelf were dominated by warm (>8.0°C) high salinity (>35.3) water of Atlantic origin. Development of seasonal thermal stratification was found only in the North Sea watermass (<7.2°C, <35.2). Chlorophyll and nitrate data indicated that the spring bloom was already under way in the central North Sea, but had not yet started on the outer shelf.

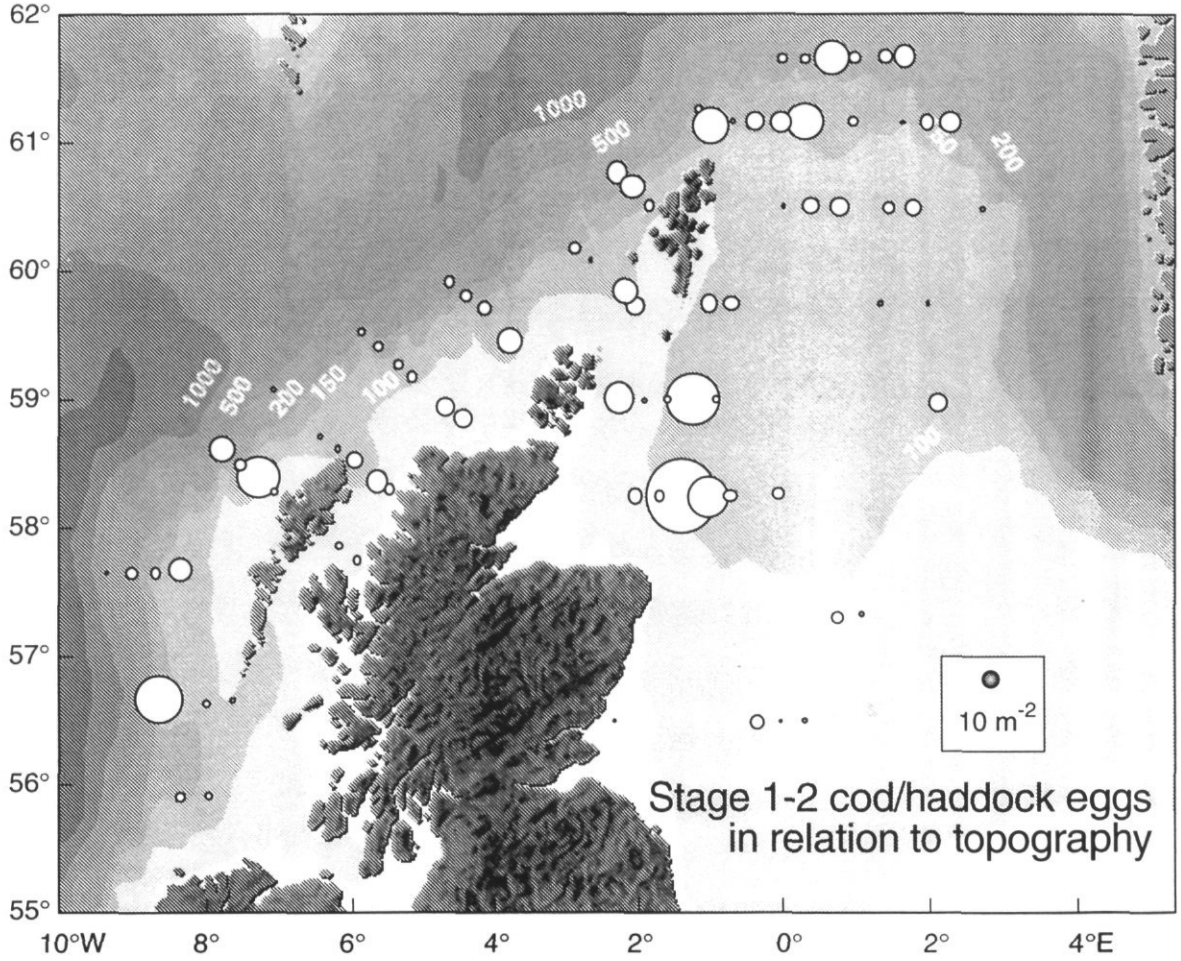


Figure 1. Distribution and abundance of stage 1–2 cod/haddock eggs in relation to topography during April 1992.

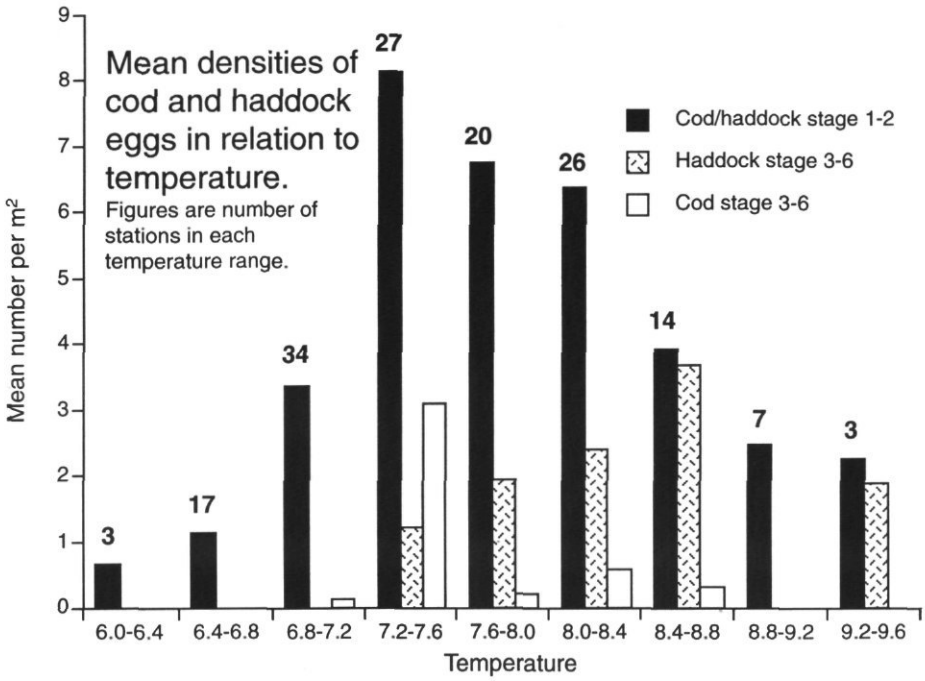


Figure 2. Mean concentration of cod and haddock eggs in relation to average water temperature over the upper 40 m.

Spawning haddock were caught at almost all trawl sites. Few spawning cod were caught. The distribution of early stage (1–2) cod and haddock eggs, which cannot be distinguished by light microscopy, was mainly confined to the outer shelf north and west of Scotland. Few early stage eggs were found in the North Sea (Fig. 1). Later stage (3–6) eggs of haddock were more restricted to the warm outer shelf waters than early stage eggs, whilst late stage cod eggs were found mostly in the cooler North Sea waters (Fig. 2). Over the whole survey, late stage haddock eggs were approximately twice as abundant as cod eggs (mean concentrations over whole survey: haddock 1.3 m^{-2}, cod 0.7 m^{-2}, number of stations containing eggs: haddock 31, cod 13).

The only previously documented widespread surveys of cod and haddock egg distributions over the same area were carried out during the period 1952–1957 (Saville, 1959; Raitt, 1967). Cod eggs were apparently more widespread and present in higher concentrations in the historical surveys than in 1992, but the historical locations of maximum cod egg concentration seem to be similar to those of the present day. Haddock egg concentrations were comparable to the recent results, but the distribution in 1992 was concentrated further north and west than in the 1950s.

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Distribution of early juvenile Arcto-Norwegian cod (*Gadus morhua* L.) in relation to food abundance and watermass properties

Kristin Helle

Helle, K. 1994. Distribution of early juvenile Arcto-Norwegian cod (*Gadus morhua* L.) in relation to food abundance and watermass properties. – ICES mar. Sci. Symp., 198: 440–448.

In 1989, the spatial distribution of early juvenile Arcto-Norwegian cod (*Gadus morhua* L.) in the Barents Sea differed from the usual distribution. The juveniles were distributed much farther east than was observed in previous years, and the largest juveniles were also found farther east than usual. The highest abundance of early juvenile cod coincided with the areas of highest zooplankton biomass and a significant positive correlation was found between the abundance of early juvenile cod and the abundance of zooplankton. Although the largest juveniles (>40 mm) were found in the areas with the highest zooplankton biomass, there was no significant correlation between the length of early juvenile cod and zooplankton biomass. No significant correlation was detected between length or abundance and temperature. However, there appeared to be a positive but not significant correlation between length and salinity.

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Introduction

Arcto-Norwegian cod (*Gadus morhua* L.) spawn on the continental shelf, primarily around Lofoten and in Vestfjorden (Sundby and Bratland, 1987). Eggs and larvae are carried to the north and east, mainly by the Norwegian Coastal Current but also by the Atlantic Current (Fig. 1). The size distribution of early juvenile cod was examined from 1983 through 1985 by Bjørke and Sundby (1987) and in 1988 by Suthers and Sundby (1993). For all these years the early juvenile cod found in areas farthest from the spawning grounds were, on average, 2–4 mm smaller than those in areas closer to the spawning grounds. The early juveniles in the north-eastern part of the survey area should have been larger and older if they had, as assumed, drifted from the main spawning areas around Lofoten. It was conjectured that the observed size distributions were due to higher water temperatures or greater zooplankton abundance in the region nearer the spawning grounds.

During the early juvenile survey in 1989, zooplankton was sampled and the usual measurements of temperature and salinity were taken. These three factors were correlated to the abundance and length of early juvenile cod in order to examine whether any of them could explain the observed size distributions.

Materials and methods

Early juvenile surveys were conducted from 1977 to 1991 during June and July in the western Barents Sea. The purpose of these surveys was to generate abundance indices and to investigate the relation between the distribution of juveniles and the distribution of water-masses.

In 1989, two research vessels were used during the survey, the RV "G. O. Sars" covered 97 stations from 6 to 23 July, and the RV "Michael Sars" covered 63 stations from 2 to 11 July. The stations are marked with dots on Figs. 3 and 4. Early juvenile cod were sampled using a 29 × 29 m midwater trawl. The codend contained a 4-m long inner net which had a 5 mm mesh (stretched hexagonal meshes). The gear was towed at 2.5–3 knots. For a standard tow, the gear was towed sequentially at three depths; first at 40 m for 7.5 min, then raised to 20 m and towed for 7.5 min, and finally towed at the surface for 15 min.

The number of juveniles was counted for each trawl haul. For smaller catches (<50) all the early juveniles were measured to the nearest mm for standard length (SL), and a random subsample was measured if the catch was larger than 50.

Salinity and temperature were recorded using a Neil

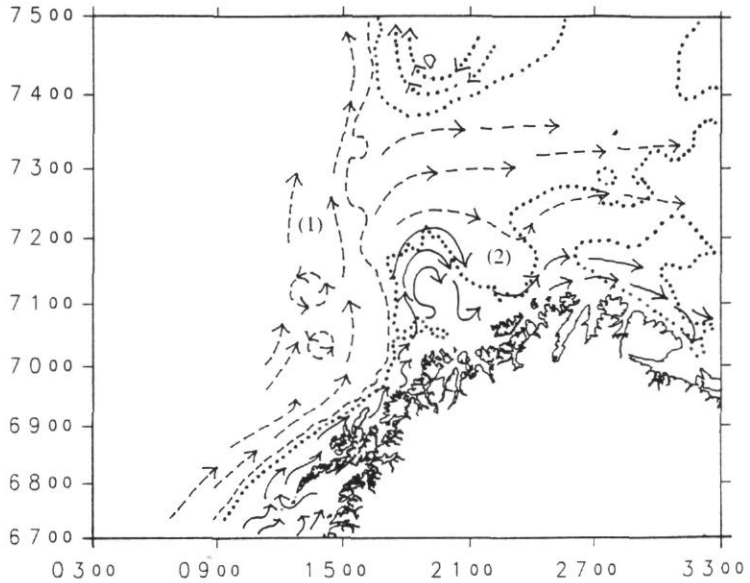


Figure 1. General system of water currents in the Norwegian Sea and the Barents Sea. Solid arrows denote the Norwegian Coastal Current, dashed arrows the Atlantic Current, and dotted arrows the Arctic Current. Dashed line is the 500 m depth contour, dotted line the 300 m contour. 1 denotes the West Spitsbergen Current, 2 denotes the North Cape Current (modified after Loeng, 1989).

Brown CTD microprofiler. Measurements were taken from the surface down to the bottom if the depth was less than 500 m and to 500 m in deeper water. A Juday plankton net was used to sample the zooplankton. The net's opening diameter was 36 cm and the mesh size was 180 μm. The Juday net was lowered to 60 m and then raised vertically to the surface.

For the calanoid copepod *Calanus finmarchicus*, each copepodite stage was identified. Stages I and II were counted as stage II. Other copepods were determined to species, and the copepod nauplii were neither staged nor species determined. The remainder of the zooplankton in the samples, the different species of krill, the hyperid amphipods, and the chaetognaths, were divided into groups. Following Bjørke and Sundby (1987), the survey region was divided into four areas. For 1989, areas 2 and 4 were further divided into subareas (Fig. 2).

The early juvenile fish surveys take two to three weeks to complete, therefore, early juveniles caught at the beginning of the survey are, on average, younger than those caught toward the end. In order to compare length distributions from different areas, the length of each early juvenile cod was adjusted to its estimated length at or about the middle of the survey period using a growth rate of 0.5 mm per day. This is the growth rate used by Bjørke and Sundby (1987) and is consistent with the daily growth rate determined by Pedersen *et al.* (1989) and Olsen *et al.* (1991), but slightly less than that estimated by Suthers and Sundby (1993), (0.65 mm). For 1989, the adjustment date was 9 July, which is slightly before the middle of the survey. This date was selected because most of the early juvenile cod were caught near this date and, therefore, the average size of the adjustments was minimized. Based on the adjusted length, the early juveniles were divided into three groups; <30, 30–40, and >40 mm, so that the length distributions could be compared with those reported by Bjørke and Sundby (1987).

The zooplankton biomass was estimated using methods described by Thorisson (1989). Abundance data were analysed in the log scale in order to stabilize the variance. Regression analysis was used to relate length to salinity and temperature, and to relate the abundance of early juvenile cod to zooplankton biomass. A two-way analysis of variance (Box *et al.*, 1978) was used to compare zooplankton biomass at stations with and without cod. Since the early juveniles were subsampled, weighted averages (Cochran, 1977) were used to estimate the mean length of the early juvenile cod. Statistical significance was assumed if $p \leq 0.05$.

Results

In 1989, early juvenile cod were mainly found north of 67°N. The largest concentrations were found at Nordkappbanken and near Sørøya. In these areas, more than 1000 juveniles per trawl haul were caught (Fig. 3a). The eastern boundary of the distribution was not located.

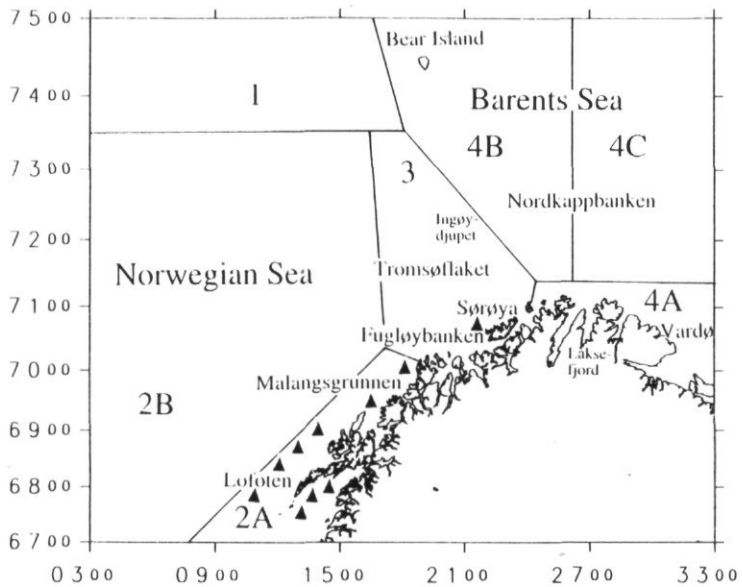


Figure 2. The four areas and subareas of the survey region, the local names used in the text, and the main spawning area for Arcto-Norwegian cod (▲, Godø and Sunnanå, 1984; Sundby and Bratland, 1987).

The lowest concentration levels were found in area 2B followed by 2A and 4B. The highest concentration levels were observed in areas 4A, 4C, and 3 (Table 1). No cod were caught at the one station sampled in area 1. The largest average cod lengths were observed in areas 4B and 4C, which is the region east of Tromsøflaket and Nordkappbanken. The smallest juveniles were found in area 2A near the spawning areas in Lofoten.

The main concentrations of cod <30 mm were found in Fugløybanken, at Nordkappbanken, and to the east of Tromsøflaket (Fig. 3b). Small concentrations were also found in the Lakesfjord and outside the spawning areas around Lofoten. For the juveniles in the length group 30–40 mm, the main concentrations were located on Nordkappbanken and in the coastal areas to the north of Vardø (Fig. 3c). A small concentration was found at Tromsøflaket. The main concentration of cod >40 mm extended from Tromsøflaket, over Ingøydjupet to Nordkappbanken (Fig. 3d). In contrast to the usual distribution, very few juveniles were found in the western parts of the survey area or in the West Spitsbergen Current.

The salinity appeared to be consistently lower in areas with cod than at stations without cod, except in area 4A (Table 2). For temperature, the relation was not as consistent as for salinity (Table 3). In areas 2A and 2B, the temperature was lower in areas with cod than in areas without cod, while in the east (areas 4A, 4B, and 4C), the temperature appeared to be higher in the areas with cod than in the areas without cod.

Table 1. Estimated mean concentration (number per trawl hour, log scale) and estimated mean length (adjusted) of early juvenile cod for each subarea in 1989. The standard error is denoted by s.e.

Area	Total no. of stations	No. of stations with cod	Concentration level of early juvenile cod	s.e.	Average length (mm) of cod adjusted	s.e.
2A	21	14	2.38	0.35	29.77	1.5
2B	56	22	1.60	0.21	31.02	1.1
3	34	34	4.36	0.25	33.31	0.6
4A	9	6	5.66	0.24	31.58	1.0
4B	19	14	3.39	0.54	36.27	1.2
4C	21	9	4.86	0.47	35.29	1.1

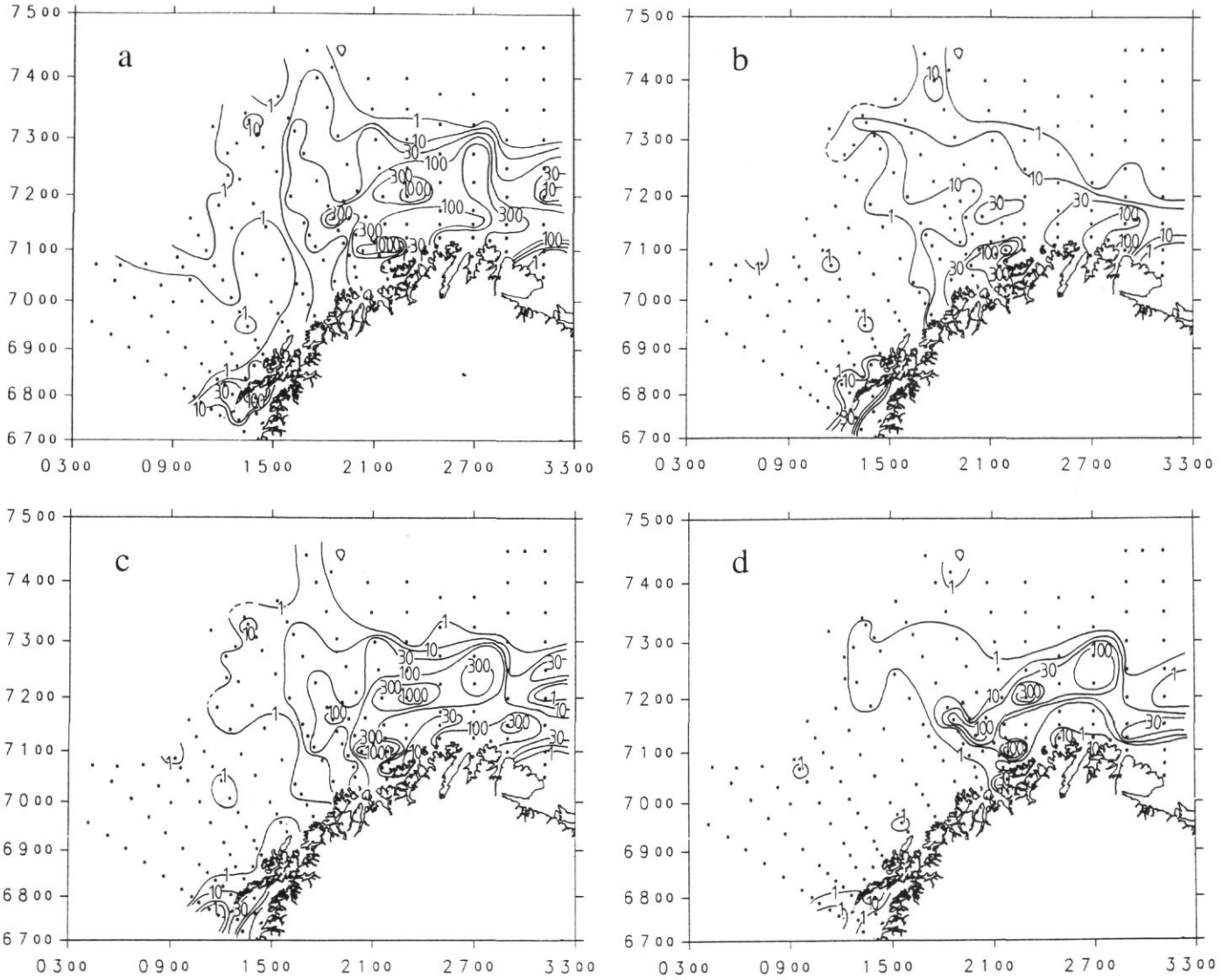


Figure 3. Distribution of early juvenile cod 2 to 23 July 1989. Number per trawl hour. (a) all early juveniles, (b) <30 mm, (c) 30–40 mm, (d) >40 mm. The dots denote the stations.

Table 2. Estimated mean salinity at 20 m depth for all stations in the survey area, for the stations where cod were caught and for the stations without cod for 1989. Cod were caught at all stations in area 3.

Area	Average salinity for all stations	s.e.	Salinity at stations with cod	s.e.	Salinity at stations without cod	s.e.
2A	34.04	0.14	33.91	0.16	34.31	0.24
2B	34.92	0.03	34.87	0.06	34.96	0.02
3	34.56	0.07	34.56	0.07	—	—
4A	33.95	0.13	34.03	0.17	33.80	0.16
4B	34.83	0.04	34.80	0.05	34.92	0.05
4C	34.77	0.05	34.61	0.09	34.90	0.04

There appeared to be no relation between temperature and length. For salinity and length of early juvenile cod there was a positive though not statistically significant correlation. The most prevalent copepod species in 1989 was *Calanus finmarchicus* followed by *Oithona similis*. The other copepod species were much less abundant and contributed little to the total bulk of biomass. It was not possible to estimate the abundance of krill because the Juday net does not catch krill efficiently.

The main concentrations of the nauplii were located west and southwest of Lofoten and at Malangsgrunnen (Fig. 4a). Stages II and III had high concentrations in the area west of Lofoten and near the coast. High concentrations were also found in the northern and southern parts of the survey area (Fig. 4b). Stages IV and V were found over Tromsøflaket, Nordkappbanken, and in the eastern parts of the survey area (Fig. 4c). The adults (stage VI) were found in the same areas as the nauplii and stages IV and V (Fig. 4d). *Oithona similis* was observed in the entire survey area, but was especially abundant around Tromsøflaket and in the area east of Nordkappbanken.

There appeared to be a large overlap of the areas with high cod abundance and large zooplankton biomass. A significant positive correlation was found ($r = 0.41$, $p = 0.0005$) between the abundance of cod and the zooplankton biomass. The stations with cod had significantly higher zooplankton biomass than did the stations without cod ($p = 0.0003$). On average, the smallest prey, the nauplii and the copepodite stages II and III of *C. finmarchicus* and *O. similis*, had a larger biomass in the areas without cod than in the areas with cod (Table 4). The largest stages, stages IV, V, and VI of *Calanus finmarchicus* had, on average, higher biomass in the areas with cod than in those without cod. The largest early juvenile cod were found in the areas with the highest zooplankton biomass, but there was not a significant correlation between the length of the early juvenile cod and zooplankton biomass.

Discussion

The distribution of early juvenile cod in 1989 differed from the distribution observed previously (e.g., Bjørke and Sundby, 1987; Suthers and Sundby, 1993) and in the two succeeding years (Bjørke *et al.*, 1991a and b). Not only was the area of highest abundance more easterly than usual, the size distribution was also the opposite of what was observed before 1989 (Bjørke and Sundby, 1987; Suthers and Sundby, 1993) and in 1990 and 1991 (Helle, 1993). For 1983 to 1985, Bjørke and Sundby (1987) found the highest concentration and the largest juveniles in the west, especially above Tromsøflaket.

Table 3. Estimated mean temperature (°C) at 20 m depth for all stations in the survey area, for the stations where cod were caught and for the stations without cod for 1989.

Area	Average temp. for all stations	s.e.	Temperature at stations with cod	s.e.	Temperature at stations without cod	s.e.
2A	9.30	0.16	9.29	0.12	9.34	0.11
2B	8.21	0.10	7.86	0.11	8.41	0.14
3	7.99	0.05	7.99	0.05	—	—
4A	8.06	0.16	8.12	0.12	7.93	0.48
4B	6.49	0.39	6.62	0.5	6.12	0.47
4C	7.12	0.16	7.67	0.09	6.72	0.19

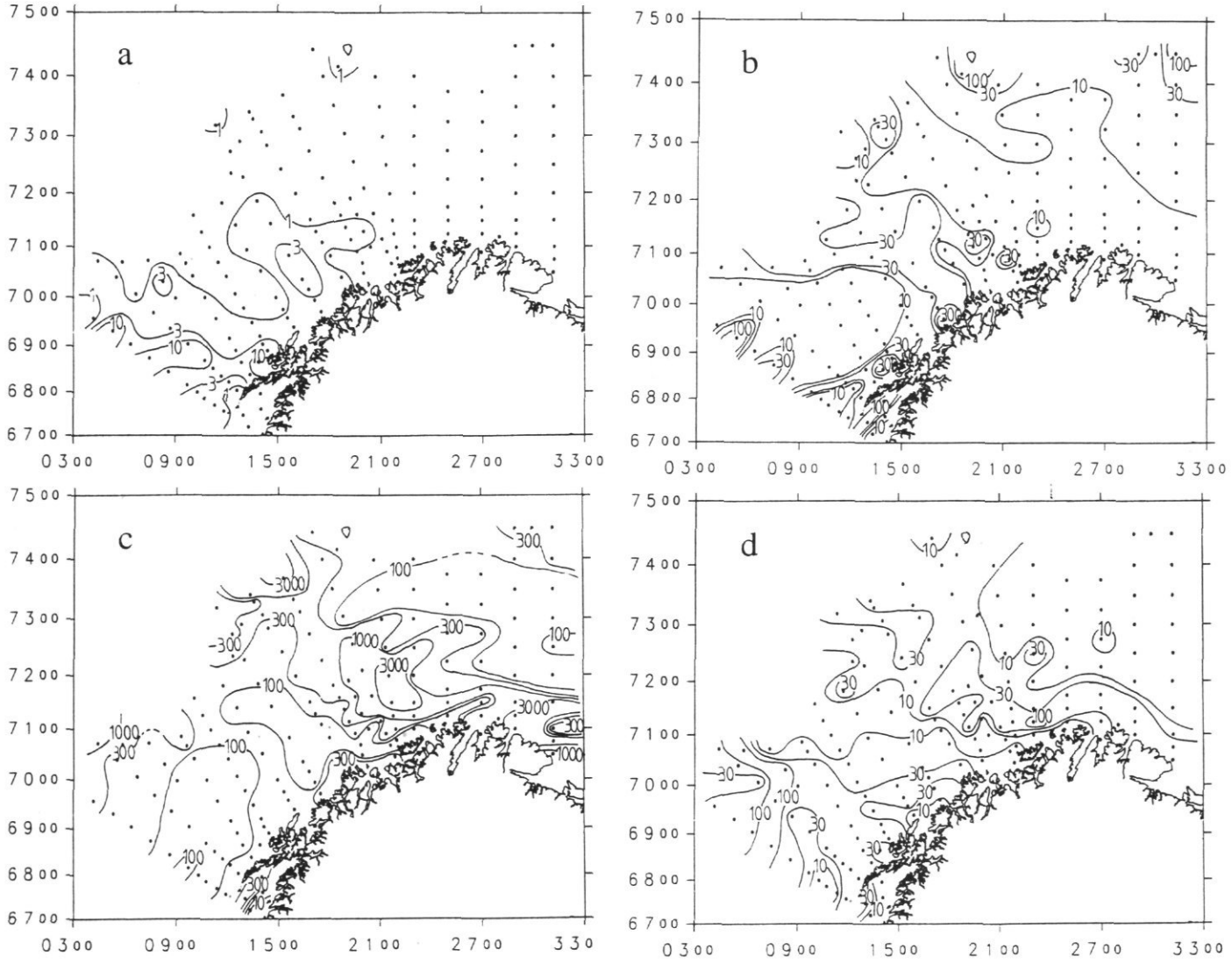


Figure 4. Distribution of biomass of *Calanus finmarchicus* (μg m^{-3}), (a) nauplii, (b) copepodite stages II and III, (c) copepodite stages IV and V, (d) the adult stage VI.

Table 4. Average biomass ($\mu g\ m^{-3}$, log scale) for the different copepodite stages of *Calanus finmarchicus*, the nauplii and *Oithona similis* for the whole survey area.

Species/stage	Average biomass for all stations	95% CI	Biomass at stations with cod	95% CI	Biomass at stations without cod	95% CI
Nauplii	0.41	0.32–0.51	0.28	0.20–0.37	0.63	0.42–0.83
C. finmarchicus II	0.49	0.40–0.58	0.46	0.35–0.57	0.53	0.38–0.68
C. finmarchicus III	1.97	1.76–2.17	1.93	1.68–2.17	2.03	1.70–2.36
C. finmarchicus IV	3.60	3.35–3.85	3.91	3.59–4.22	3.09	2.69–3.50
C. finmarchicus V	4.58	4.33–4.83	5.15	4.84–5.45	3.65	3.29–4.00
C. finmarchicus IV	2.59	2.40–2.77	2.62	2.41–2.83	2.52	2.21–2.85
O. similis	0.96	0.86–1.06	0.84	0.72–0.97	1.15	0.99–1.32

Usually, 40 to 90% of the early juveniles are concentrated above Tromsøflaket (Sundby *et al.*, 1989). In early 1989, a large inflow of warm Atlantic water began (Loeng *et al.*, 1992) and appears to have caused the early juvenile cod to be more easterly distributed than usual. Randa (1984) and Muchina *et al.* (1987) suggest that the intensity of the inflow of Atlantic water into the Barents Sea has an influence on the distribution of 0-group cod, and that the spatial distribution is determined by the strength of the current transport from the spawning ground. They conclude that an easterly distribution of the 0-group is probably caused by a high level of Atlantic inflow.

Although temperature is assumed to have the largest effect on growth rates (Sætersdal and Loeng, 1987; Ellertsen *et al.*, 1989; Pedersen and Jobling, 1989; Sundby *et al.*, 1989; Suthers and Sundby, 1993), no correlation between temperature and length was detected for 1989. For salinity and length, a weak but not significant correlation was found. Similarly, no relation between length and temperature was detected for 1990 and 1991 (Helle, 1993), but there was a significant positive correlation between salinity and length (1990: $r = 0.68$, $p < 0.05$, 1991: $r = 0.57$, $p < 0.05$). Length correlated with salinity but not with temperature might be due to the fact that salinity changes to a lesser extent and more slowly than temperature after a watermass enters the Barents Sea. Salinity may, therefore, better reflect the history and origin of the watermasses than temperature (Loeng, 1989). Gundersen (1993) found a relation between length and salinity but not between length and temperature for capelin larvae and for the 0-group capelin during the period 1981–1991.

Usually, after warm and saline Atlantic water enters the western Barents Sea it takes about six months before it can be detected in the east (Loeng, 1989; Loeng *et al.*, 1992). In 1989, temperature and salinity increased simultaneously in the southern Norwegian Sea, the West Spitsbergen Current, and in the Barents Sea (Loeng *et al.*, 1992). Thus the watermass properties were similar over the entire survey area, which might explain the weak correlation between the length of cod and salinity in 1989 compared with the following two years.

Also the distribution of zooplankton in 1989 differed from that previously observed (Nesterova, 1990). The abundance of zooplankton during summer is usually high in the main current branches at the western entrance of the Barents Sea and lower in the central areas (Bliznichenko *et al.*, 1984; Degtereva *et al.*, 1985, 1986a, b; Nesterova, 1990). The advective transport of zooplankton by currents is known to vary with the rate of Atlantic inflow (Ozhigin and Ushakov, 1985). The large interannual variation in biomass is mainly due to variation in the stock of *C. finmarchicus* (Skjoldal *et al.*, 1987), which is the main zooplankton species in the Barents Sea (Sysoeva and Degtereva, 1965; Skjoldal and Rey, 1989). Nesterova (1990) examined the zooplankton biomass from 1959 to 1990 in the Barents Sea and found that it varies with the water temperature. In warm years there is a large biomass, while in cold years biomass is low. The zooplankton distribution in 1989 confirms this observation. This result, together with the distribution of the different stages of *C. finmarchicus* observed in 1989, supports the theory that *C. finmarchicus* is for the most part recruited from the Norwegian Sea (Skjoldal *et al.*, 1992).

Although the distribution of early juvenile cod in 1989 differed from that in previous and successive years, the relation between early juveniles and zooplankton biomass was consistent with other investigations. Sysoeva and Degtereva (1965) examined the distribution of zooplankton and cod juveniles for 1959 through 1961. They found the highest concentration of cod larvae and juveniles in areas with the highest concentrations of *C. finmarchicus*. This also appears to be the case for the period 1977–1990 (Nesterova, 1990). Blom *et al.* (1991) studied the relation between the feeding conditions and production of cod fry in semi-enclosed marine ecosystems in western Norway, and Astthórsson *et al.* (1994) examined the distribution, abundance, and length of early

juvenile cod in relation to environmental conditions in Icelandic water. In both studies there was a significant correlation between zooplankton abundance and the abundance of cod fry, and no correlation between the length of cod and zooplankton biomass, which is consistent with that observed in the Barents Sea in 1989.

Early juvenile cod have limited ability to move over large distances (Sundby, 1993). The high abundance of cod juveniles and zooplankton in the same areas may, therefore, be due to the current patterns or it may indicate better cod survival in areas with high zooplankton biomass. The highest abundance of early juvenile cod was observed in the areas with the largest zooplankton biomass, which were also the areas with the largest copepodite stages (IV and V). This observation supports the theory of Jones and Hall (1974), who suggested that larval survival depends not only on food density, but also on the size range of the available food. A synchronized spawning of *C. finmarchicus* and cod will enhance cod survival, since their parallel growth provides the optimum size of food for cod from first-feeding to the early juvenile stage. The distribution of early juvenile cod in the Barents Sea in 1989 supports the hypothesis that the zooplankton distribution is an important factor affecting the distribution and abundance of early juvenile cod.

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Recruitment variability and growth of Northeast Arctic cod: influence of physical environment, demography, and predator–prey energetics

E. M. Nilssen, T. Pedersen, C. C. E. Hopkins, K. Thyholt, and J. G. Pope

Nilssen, E. M., Pedersen, T., Hopkins, C. C. E., Thyholt, K., and Pope, J. G. 1994. Recruitment variability and growth of Northeast Arctic cod: influence of physical environment, demography, and predator–prey energetics. – ICES mar. Sci. Symp., 198: 449–470.

Large-scale oceanic and climatic variability greatly affects the distribution and abundance of Northeast Arctic cod off Northern Norway and in the Barents Sea. Abundance estimates of 0-group cod exhibit a close relationship with sea-temperature variability at the Kola meridian section in the eastern Barents Sea, with good year classes tending to coincide either with temperature peaks or with increasing temperatures, and declining recruitment and poor year classes tending to coincide with decreasing or low temperatures. Construction of a simple multiplicative regression model describing the recruitment of Northeast Arctic cod, incorporating sea temperature along the Kola meridian, spawing-stock biomass (SSB), and cannibalism as predictors, explained about 46% of the 1946–1988 recruitment variability. Temperature, or its environmental associates, affected recruitment by a factor of about 4 between the coldest and the warmest years, while SSB and cannibalism influenced recruitment by a factor of about 2.6 each. The biomass of the 3+ ages of Northeast Arctic cod declined from about 5 million tonnes in the late 1940s to about 1 million tonnes in 1992, mainly as a result of a concerted increase in fishing mortality before a marked reduction occurred in the late 1980s. The abundance of younger cod (<6 years old) was generally stable during this period, but that of older cod (>10 years old) declined to present levels, <1% of these in the late 1940s. The greatest variability in weight-at-age and growth rates of cod ≥4 years old occurred in the late 1970s and in the mid-1980s, after the demise in recruitment of Atlanto-Scandian herring to the Barents Sea and the establishment and subsequent failure in the capelin fishery. Statistical analyses of data from about 1955 onwards showed a clear inverse relationship between the numbers of fish at age and their specific growth rates (SGR, % change per day), i.e., evidence of density-dependent growth. An SGR model for the Northeast Arctic cod stock, incorporating a solution for a density-dependent or food-effect in addition to sea temperature (Kola meridian) for the 1950s onwards, showed good agreement between modelled and observed values for 4–9-year-old fish for which data were available. Compilation and subsequent analysis of a data set from Norwegian and Russian sources showed a positive correlation between the availability of capelin (expressed either as capelin biomass or as the ratio of capelin:cod biomass) and the percentage of prey individuals in cod stomachs that are capelin (i.e., percentage frequency of occurrence: % FoO). The % capelin FoO was also positively related to the SGR of 4–9-year-old cod, as well as to the liver index (% of body weight formed by liver) of prespawning cod caught at Lofoten, probably reflecting a tendency for increased relative and absolute levels of feeding on the lipid-rich capelin to result in proportionately larger cod livers.

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Introduction

The Barents Sea is a neritic shelf area covering about 1.5 million km^2 (Zenkevitch, 1963; Dragesund and Gjøsæter, 1988). The southern Barents Sea is ice-free throughout the year owing to the intrusion of relatively warm, Atlantic water masses, while the northern part is covered by annually formed sea ice in winter, and is dominated by cold water masses of Arctic origin (Loeng, 1991). The inflow of Atlantic water into the Barents Sea may vary greatly, resulting in changes in temperature and ice cover (Loeng, 1991; Ådlandsvik and Loeng, 1991).

The Barents Sea's fisheries occur mainly within the Atlantic domain, with total landings of fish ranging from about 1.5 to 4.5 million tonnes annually since 1950 (Hjort, 1914; Dragesund and Gjøsæter, 1988; Anon., 1992; Nilssen and Hopkins, 1992). Both the fish stocks and landings sustained from the Barents Sea have fluctuated greatly in the past as well as in recent times (Helland, 1908; Helland-Hansen and Nansen, 1909; Hjort, 1914; Anon., 1948; Rollefsen, 1954; Bergstad *et al.*, 1987; Hopkins and Nilssen, 1991; Anon., 1992). Before the collapse of the Atlanto-Scandian herring (*Clupea harengus*) about 1970, the Barents Sea served as a feeding area for young herring (Dragesund *et al.*, 1980; Dragesund and Gjøsæter, 1988). A profitable capelin (*Mallotus villosus*) fishery arose after the demise of the herring stock: nominal catches peaked at 2.9 million tonnes in 1977, falling to moratorium levels in the late 1980s, before rising again in the early 1990s (Røttingen, 1990; Hopkins and Nilssen, 1991; Anon., 1992a). The Northeast Arctic cod (*Gadus morhua*) stock is potentially the largest cod stock in the world, with annual catches reaching about one million tonnes from the 1950s to the mid-1970s (Cushing, 1966; Jakobsson, 1992), but fell in the mid-1980s to about 300 000 t and has remained at 200 000–500 000 t yearly (Anon., 1992).

The climate of the Barents Sea oscillates between a warm and a cold state. The warm state is characterized by high temperatures, low pressure, and cyclonic circulation in the atmosphere, increased Atlantic inflow, and little ice cover, while the cold state is characterized by reverse conditions (Ådlandsvik and Loeng, 1991). Climate variability in North Norwegian waters and in the Barents Sea affects the recruitment and distribution patterns of several economically important fish species, as well as the geographic location of the fisheries (Eggvin, 1938; Loeng, 1989a, b; Nilssen and Hopkins, 1992).

The majority of the high and medium abundance year classes of the Northeast Arctic cod are either associated directly with positive temperature anomalies in the early part of a warm period in the Barents Sea, when feeding areas are expanding, or they occur immediately before a shift to a warmer regime (Sætersdal and Loeng, 1987; Loeng, 1989a). Sætersdal and Loeng (1987) calculated that weak year classes are common, occurring in about 66% of years since the early 1900s, and are as likely to arise in both cold and warm years. Medium strength year classes arise twice as often in warm years as in cold ones, while strong year classes are about 12 times more common in warmer than colder years. A strong cod year class is about 10 times more abundant than a weak year class, and about twice as abundant as a medium one (Sætersdal and Loeng, 1987).

This marked, climate-related variability in the recruitment of Northeast Arctic cod also influences predator–prey relationships. If food is limited, larger cod resort to cannibalism (Korzhev and Tretyak, 1989; Mehl, 1989, 1991), with potentially major effects on recruitment. In this article an attempt is made to develop a recruitment model for Northeast Arctic cod incorporating spawning-stock biomass, environmental temperature and cannibalistic predation mortality as predictors of year-class strength. Further, as the Barents Sea ecosystem has seen several major perturbations over the course of the last four decades (Hamre, 1988; Skjoldal and Rey, 1989; Hopkins and Nilssen, 1991), including marked year-class strength changes in cod, and oscillations in several of its prey (e.g., herring, capelin, and the shrimp *Pandalus borealis*), sufficient variability should have taken place to discern key features affecting prey–predator supply-and-demand relationships (Ney, 1990). This article thus also focuses on detecting changes in growth rates owing to density-dependence and variations in prey availability, as well as searching for informative indicators of functional trophodynamic responses.

Materials and methods

Temperature data

The longest temperature (°C) time series in the Barents Sea is the Russian record on the Kola Section (from the upper 200 m along the 33°30′E meridian from 70°30′N to 72°30′N), which started in 1900. The period 1906–1919 has quarterly measurements, while the rest of the series is based on monthly measurements, with the exception of two periods, 1906–1919 and 1941–1944. Data for the missing periods have been filled by a combination of interpolation and other observations (Bochkov, 1982). The present article uses the post-1945 data set, 0–200 m depth integrated along the whole section, as an index of gross temperature fluctuations for North Norwegian waters and the Barents Sea.

The temperature data have been treated by Fourier analysis to remove seasonal trend components using the TIME SERIES module of SYSTAT, and further treated by Cleveland-Lowess smoothing (Wilkinson, 1988) to remove high frequency "noise" and thus emphasize

more robust trends. The data have been used to assess the relationship between temperature fluctuations and the year-class strength of cod; a recruitment model is developed. The temperature data have also been used as input for model estimation of cod growth rates.

Cod numbers and weight-at-age

Data on size (body length and body weight) and age composition of Northeast Arctic cod have been compiled from the literature (ICES, 1992; Lebed, 1981; Lebed and Ponomarenko, 1983–1985, 1986a, b; Lukmanov and Ponomarenko, 1976, 1977, 1979; Ponomarenko, 1968–1970, 1972, 1973a, 1978; Ponomarenko *et al.*, 1980; Shevelev *et al.*, 1988).

For the purpose of estimating spawning stock biomass from the virtual population analysis (VPA) results, weights-at-age were required for all years from 1946 to 1988. Since observational data are not currently available for the year classes earlier than 1946 the weights were estimated by first calculating the sum of product corrections each year for the average catch weight-at-age (ICES, 1993) and applying these corrections to the average stock weights-at-age given in ICES (1993). Comparisons of the weights of spawning age fish were compared with the observational data and were found to be in broad agreement. The corrected average weights were therefore adopted for all years to estimate spawning stock in a consistent fashion.

Percentage maturity-at-age estimates (mat(a,y)) for each year were calculated from these spawning stock weights at age (Ws(a,y)) using the equation:

$$\ln\left(\frac{\text{mat}(a, y)}{1 - \text{mat}(a, y)}\right) = -3.473 + 3.094 \times \ln(\text{Ws}(a, y)) + \varepsilon \quad (1)$$

This was obtained from a logit regression of the maturity-at-age data on stock-weight-at-age data available in ICES (1993).

Estimates of cod population numbers at age were obtained from single species VPA runs made for the period 1946–1992. The catch-at-age data used in this analysis were taken from ICES (1993) for 1962–1992 with data for the years 1946–1961 being kindly provided by Dr T. Jakobsen (Institute of Marine Research, Bergen, Norway) from the ICES Arctic Working Group data files. The biomass of juveniles each year was estimated using estimates of mid-year weight-at-age. Estimates of spawning biomass for each year were obtained from the sum of the product of the estimates of numbers-at-age, the weight-at-age at spawning, and the maturity (%)-at-age.

Modelling recruitment

Multiple regression techniques were used to relate logarithms of recruitment estimates to depth integrated (0–200 m) temperature on the Kola section, the logarithm of spawning stock biomass and to the biomass of 3- and 4-year-old fish. This approach thus attempts to relate recruitment to temperature, spawning stock, and cannibalism effects. It follows similar approaches used in the North Sea (Pope and Woolner, 1981) and at Iceland (Pope, 1992; Olafsson *et al.*, 1993).

To further investigate the role of cannibalism on cod recruitment, a simple VPA model of cod cannibalism was developed as an EXCEL spreadsheet, following the general approach of Pope and Macer (1991). Predation mortalities generated by older ages of cod were estimated, assuming that a unit biomass of cod of a particular weight exerts a constant predation mortality on each age group. This constant per unit biomass predation mortality of cod by cod, UM2, per unit biomass (megatonne) is usually modelled as:

$$\text{UM2} = \alpha 1 * \exp\left[-0.5\left(\frac{\ln\left(\frac{\text{Wt (pred)}}{\text{Wt (prey)}}\right) - \alpha 2}{\alpha 3}\right)^2\right]. \quad (2)$$

Given the tendency of the Barents Sea cod to separate by age due to spawning migrations (Rollefsen, 1954; Garrod, 1967; Wielgolawski, 1990) this form was attenuated by a term:

$$\beta^{\text{Age(pred)} - \text{Age(prey)} + 1} \quad (3)$$

Initial values of $\alpha 1$, $\alpha 2$, and $\alpha 3$ were taken from the relationship found for cod cannibalism in the North Sea (ICES, 1988).

With the resulting form of UM2, a VPA of the Northeast Arctic cod that includes the predation mortality M2 generated on younger ages by older ages can be developed on an EXCEL spreadsheet. Manipulations of the α and β terms in the above equations can be made to bring recruitment at ages 0, 1, 2, and 3 as close as possible to the international and national recruitment survey estimates for these ages given in ICES (1993).

Amounts (biomass) of cod eaten at age by older cod, available for example in Skagen *et al.* (1990), were used for model verification.

Weight, growth rates, and estimates of temperature and density effects

The geometric weight (GW, kg) of cod has been calculated from weight-at-age data for particular year classes:

$$GW_{n+1} = \exp\left(\frac{\ln W_n + \ln W_{n+1}}{2}\right) \quad (4)$$

where W_n and W_{n+1} are fish weights at the start and end of the period examined.

The specific growth rate (SGR) is particularly useful for discerning *changes* in growth trends and periodicity with age or time (Hopkins *et al.*, 1984, 1993; Pedersen and Jobling, 1989). SGR (as % change per day) has been calculated as:

$$SGR_{n+1} = \left(\frac{\ln W_{n+1} - \ln W_n}{360}\right) \times 100 \quad (5)$$

Jobling (1988) has provided an equation for predicting the effects of water temperature (T°C) and body weight (W, kg) on the growth of cod in the laboratory, when fed either to satiation or in excess:

$$\ln SGR = (0.216 + 0.297 \times T - 0.000538 \times T^3) - 0.441 \ln W \quad (6)$$

which gives:

$$SGR = e^{A(T)} \times W^b \quad (7)$$

where A(T) is the polynomial in parentheses in Equation (6) above. The step $e^{A(T)}$ expresses the functional relationship between SGR and T.

Jobling's (1988) equation has been used in this study to provide reference growth rates for cod of various ages/sizes at temperatures of 2 to 5°C (spanning the observed mean range of ambient temperature observed at the Kola meridian section), for comparison purposes with those calculated for observed "field" data for particular age groups or year classes of cod.

In this paper we have modified and extended Jobling's (1988) equation in order to model the SGR of Northeast Arctic cod, taking into account both ambient water temperature and population density changes for 4–9-year-old fish during the period 1950–1991. In our model the expression ($e^{A(T)}$) is replaced with a simple exponential relationship $C \times e^{aT}$ between SGR and T. Thus, in our model:

$$SGR = C \times e^{aT} \times GW^b \quad (8)$$

The expression $C \times e^{aT}$ is a simple description of the functional relationship between SGR and T for low temperatures which can be expected to perform well at temperatures which lie under that for maximum growth rates. This, however, means that our model ought not to be used for cod stocks which live at higher ambient temperatures.

The parameters of the regression model were fitted by the NONLIN module of SYSTAT using the quasi-Newton iteration procedure (Wilkinson, 1988).

Trophodynamics

Food and feeding data, including the relative proportions of different prey in Northeast Arctic cod stomachs, have mainly been extracted from Russian and Norwegian literature (e.g., Ponomarenko and Ponomarenko, 1975; Ponomarenko and Yaragina, 1978, 1979, 1984; Ponomarenko *et al.*, 1978; Berenboim *et al.*, 1991; Drobysheva *et al.*, 1991; Korsbrekke *et al.*, 1991; Tretyak *et al.*, 1991). These data are presented as percentage frequency of occurrence (% FoO, the relative numerical abundance of prey species x per 100 individuals of all prey species registered in the stomach). They do not *per se* indicate the abundance of prey items in the stomach (i.e., whether stomachs are full or only partly full), but rather provide an insight about the contribution of a given prey species as a *per capita* proportion (%) of the sum of prey individuals registered. However, where it can be shown that there is some significant correlation between % FoO of a given prey species and its own biomass and/or its predator in the ecosystem, sufficient grounds may be present to make an associated pronouncement regarding an index of the abundance of prey in predator stomachs.

The stomach data have been analysed, together with various other relevant data (e.g., stock size of prey and predator, liver-indices [% of the body weight comprised by the liver after the gonads have been removed from prespawning cod caught in the Lofoten fisheries; Anon., 1946–1988; T. Pedersen, unpubl.]), to try to discern functional prey–predator relationships, including whether changes in the absolute and relative abundance of one or more of the actors in the trophodynamic play contribute to enhanced or depressed growth and changes in cod condition indices.

Principal components analysis

Principal components analysis (PCA, implemented in the FACTOR module of SYSTAT, Wilkinson, 1988) has been used to examine the relationship between abundance at age, body weight, SGR and liver index of cod, as well as trying to analyse interrelated changes in these features with the % FoO of capelin and *P. borealis* in cod stomachs. A similar approach has been used successfully in examining growth relationships in the capelin (Hopkins and Nilssen, 1991).

Results

Temperature and recruitment

A gross index of ambient temperature, integrated from 0 to 200 m depth along the Kola meridian section between 1945 and 1993 illustrates the flow frequency periodicity of peaks and troughs, with an average amplitude over

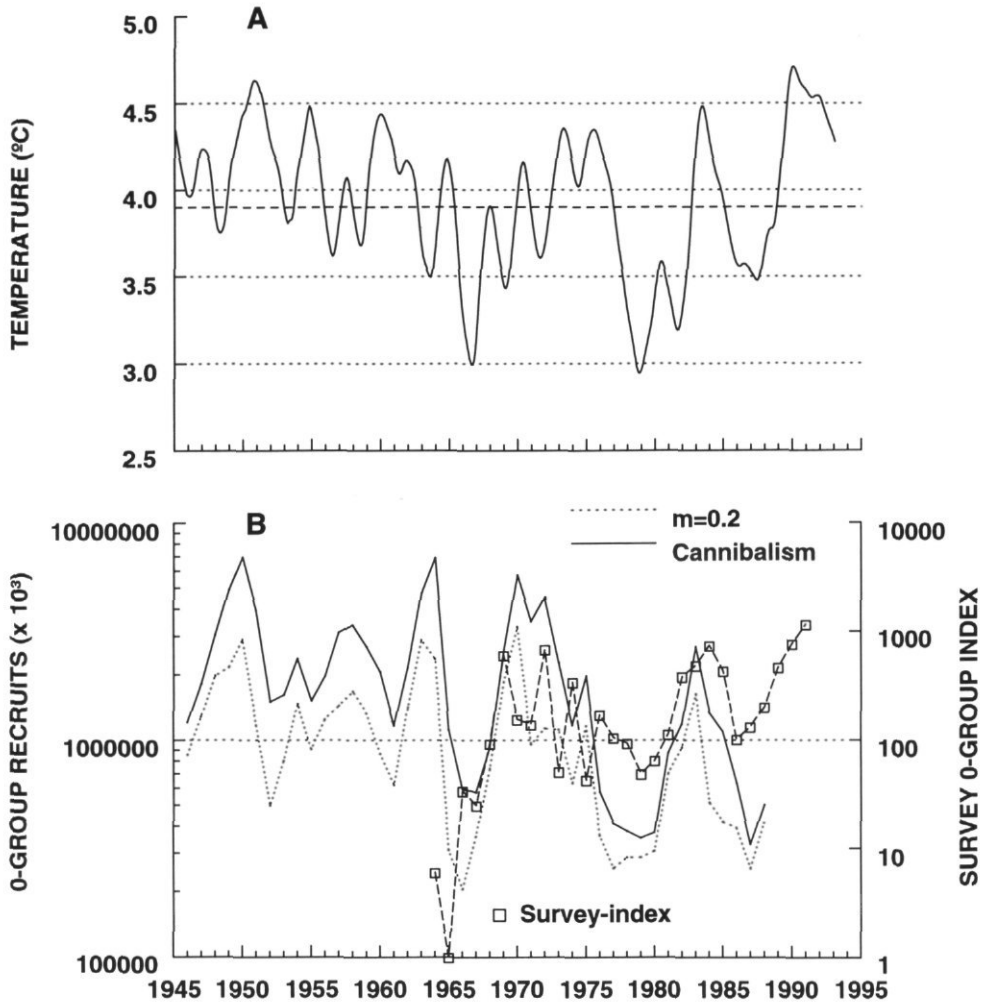


Figure 1. Variation in (A) temperature (integrated 0–200 m, Fourier treated and smoothed) at the Kola meridian section of the Barents Sea, and of (B) various measures (survey index; VPA estimated with natural mortality, M = 0.2; estimates from a stock–recruitment model which includes a cannibalistic predation component) of 0-group Northeast Arctic cod abundance.

the whole period of about 5 years (Fig. 1A). Major cold periods, with mean temperatures falling to 3°C, occurred from about 1966 to 1967 and from about 1977 to 1980. Compared with before 1975, the post-1975 period is characterized by relatively prolonged, low-temperature troughs. Comparison of the temperature cycle and the abundance estimates of 0-group cod (Fig. 1B) generally shows a substantial degree of similarity in pattern between temperature and recruitment, with recruitment pulses of strong year classes tending to coincide either with temperature peaks or with increasing temperatures, while declining recruitment and poor year classes tend to coincide with decreasing or low temperatures.

In general there is quite good coincidence between the 0-group survey index and the 0-group recruits as estimated by VPA (with natural mortality = 0.2), adjusted for the affects of cannibalism (see below for details) (Fig. 1B). There is, however, a greater discrepancy in the pattern exhibited between the 0-group survey data on the one hand and the two other estimates of 0-group abundance on the other during the post-1975 cold-water troughs.

Age structure of the stock

Long-term changes in the relative composition of the stock are apparent when a logarithmic plot of VPA estimated abundance by age (for 4–14-year-olds) is made (Fig. 2). Although there are some shorter-scale

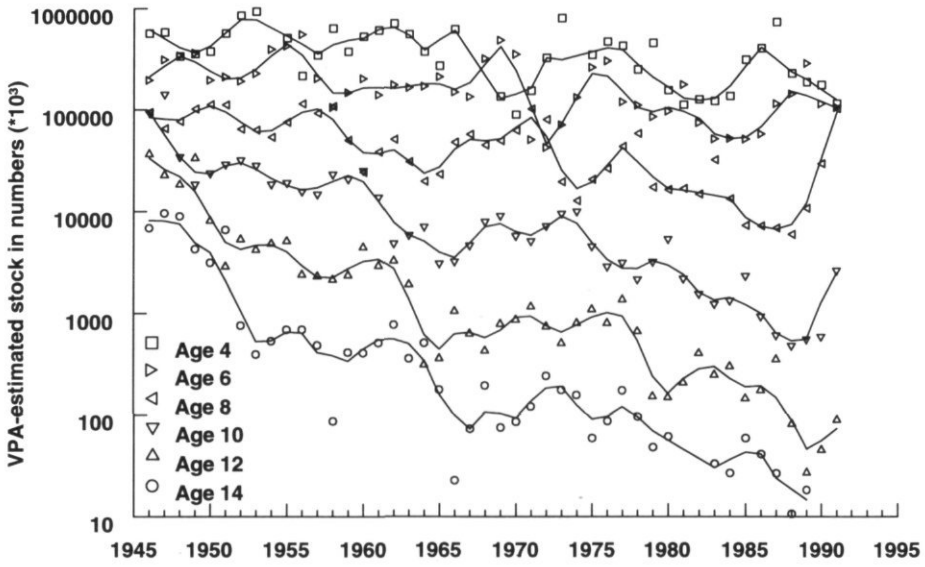


Figure 2. Variation in VPA-estimated stock abundance (logarithmic plot) of 5 age groups (4–14 years) of Northeast Arctic cod between 1945 and 1991.

oscillations owing to good or poor year classes entering the stock, the abundance of 4–6-year-olds has been relatively stable from 1945 up to the present. The decrease in the absolute and relative abundances of older cod (>10 years) has been more marked (Jakobsen, 1992). The present abundance of 12–14-year-olds is only about 1/1000 of the abundance level in the latter half of the 1940s. The abundance of 8–10-year-olds has, fortunately, increased in recent years.

A stock and recruitment model

Recruitment estimates, juvenile biomass estimates and spawning stock estimates were obtained as described in the Materials and methods section. Logarithmic transformations were made on the recruitment estimates and spawning stock biomass estimates. The recruitment transformation was used to normalize the variance since, as shown by Hennemuth *et al.* (1980), recruitment data typically have a lognormal distribution. The logarithmic transformation of the spawning stock estimates was used to fit a power curve relationship between recruitment and spawning stock. Other potential independent variables were used untransformed. Simple regression analysis of log recruits on each of the independent variables gave R-squared values of 0.28 for temperature, 0.28 for log spawning stock size, 0.07 for juvenile biomass (ages 3 and 4), and 0.05 for the cod liver index. These were all made for the years 1946–1988, giving 41 degrees of freedom for each regression. Thus the temperature and spawning stock R-squared values differ significantly from zero at the 1% level, but the other effects do not differ from zero at the 5% level.

Including terms progressively in a multiple regression of log recruits on temperature at the Kola section, the juvenile biomass and log spawning stock biomass gave sum of square increments which were significantly different from zero at least at the 5% level (Table 1). Table 1 also gives the parameter estimates obtained by this fit and their standard errors. As an additional check on the stability of these estimates, regression fits were made using data from the odd years and data from the even years. The resulting estimates are contrasted with the overall estimates in Table 1 and indicate that the estimates only varied within the range of the standard errors.

Inclusion of the cod liver index and the percentage frequency of occurrence of capelin (% capelin FoO) in cod stomachs, both for the recruiting year and also for the preceding year, made little improvement to the fit and were thus omitted in the final model. The correlation between the estimates of the coefficients of the independent variables was observed to be quite small. The residuals were approximately normally distributed. The main outlier (Fig. 3A) was the very large 1964 year class. The fit between the log recruitment estimators and the multiple regression fitted predictors explained about 46% of the variation in log recruits (see Fig. 3A). After retransformation the model can be expressed as:

$$\text{recruits} = 3429 \times \exp(0.772 \times \text{temp} - 5.408\text{e}-7 \times \text{juvenile biomass}) \times \text{SSB}^{0.456}$$

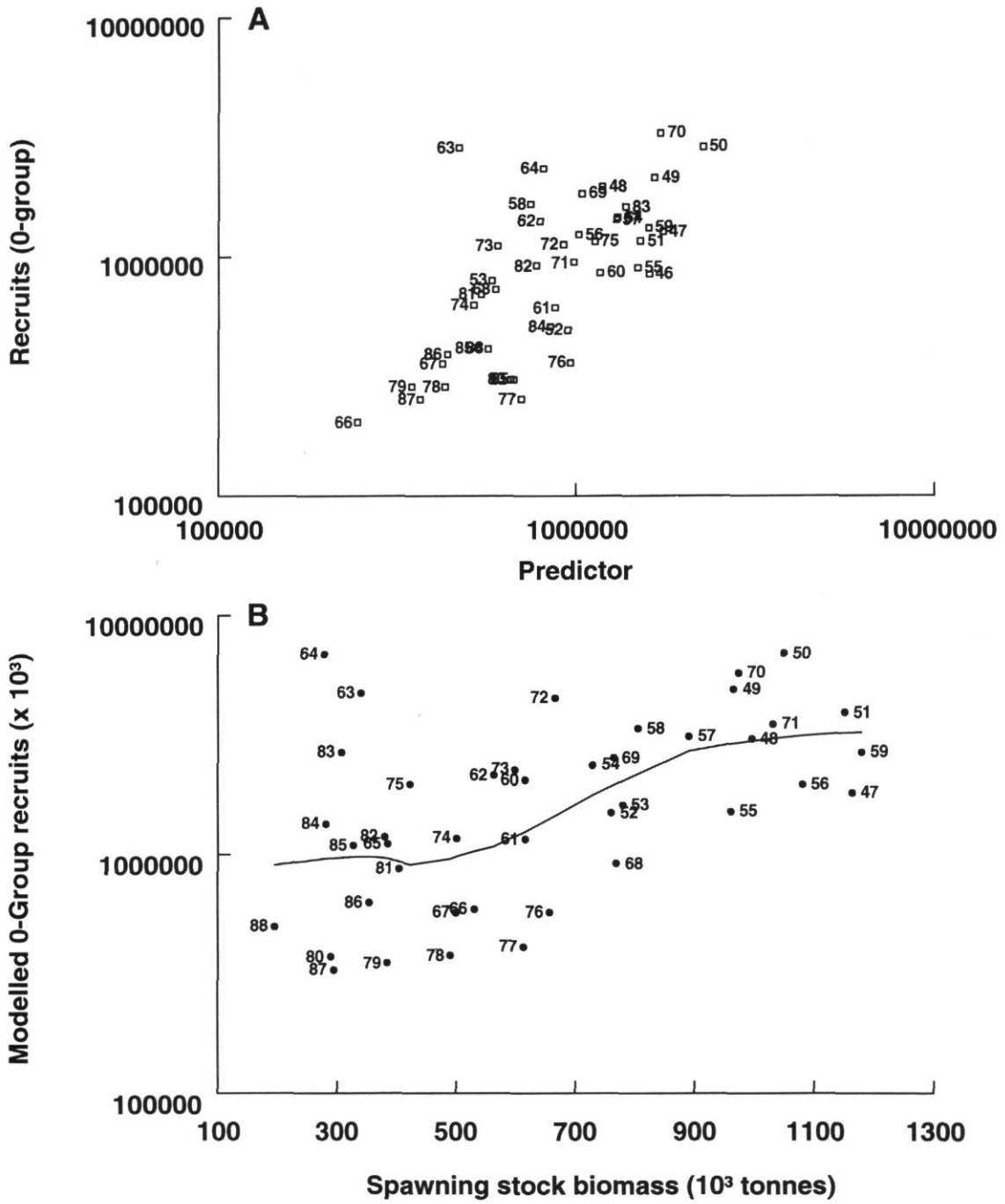


Figure 3. 0-group recruitment of Northeast Arctic cod. (A) Comparison of the "observed" with the "modelled" (predictor) results, (B) modelled recruitment (logarithmic scale) as a function of spawning-stock biomass (data 1946–1988).

Table 1. Multiple regression model of log 0-group recruits of Northeast Arctic cod, for 1946–1988, on three predictors (mean temperature on the Kola-meridian section, juvenile biomass, and log SSB (spawning-stock biomass)), with analysis of variance and parameter solutions.

Predictors	DF	SS	MS	F	p
Temperature	1	6.69	6.69	20.41	<0.01
Juvenile biomass	1	2.42	2.42	7.36	<0.01
Log SSB	1	1.97	1.97	6.01	<0.05
Residuals	39	12.80	0.33		
Total	42	23.88	0.57		

Predictors	Estimate	SE	Estimate odd years	Estimate even years
Constant	8.14	1.21	9.21	7.12
Temperature	0.77	0.21	0.72	0.84
Juvenile biomass	−5.4e-7	2.0e-7	−5.0e-7	−6.0e-7
SSB	0.46	0.19	0.31	0.58

SS = sum of squares, DF = degrees of freedom, MS = mean square, F = Fisher ratio, SE = standard error, p = significance level.

Table 2. Estimates of natural mortality of Northeast Arctic cod obtained from multiple regression fits of ln (VPA) recruits to mean temperature (Kola-meridian section), spawning-stock biomass and to juvenile biomass and from a simple MSVPA. Results shown are the cumulative M2 values on ages 0–3.

Year	M2 from multiple regression	Cumulative M2 from MSVPA	Year	M2 from multiple regression	Cumulative M2 from MSVPA
1946	0.33	0.30	1968	0.64	0.21
1947	0.24	0.31	1969	0.10	0.30
1948	0.19	0.39	1970	0.11	0.54
1949	0.23	0.77	1971	0.23	1.28
1950	0.32	0.81	1972	0.49	1.36
1951	0.55	1.13	1973	1.10	0.70
1952	0.61	1.05	1974	0.90	0.61
1953	0.82	0.67	1975	0.35	0.52
1954	0.72	0.45	1976	0.48	0.44
1955	0.32	0.49	1977	0.36	0.46
1956	0.22	0.44	1978	0.33	0.27
1957	0.37	0.75	1979	0.35	0.20
1958	0.44	0.68	1980	0.13	0.19
1959	0.47	0.68	1981	0.13	0.18
1960	0.46	0.84	1982	0.13	0.24
1961	0.56	0.60	1983	0.13	0.48
1962	0.58	0.39	1984	0.22	0.92
1963	0.37	0.46	1985	0.44	0.93
1964	0.26	1.01	1986	0.64	0.46
1965	0.35	1.22	1987	0.57	0.26
1966	0.78	1.03	1988	0.18	0.22
1967	0.97	0.45			
Max	1.10	1.36	Min	0.10	0.18

Recruitment thus increases with temperature and with higher spawning stock biomass, but declines with increasing biomass of juveniles. Recruitment increases roughly as the square root of spawning stock abundance. The power curve form, however, is incorrect at low stock size, as it indicates an infinite slope at the origin.

The exponential form of the term for the juvenile biomass effect allows it to be interpreted as a predation mortality. The resulting estimates of predation mortalities (Table 2) vary between 1.103 in 1973 and 0.101 in 1969. They thus appear to represent a predation-induced variation in recruitment of a factor of slightly less than 3. This initial multiple regression approach indicates that predation mortality could have a significant impact on recruitment. The standard VPA recruitment estimates may be adjusted by multiplying them by the exponential of the M2 values given in Table 2 to account for the predation mortality. Such adjustments might be expected to improve the fit of the VPA recruitment estimates to the available recruitment survey series, because the surveys might have been made before the predation mortality acted. This possibility was examined. Table 3A shows the improvements/reductions in the R-squared values of the log-log fits of the various survey series to the revised recruitment series compared to those obtained from single species VPA recruitment estimates. Table 3A indicates that fits were in general worse with the revised series, thus casting some doubt on the interpretation of the juvenile biomass effect as a reflection of cannibalism.

To examine the existence of within cod stock predation mortality further, a simple multispecies VPA was investigated. This was used to test whether a reasonable model of predation could provide estimates of recruitment that better reflected changes in the survey series. A number of model trials were made using different combinations of the parameters $\alpha 1$, $\alpha 2$, $\alpha 3$, and β of the predation relationship described in Equations (2) and (3). It was a feature of these trials that combinations that gave rational levels of M2 also provided recruitment series, which in many cases correlated with available recruitment survey series better than the normal VPA estimates of recruitment. The final parameter combination adopted was a value of $\alpha 1 = 2$ per megatonne, with $\beta = 0.27$. The mean of the lognormal feeding relationship ($\alpha 2$) was maintained at the North Sea estimate of 3.26 (a mean predator to prey weight ratio of 26:1), but the SD of their feeding relationship ($\alpha 3$) was reduced to 1 on statistical grounds.

With the above parameter combinations all recruitment surveys were fitted at least marginally better than with the constant M results. Table 3B shows the improved, although still low, R-squared estimates of the log-log fits of the 0-group surveys to the recruitment estimates compared to those obtained with single species VPA. Results were very similar to constant M results for the Russian survey series. Considerable improvements were noticed with the various Norwegian surveys, particularly on the 1- and 2-year-old fish. In general, the shorter Norwegian series would have been fitted better with higher M2 terms while the longer Russian series favoured lower M2 terms. This may suggest that the α-term has increased in recent years. It is striking that all 16 series showed some improvement, even though some were small.

A further check on the series is provided by comparing the consumption of 1-, 2-, and 3-group cod with results calculated by Skagen *et al.* (1990) from stomach content analyses made in 1984–1988. The results obtained are generally lower than those of Skagen *et al.*

Table 3. Improvement of the R-squared values of log-log fits of "predation" (cannibalism) adjusted recruitment survey series compared with the values obtained by fitting to VPA for Northeast Arctic cod.

	International	Russia			Norway		
Age	0	1	2	3	1	2	3
A. Difference in R-squared fit values for survey series regressed on single species VPA recruits and upon recruits estimated by multiple regression.							
Region							
1		0.02	−0.01	−0.04	0.06	0.02	−0.03
2b		−0.11	−0.18	−0.18	0.03	−0.02	−0.04
Both	−0.09				0.02	0.05	−0.19
B. Difference in R-squared fit values for the survey series regressed on single species VPA recruits and upon recruits estimated by MSVPA.							
Region							
1		0.00	0.00	0.00	0.15	0.17	0.04
2b		0.00	0.04	0.01	0.23	0.19	0.04
Both	0.04				0.21	0.07	0.00

(1990) for ages 0–2, suggesting that predation mortality might be underestimated in these cases but slightly higher for the 3-year-olds.

Fitting a similar multiple regression to the new recruitment estimates to that applied to single species results (as in Table 1) produced significant correlations with temperature and spawning stock biomass, but as would be expected the juvenile biomass did not correlate. Overall, the residual variance was increased, which suggests that the model had increased the noise in the recruitment series.

The levels of cumulative predation mortality from ages 0–3 on each year class were calculated (Table 2) and show that these are generally similar in size to those obtained from multiple regression and peak on 1-year-old fish. They increase markedly in the shadow of the exceptionally large 1950, 1963–1964, and 1970 year classes, but are slightly out of phase with the multiple regression estimates.

Figure 3B shows the new stock recruitment plot together with a Cleveland–Lowess smoothed line. In general, although the peaks and troughs overlap with the old series, the new recruitment series is somewhat higher in earlier years, showing a stronger relationship with spawning stock biomass.

Growth and trophodynamics

The geometric mean weight (kg) of 4–9-year-old cod has varied appreciably between the early 1950s and 1991 (Fig. 4). The expected scalar biology trend for decreases in specific growth rates with increasing age is clearly visible, and so too is the trend for specific growth rates within given age groups clearly to increase and decrease as the mean weights also increase and decrease respectively. The greatest specific growth rates are achieved as the weight-at-age increases, but specific growth rates have already begun to decline by the time that peak weights-at-age have been attained, i.e., growth rates *sensu stricto* are not necessarily akin to weights-at-age. Further, the greatest variability in weight-at-age (for ≥4-year-olds) occurs in the period after 1970, being particularly as prominent peaks in the younger ages examined, and becoming progressively less evident with increasing age. The two major epochs of growth variability are visible in the population sampled in the early 1970s and mid-1980s.

The change in the magnitude and the cycle of the specific growth rates for 4–7-year-old cod are well illustrated for the period 1982–1992 (Fig. 5). In addition to the declining trend in cod growth rates with increasing age, it is clear that fish sampled in 1986 and 1987 had substantially slower growth rates than fish sampled in 1990 and 1991. Estimated in the same diagram (from the equation of Jobling, 1988) are specific growth rates of cod, fed "in excess" (i.e., these growth rates are unlikely to be affected by density dependence), at ambient temperatures of 2–5°C. An examination of the growth rates of cod at the ambient temperatures (e.g., "cold" or "warm") prevalent for particular years in the Barents Sea, seen in conjunction with the respective population densities (e.g., "high" or "low") and food availability (e.g., "plentiful" or "scarce"), allows the presentation of some scope for growth scenarios relative to the optimum

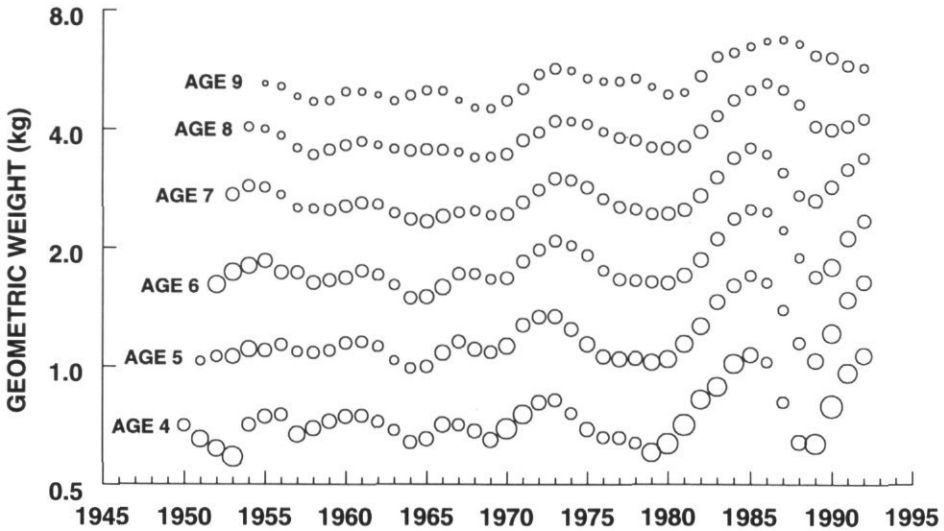


Figure 4. Variation in the geometric mean body weight (kg) and specific growth rate (denoted by the diameter of the plotted circles) of 4–9-year-old Northeast Arctic cod between 1951 and 1991. The plotted geometric weights and specific growth rates have been smoothed by a 3-year running mean.

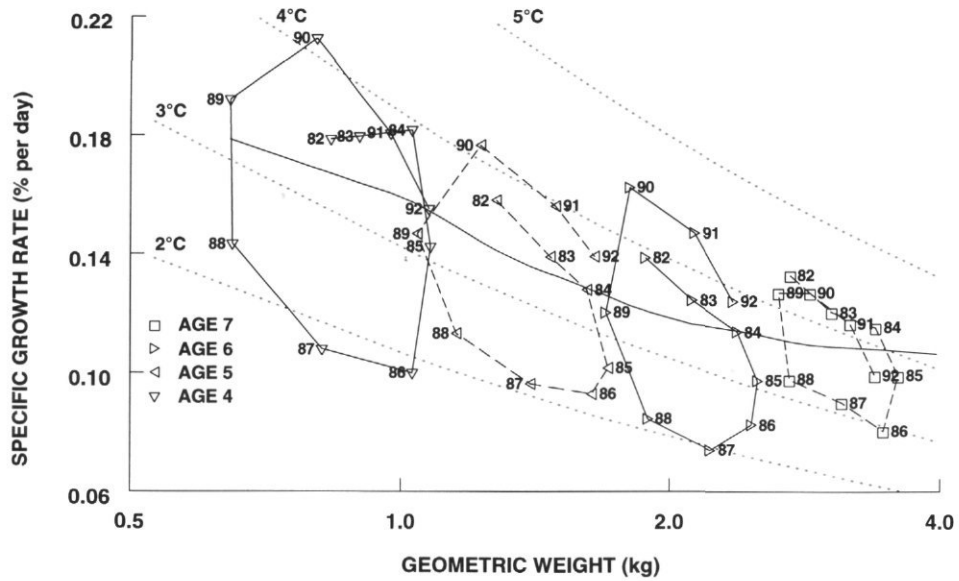


Figure 5. Change in the specific growth rate (SGR, % per day) as a function of geometric body weight (kg) of 4–7-year-old Northeast Arctic cod between 1982 and 1992. The dotted lines represent estimated SGR (equation of Jobling, 1988) for cod with "excess" food at water temperatures of 2–5°C.

(i.e., not limited by food or density effects) metabolic reference points (Jobling, 1988) for 2–5°C. A *worst case growth scenario* can be envisaged when population densities are high, temperature is high (i.e., metabolic demands are also high) but not above environmentally acceptable maxima for cod, and food is highly limited (i.e., not sufficient to provide the fuel to sustain the elevated metabolism at higher temperature). An example of a *best case growth scenario* would arise when population densities are low, temperature is high but acceptable, and food is plentiful (i.e., not growth limiting). In the case of the relatively low growth rates sampled for fish of 4–7 years old in 1986–1987, these are the product of relatively high population densities (after the production of the strong 1983 year class) coupled with relatively low temperatures (ca. 3.5°C), and relatively scarce food (reduced capelin stock and absence of herring). In the case of the relatively high growth rates sampled for the same ages of fish in 1990–1991, these are the product of increased food (capelin) availability and high temperature (ca. 4.7°C).

At attempt at modelling the specific growth rate of cod was carried out, taking population density and ambient temperature into account, for the complete data set (1950–1991). The regression equation, with non-linear parameter solutions using quasi-Newton iteration, are given in Table 4.

Comparisons of the model-estimated specific growth rates with the observed rates, when presented as a

Table 4. Nonlinear regression model, with analysis of variance and parameter solutions, estimating the specific growth rate of Barents Sea cod (1950–1991).

Source	SS	DF	MS
Regression	3.213	4	0.803
Residual	0.080	233	0.000
Total	3.293	237	
Corrected	0.215	236	
Raw R^2 (1-residual/total) = 0.976			
Corrected R^2 (1-residual/corrected) = 0.630			

Parameter	Estimate	ASE	L_{95}%	U_{95}%
D	0.176	0.019	0.139	0.213
C	1.266	0.355	0.566	1.965
β	−0.277	0.015	−0.307	−0.247
α	0.064	0.023	0.0200	0.109

$$SGRS3 = \left[\frac{1}{(N3 + N4 + N5 + N6)^D}\right] \times C \times GWS3^{\beta} \times e^{\alpha T}$$

where SGRS3 = 3-year running averaged specific growth rate (% change per day), N3, N4, N5, N6 = numbers of cod age 3, 4, 5, and 6 respectively, D = an exponent, C = a measure of food/population density, GWS3 = 3-year running averaged geometric weight (kg), α = temperature-related coefficient, β = weight-related coefficient, and T = mean temperature (°C) at the Kola-meridian section. SS = sum of squares, DF = degrees of freedom, MS = mean square, ASE = asymptotic standard error, L_{95}% = lower 95% confidence limit, U_{95}% = upper 95% confidence limit.

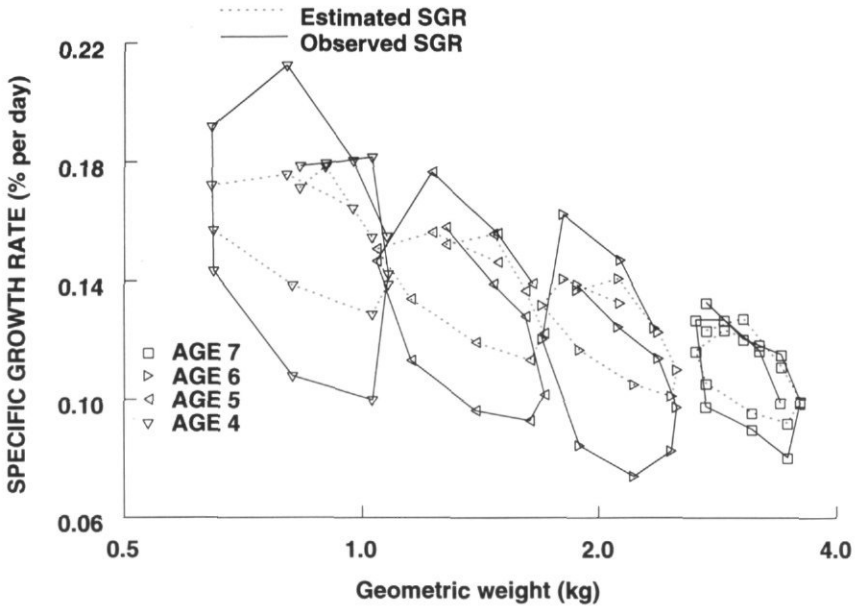


Figure 6. Comparisons of model estimates and field observations of specific growth rate (SGR, % per day) as a function of geometric body weight (kg) of 4–7-year-old Northeast Arctic cod. The field observations are identical with those in Figure 4.

function of geometric fish weight, for the period 1982–1992 (Fig. 6), show a good similarity of pattern between the two, but also emphasize that the model estimates tend to fail in fully following the observed data when peaks and troughs of growth rates occur (Fig. 6). However, a further examination of the model estimates for the ca. 40-year period of the full data set shows that a substantial degree of the observed variation in cod specific growth rate is well represented in the model (Fig. 7).

The numbers of cod at age (abundance of 3–9-year-olds, N3–N9), the observed specific growth rates (for 4–9-year-olds, SGR4–SGR9), the biomass of cod (BIOCOD, sum of 3–9-year-olds in tonnes), the liver index (LIVERIND), and the percentage frequency of occurrence of capelin (ACPOC) and *Pandalus borealis* (SHRIMPOC) in cod stomachs have been treated by principal components analysis (PCA, based on rank correlation) (Fig. 8). The juxtaposed position of the numbers of 4- and 5-year-old cod, and to a lesser extent 3-year-olds, on the one side and the specific growth rates on the other along Axis I are indicative of a trend for high abundances of cod to be associated with diminished growth rates and low abundances to be correlated with elevated growth rates, i.e., the presence of density-dependent growth. Specific growth rates of cod also appear to be positively correlated along Axis I with % FoO of both capelin and *P. borealis*. Along Axis II the % *P. borealis* FoO is negatively related to the numbers of cod and cod biomass.

From 1945 to 1991, the % FoO of the various prey species recorded in Barents Sea cod stomachs has varied greatly, with capelin and *P. borealis* exhibiting pulses ranging from minima of about 10% up to maxima of about 55% in both cases (Fig. 9A). The liver index of cod has tracked, in the main, the % capelin FoO in cod stomachs. Unfortunately, although stock abundance data have existed for cod, reliable abundance data for these two prey species have only been available since 1973 in the case of capelin, and since 1981 in the case of *P. borealis* (Fig. 9B).

Plots of the % FoO of capelin and *P. borealis* in cod stomachs as a function of their respective biomass indicate that the % capelin FoO clearly rises as their own population abundance increases (Fig. 10A), and a weaker but basically similar trend is apparent for *P. borealis* (Fig. 10B). Thus, there is a trend that the proportionate selection of both these prey species by cod reflects the prey abundances in nature. A longer data set (1950–1987) presenting variability in the cod liver index as a function of the % capelin FoO in cod stomachs shows that there is a strong positive correlation between the two (Fig. 10C). High liver indices in cod, however, are associated with low % *P. borealis* FoO, although there is a marked flattening out, with signs of a small upturn, of the relationship at low liver indices and high FoO of *P.*

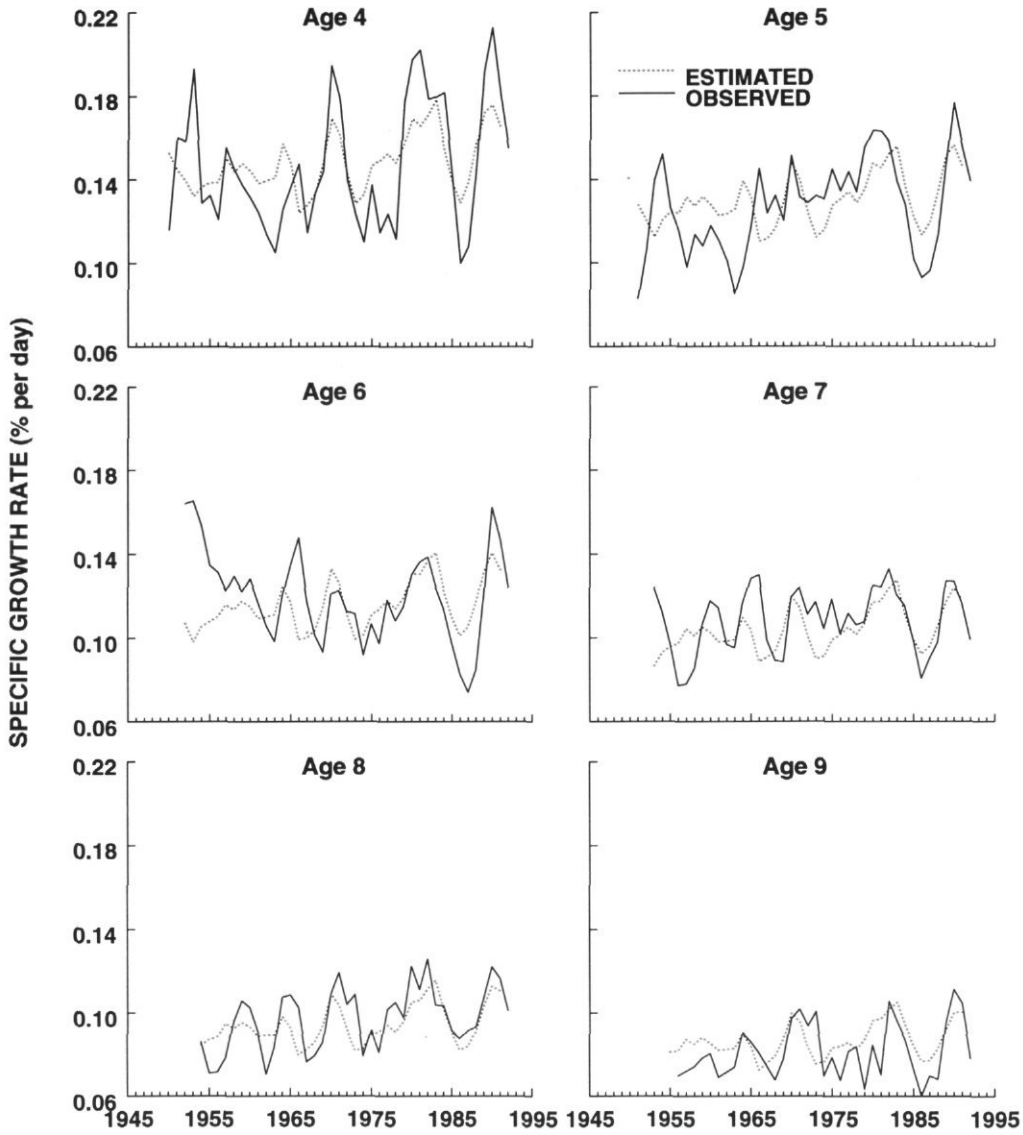


Figure 7. Comparisons of annual (1953–1992) variability in model estimates and field observations of specific growth rate (% per day) in 4–9-year-old Northeast Arctic cod.

borealis (Fig. 10D): the two "wings" of the curve are skewed regarding the weighting of years, with low % (0–20) *P. borealis* FoO being mainly associated with the 1950s to mid-1970s data and high % (25–50%) *P. borealis* FoO being mainly associated with the later 1970s' and earlier 1980s' data. Interestingly, the 1986–1988 years are distinguished by having unusually low cod liver indices and low % capelin and *P. borealis* FoO (Fig. 10A, B) concurrent with extremely low stock biomass of these two prey species: this occurred as the recruitment of the strong 1982 year class of cod manifested itself (Fig. 9B).

The % capelin FoO in cod stomachs, from 1973 to 1989, increased from about 10% in an approximately linear manner with increasing ratio of capelin to cod stock biomass (i.e., standardized per unit of cod biomass and thus an index of food availability) before flattening off at about the 35% level (Fig. 11). This response supports, in a more independent manner, the implied functional response that cod select capelin relative to the latter's biomass and availability in the ecosystem.

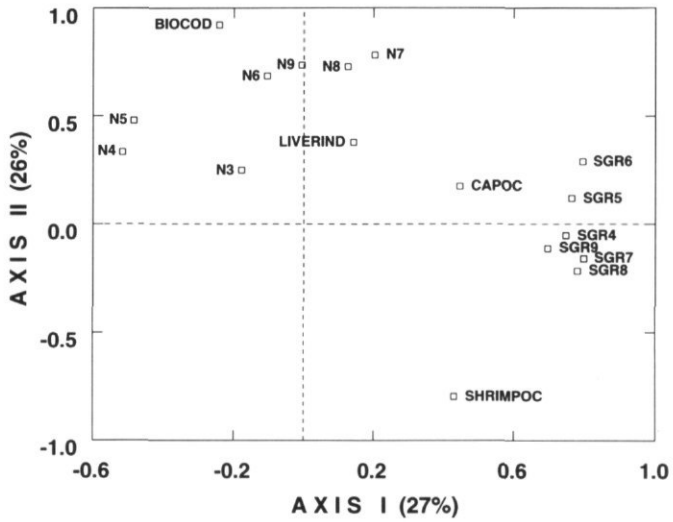


Figure 8. Principal Components Analysis plot (Axes I and II) of Northeast Arctic cod and their feeding relationships, involving numerical abundance of 3–9-year-olds (N3–N9), specific growth rate of 4–9-year-olds (SGR4–9), biomass in tonnes of 3+ year-olds (BIOCOD), liver index (LIVERIND) of prespawning cod caught at Lofoten, and percentage frequency of occurrence of capelin and *Pandalus borealis* (CAPOC and SHRIMPOC respectively) in cod stomachs.

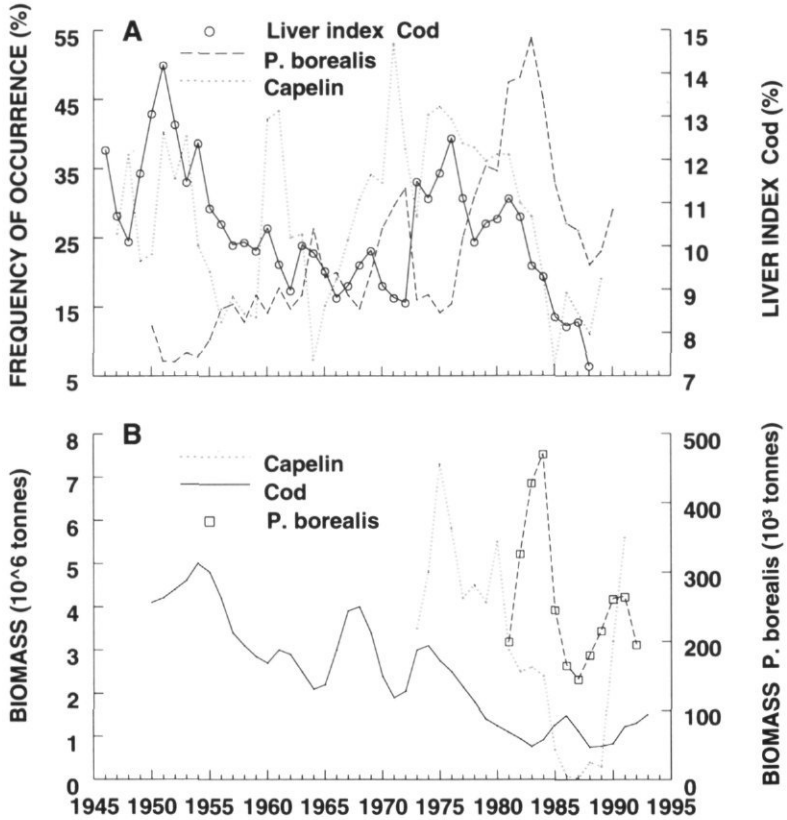


Figure 9. Variation in (A) the percentage frequency of occurrence of capelin and *Pandalus borealis* recorded in the stomachs of Northeast Arctic cod, and the liver index (percentage of round body weight after the gonads and guts have been removed) of prespawning cod caught in the Lofoten fishery, and (B) stock size (biomass) estimates of Northeast Arctic cod (at age 3+), capelin (at age 2+), and *Pandalus borealis* in the Barents Sea.

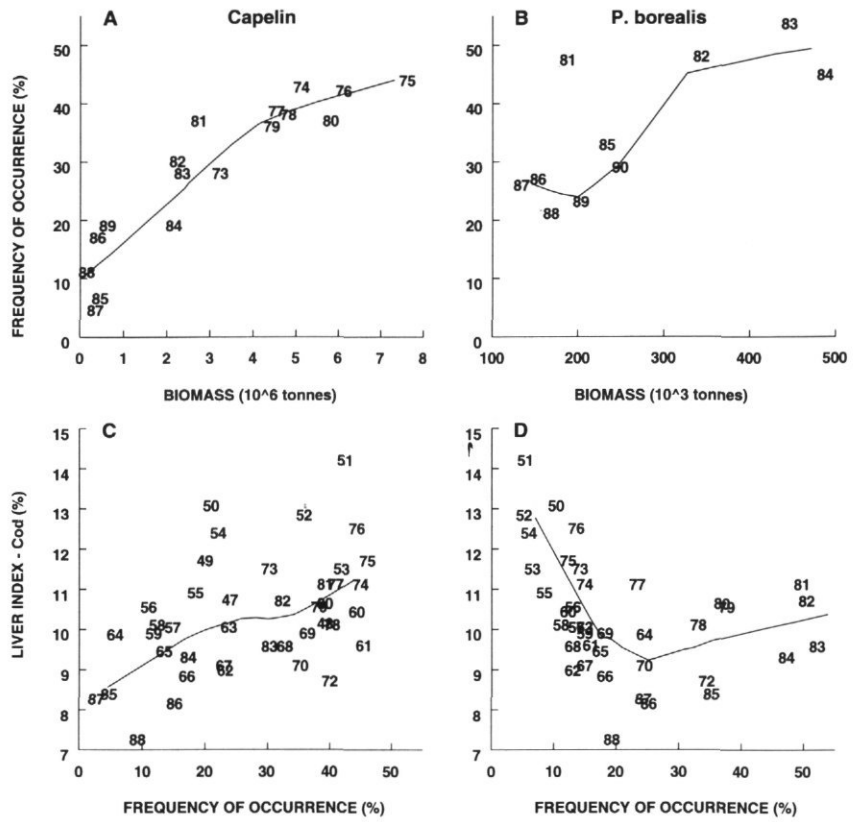


Figure 10. Variation in the percentage frequency of occurrence of (A) capelin, and (B) *Pandalus borealis*, in the stomachs of Northeast Arctic cod as a function of their own stock biomass, and variation in the liver index of cod as a function of the percentage frequency of occurrence of (C) capelin and (D) *Pandalus borealis*.

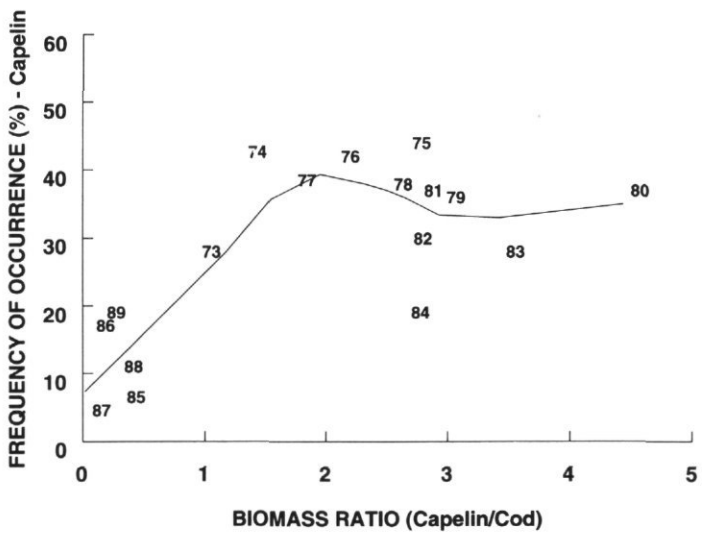


Figure 11. Percentage frequency of occurrence of capelin in the stomachs of Northeast Arctic cod as a function of the biomass ratio of capelin to cod.

Discussion

Recruitment

The recruitment of marine fish stocks commonly varies by one or two orders of magnitude, for reasons that are generally not fully understood (Hjort, 1926; Pitcher and Hart, 1982; Houde, 1987). Of the 43 year classes recruited to the Northeast Arctic cod stock between 1946 and 1988, the 10 least abundant had an average VPA abundance (notionally estimated at age 0) of 302 million. By contrast, the 10 most abundant year classes had an equivalent abundance of 2222 million and the top 4 (those of 1950, 1963, 1964, and 1970) of 2864 million. The middle range year classes had an abundance of about 920 million. Hence, the lowest 10 year classes were 1/3 of the level of the mid-range year classes which were in turn about 1/3 of the average of the four most abundant year classes. There was a ratio of 1:16 between the least abundant, the 1966 year class, and the most abundant, the 1970 year class.

A number of environmental factors might influence recruitment to the stock. Of these, temperature, measured at the Kola section, is available for the longest time series. Moreover, temperature at the Kola section might reasonably be expected to act as a full or partial proxy for factors such as Atlantic inflow, westerly winds, plankton production, and possibly turbulence (Izhevskii, 1961, 1964; Corlett, 1965; Cushing, 1975, 1990; Sundby and Gossum, 1990). A description of which of these factors are inherently correlated could form the basis for a fruitful dialogue between physical and biological oceanographers.

The increased occurrence of strong and medium year classes of Northeast Arctic cod in years with elevated temperatures along the Kola section (Sætersdal and Loeng, 1987) is not unexpected for a species at the northernmost extent of its biogeographical distribution (Ekman, 1967). The same variations are also reflected in the Lofoten spawning area. The spawning success of the Northeast Arctic cod is coupled with the temperature triggered spawning of *Calanus finmarchicus,* while the time of cod spawning appears to be relatively constant and unrelated to temperature variations (Ottestad, 1942; Pedersen, 1984; Ellertsen *et al.*, 1989). Ellertsen *et al.* (1989) demonstrated that only small year classes were produced when temperatures on the spawning grounds were low, but that as both good and poor year classes were produced in years with elevated temperatures it is also apparent that high environmental temperature alone is not adequate for the formation of strong year classes.

The distribution and survival of fish, both as larvae and as adults, is greatly affected by the strength of the water currents and temperature regime in the Barents Sea (Lee, 1949; Konstantinov, 1967; Ponomarenko, 1973b; Nakken and Raknes, 1987; Shevelev *et al.*, 1987; Loeng, 1989a). Increased inflow of warmer water into the Barents Sea will be beneficial to young cod in distributing them over a larger warmer domain, thereby reducing the intraspecific competition and possibly aiding the survival of young bottom-dwelling cod (Ponomarenko, 1973b; Sætersdal and Loeng, 1987; Nilssen and Hopkins, 1992). Although large-scale oceanic and climatic variability greatly affects marine resources in the Barents Sea, research on the feeding conditions of Northeast Arctic cod larvae also corroborates the Rothschild–Osborn theory of small-scale turbulence and plankton contact rates (Sundby and Fossum, 1990). Nevertheless, too strong westerly winds, although being correlated with high temperatures, are likely to be accompanied by excessive turbulence for, for example, the successful feeding of larval cod (Ellertsen *et al.*, 1989; Sundby and Fossum, 1990). Cury and Roy (1989) have emphasized the presence of an optimal environmental window for wind and turbulence affecting successful recruitment.

The significance of the temperature effect on the regressions of recruitment shown singly and in conjunction with other factors in the present article propounds the importance of this factor and/or the factors for which it acts as a proxy. The relationship modelled in the multiple regression suggests that temperature (or its aliases) might affect recruitment by a factor of slightly less than 4 between the coldest and warmest years. However, an adequate spawning stock biomass is ultimately the *sine qua non* for adequate recruitment. Examples exist of stocks where this requirement has been violated and recruitment has collapsed. In vigorous stocks, however, recruitment appears to have little relationship with the size of the spawning stock. In Northeast Arctic cod, Garrod (1973) suggested a recruitment–survival relationship with both temperature and spawning stock biomass, while Garrod and Jones (1974) fitted a Ricker curve to the stock. In the present article, the statistically significant results of regression of recruitment on spawning stock biomass as a single factor and in conjunction with other factors suggests that such a relationship is highly likely. The precise form of this relationship is unlikely to be the power curve modelled, however, since this form was chosen for statistical rather than biological reasons. Nevertheless, it does indicate a decline of recruitment with reduced spawning stock biomass. The relationship modelled in the multiple regression has a fitted exponent for the power curve of 0.456, thus suggesting a near square root relationship between recruitment and spawning stock. Given the range over which recruitment has varied between 1946 and 1988 (the first and last years had respectively the highest and lowest spawning stock biomass of the series) the relationship would suggest that this could generate a factor of about 2.6 in recruitment.

Predation by larger fish, including cannibalism by older age groups of the same species, has been recognized as a potential modifier of yearly natural mortality by age class. Multispecies virtual population analysis (MSVPA) applied to the North Sea (ICES, 1988), to the Baltic Sea (Sparholt, 1991), and analogous methods applied to other areas including the Barents Sea (Mehl, 1989, 1991) also indicate this to be the case. The effect of the varying natural mortality levels in MSVPA is to increase the relative estimates of recruitment for year classes which have suffered the most natural mortality. Thus, it might be expected that single species VPA recruitment estimates would show negative correlations with the biomass of significant predators. Such relationships have been found for a number of stocks (Pope and Woolner, 1981; Pope, 1992; Olafsson *et al.*, 1993). For the Northeast Arctic cod the abundance of 3- and 4-year-old fish had the highest negative correlations with recruitment estimates and, hence, were selected as the appropriate measure of juvenile biomass. Fish older than 3 or 4 years would be large enough to prey on recruits in their first year and possibly on recruits up to age 3. A large year class of 3- or 4-year-olds could therefore potentially reduce the abundance of a recruiting year class. The biomass of 3- and 4-year-olds did not show a significant correlation with recruits when considered in a simple regression, but did show a significant effect when the Kola section temperature was included. The relationship between juvenile biomass and recruits could be interpreted to give a direct estimate of predation mortality. For cod, cannibalism by adults can produce mortality dependent on the density of both the young and the stock (Pitcher and Hart, 1982). Cushing (1975) considered that the average rate of cannibalism in the Northeast Arctic cod is about half a recruit per adult per year. In the present study, the range of this variable suggests that it might modify recruitment by a factor of 2.7, which is close to the factor of 3 suggested by Mehl (1991) from stomach content and consumption data.

If the 3–4-year lagged juvenile biomass term in the multiple regression is indeed related to predation, then correcting the VPA recruitment series for its effect might be expected to yield new estimates that correlate better with survey series for the younger fish, and which in turn might measure recruitment prior to cannibalism. In fact, correlations do not generally improve, and this weakens the case for the 3–4-year lag correlation describing a predation mediated interaction. An alternative explanation might be that the 3–4-year lag described by juvenile biomass is the half-cycle effect of the stock–recruitment relationship, since the age of 50% maturity is about double the lag at 7–8. It might otherwise reflect the exhaustion of some vital component of the ecosystem by large cod year classes.

A simple MSVPA designed to improve the fit to the survey series by considering size-based predation was able to do so with a plausible parameter set. However, this resulted in more variable estimates of recruitment, after the temperature and stock variables had been allowed for, which would suggest that it is not describing cannibalism exactly and is therefore adding noise. The problems with these two approaches may well be a reflection of the "time-series" nature of the recruitment data. Both spawning stock and predator variables in recruitment regressions imply lagged correlations between year classes. Thus, the negative effect of cannibalism by the preceding two year classes might be masked by positive autocorrelations due to the effects of temperature or spawning stock size. Although predation appears a plausible modifier of recruitment the various evidence required further careful scrutiny.

Other variables considered as predictors of recruitment were the cod liver index, which might reflect changes in fecundity, and the percentage frequency of occurrence (% FoO) of herring, capelin, and *P. borealis* in cod stomachs, which might influence the level of predation. None of these measures directly improved the fit of the recruitment in the muiltiple regressions. It should, however, be noted that these factors are reflected in growth rate, and hence in maturity-at-age and spawning stock biomass. Thus they may represent indirect influences on recruitment which will themselves be the subject of climatic influences.

The simple multiple regression model used to describe influences on the recruitment of Northeast Arctic cod has the form of a multiplicative model of three influences: temperature, spawning stock, and cannibalism. Temperature, possible as an alias or proxy for other climatic variables, is the most important, but the internal cod stock variables can also potentially cause changes in recruitment on the threefold scale of the differences between average and small or large year classes. Since these are the factors controllable by fisheries management, considering how they should be arranged to best endure the inevitable variation in the climatic variables should be a prime consideration for managers.

Population structure, growth, and trophodynamics

In the 1950s the biomass (3+ ages) of the Northeast Arctic cod stock was about 5 million tonnes and sustained an annual fishery of about a million tonnes (Garrod, 1967, 1977). The stock size declined before flattening out in the late 1980s and early 1990s with the recruitment of several good year classes during the coincident warm-water period (Fig. 9B). The main reason for this decline is considered to be a steadily increasing fishing mortality, rising from about 0.2 up to in excess of 0.8, before being markedly reduced in the

late 1980s (Mehl, 1989; Jakobsen, 1992). The present results emphasize that the main consistent demographic trend since World War II has been a substantial decrease (to about 0.1% of 1950s reference levels) in the absolute and relative (% contribution) abundance of older fish (>10 years) in the stock, whereas younger fish (<6 years) are virtually as common as they were earlier (Fig. 2).

Although large cod obviously abounded in the 1940s and 1950s, the largest weights-at-age registered for 4–9-year-old fish since the 1950s were attained in two major pulses, in 1973–1974 and in 1985–1986 (Fig. 4). The pattern of harmonious, only slightly age-offset, peaks and troughs evident for weight and growth rates emphasizes that the prevalent forcing factors primarily affected all of the studied age groups of cod relatively simultaneously. Figure 4 suggests that the recruitment of the strong 1970 year class to the stock of larger/older cod (4–9 years old) was a contributory factor reducing the weight-at-age and subsequent growth rates. Interestingly, the periods 1973–1979 and 1985–1988, in which weight declined consistently and growth rates were low, were periods of generally decreasing temperature, while the period 1979–1985, in which weight-at-age increased consistently and growth rates were high, was also a period of generally increasing temperature (Fig. 1A). However, growth in fish is a complex process, such that although increased temperature may elevate metabolic rates and thus set the scene for *potentially* better growth rate, population density and food availability frequently exert a predominant influence on the realized growth rates (Brett, 1979; Ricker, 1979).

Even though an inverse relationship between abundance and growth rate is indicative of density dependence, predator–prey relationships may also fluctuate greatly, sometimes obscuring possible regulatory mechanisms. In the case of Northeast Arctic cod, temperature may act simultaneously on recruitment and growth (Nakken and Raknes, 1987; Loeng, 1989a; Jørgensen, 1992). Although several authors have maintained that Northeast Arctic cod growth is density-dependent or affected by temperature (Rollefsen, 1954; Cushing and Horwood, 1977; Nakken and Raknes, 1987), they suffer from employing size- (e.g., length or weight)-at-age data rather than growth rates (Miller, 1992; Jørgensen, 1992). The use of weight-related specific growth rate and abundance-at-age data in the present study, analysed by principal components analysis (PCA), clearly demonstrates that the parameters are negatively correlated and thus that growth of Northeast Arctic cod is density-dependent. Jørgensen (1992), analysing length-based growth data of Northeast Arctic cod, concluded that although marked short-term (1–5 years) variations in length-at-age were observed, no overall trend was detectable. The present study demonstrates that weight data are appreciably more informative about growth dynamics than length data, as such mass measures are better suited to reflecting energetic (e.g., anabolic and catabolic) change.

Analysing a 10-year data set (1982–1992) of specific growth rates (SGR, % per day) of Northeast Arctic cod, spanning appreciable variability in temperature, population density, and food quantity, the present study shows that mean values decreased with fish age and size from a mean of about 0.18% per day for 4-year-olds to about 0.12% per day for 7-year-olds. Interannual variability is conspicuous when comparing a "poor-case" scenario for 1986–1987, in which slow growth rates are associated with high stock densities, low temperature (about 3.5°C) and paucity of capelin, with a "better-case" scenario for 1990–1991 in which higher growth rates are associated with elevated temperature (about 4.5°C), increased capelin availability, but high stock numbers (which would tend to reduce growth rates). Comparison of these measured values with reference points calculated from the equation of Jobling (1988) for experimentally fed in excess or satiation at 2–5°C (representing the range of mean temperatures in the cod domain of the Barents Sea) suggests the merit of comparing attained growth in a given temperature regime against what could be achieved (i.e., a "scope for growth") in the absence of density or food-scarcity-mediated restrictions. Our extension of Jobling's (1988) equation, now incorporating a solution for a density-dependent/food effect for field populations, provides a remarkably good fit to the observed SGRs from about 1950 to 1991 for 4–9-year-old cod, although there is a tendency for the model fit to underestimate SGR. At increasing temperatures, the difference between our model and Jobling's (1988) equation reflects the fact that Barents Sea cod experience a substantially lower food ration than the cod in experimental conditions fed to "satiation", and thus their temperature response is appreciably less. Further, Jobling's (1988) data are based on relatively small cod and there are clear indications that maximum growth rates of larger fish (> ca. 1 kg) occur at relatively lower temperatures, and that growth rates estimated by Jobling's model for low temperature (2–5°C) are too low (Pedersen and Jobling, 1989). Jobling's (1988) experiments were based on few observations at low temperatures, such that the uncertainty between temperature and SGR is proportionately greater at low temperatures than at higher temperatures. Despite this, the approach of incorporating temperature as well as density/food effects, as applied in this study, appears to be promising for exploring field populations.

Cod, particularly in the Barents Sea, is well known as being a generalized, opportunistic carnivore, feeding on several types of prey when these are available (Zatsepin

and Petrova, 1939; Brown and Cheng, 1946; Daan, 1974; Ponomarenko and Yarragina, 1978; Lilly, 1987; Pálsson, 1983; Magnússon and Pálsson, 1989). In the Barents Sea, however, only nine species or groups of categories contribute more than 1% by weight of food: these are hyperiid amphipods, euphausiids ("krill"), deep-sea shrimp (*P. borealis*), herring, capelin, polar cod (*Boreogadus saida*), its own siblings (i.e., cod), haddock (*Melanogrammus aeglefinus*), and redfish (*Sebastes* spp.) (Mehl, 1991). An examination of the percentage frequency of occurrence (% FoO) of capelin, herring, and *P. borealis* in the stomachs of cod since the 1940s clearly emphasizes the importance of capelin in the diet (Fig. 9A; Zatsepin and Petrova, 1939; Brown and Cheng, 1946; Ponomarenko and Yaragina, 1978), even when herring were common in the Barents Sea. The plots of the change in the % FoO of capelin and *P. borealis* prey in the stomachs of cod as a function of prey biomass during the 1973–1989 post-herring period indicate a positive relationship between the two (Fig. 10A, B). A generally similar relationship is apparent in a plot of % capelin FoO as a function of capelin availability (capelin/cod biomass ratio), although there is some sign of saturation at high capelin availability. These data thus denote that a c.p.u.e. relationship is operative, further suggesting that the % capelin FoO may offer a means of predicting capelin biomass in the Barents Sea. The present study also indicates that there is a positive correlation between the liver index of prespawning cod caught in the fishery at Lofoten and the % capelin FoO, probably reflecting a relationship in which increased relative and absolute levels of feeding on the lipid-rich capelin results in proportionately larger livers in cod, and presumably improved condition indices (see Love, 1970; Falk-Petersen *et al.*, 1990). The PCA further confirms that the % capelin FoO is positively related to the specific growth rate of 4–9-year-old cod, and that high numbers and biomass of cod are negatively related to the % *P. borealis* FoO, suggesting that a high degree of prey–predator oscillations occur between *P. borealis* and cod. Berenboim *et al.* (1986) concluded from analyses in the 1980s that there was a negative correlation between the biomass of *P. borealis* and that of the Northeast Arctic cod stock, but that the % *P. borealis* FoO in cod stomachs positively reflected the biomass of the *P. borealis* stock. Hopkins and Nilssen (1991), however, also considered that the increase from about 10% to about 55%, between 1975 and 1983 in the % *P. borealis* FoO, may have reflected a lack of capelin as primary choice prey for cod. Although the present study suggests that there was a general trend for high % capelin FoO and high capelin biomass in the mid-1970s, the trend in the 1980s data positively relating % *P. borealis* FoO with its biomass does not rule out the possibility that an increase in the *P. borealis* stock occurred during the 1975 to 1983 period. It has to be emphasized that the % FoO scale gives the same emphasis to a relatively large prey organism like capelin as it does to a smaller one like *P. borealis*, and thus a rise in % FoO of *P. borealis* from 10 to 55%, as occurred in the late 1970s and early 1980s, conceals a major change in the stomach content energetics of Northeast Arctic cod at that time.

The collapse of the capelin stocks in 1983/1984, lasting until the end of the decade, provided a major perturbation of the Barents Sea ecosystem, affecting the upper trophic levels including the cod, marine mammals, and seabirds (Hamre, 1988; Borisov and Elizarov, 1989; Skjoldal and Rey, 1989; Hopkins and Nilssen, 1991; Orlova, 1992). Norwegian studies in the Barents Sea have revealed that the capelin stock collapse was associated with a decline, between 1984 and 1988, of about 60% in the mean weight-at-age of the majority of ages of Northeast Arctic cod, coincident with model-estimated decreases in food consumption of about 40–70% in the same age groups (Mehl and Sunnanå, 1991). During this period of capelin paucity, natural mortality of cod probably increased by a factor of 3 because of prevalent cannibalism (Mehl, 1989), in general accord with the perspectives of our cannibalism embodying recruitment model. The present study independently confirms that the relationship between cod and capelin in the Barents Sea is comparable to that around Iceland, where Icelandic cod exhibited lower stomach contents, reduced feeding levels, and slower growth rates when the capelin stock declined to low levels than when it was abundant (Magnússon and Pálsson, 1989, 1991). These findings clearly substantiate the importance of capelin, particularly with the present lack of Atlanto-Scandian herring in the Barents Sea, for sustaining the production of Northeast Arctic cod at times of elevated cod recruitment.

Acknowledgments

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Influence of temperature variability on recruitment of cod in the Barents Sea

Geir Ottersen, Harald Loeng, and Askjell Raknes

Ottersen, G., Loeng, H., and Raknes, A. 1994. Influence of temperature variability on recruitment of cod in the Barents Sea. – ICES mar. Sci. Symp., 198: 471–481.

During the past fifteen years several studies have examined the influence of temperature variability on the recruitment of Arcto-Norwegian cod. The overall conclusion has been that year classes of high abundance occurred mainly during years with high temperature, while poor year classes occurred mainly during cold years. The present article quantifies the difference between year classes produced in warm and cold years. Separate calculations based on two different abundance indices from the international 0-Group Surveys in the Barents Sea for the years 1965 (1966) to 1992 show that the average production of Arcto-Norwegian cod larvae in warm years was about three times higher than in cold years. Similar calculations were done for haddock and for both species based on the virtual population analysis at age 3. The difference in both 0-group and virtual population analysis recruitment strength between warmer and colder years is statistically significant for cod and haddock for the 1965 to 1992 period. Our results show that the influence of temperature on cod recruitment has been stronger in the last 25 years than in the previous decades. In our opinion this added sensibility to environmental fluctuations is connected with the decline in size of the spawning stock and the change in its age composition.

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Introduction

The Barents Sea is the feeding and nursery area for such large commercially important fish stocks as Arcto-Norwegian cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*), and capelin (*Mallotus villosus*) and management of the resources presupposes a broad and thorough knowledge of the biological system and environmental conditions. Helland-Hansen and Nansen (1909) stressed the importance of studying how fish are influenced by variations in the physical conditions of the sea.

An important factor in the management of fish stocks is an understanding of the recruitment mechanisms. Many investigations have dealt with cod recruitment. The year-class strength of cod is mainly determined during the first six months of life (Sundby *et al.*, 1989), and there are several factors that may be responsible for the large variations observed, e.g., fecundity and egg quality (Kjesbu *et al.*, 1991, 1992), starvation at the start of exogenous feeding (Hjort, 1914, Wiborg, 1957; Kislyakov, 1961; Ellertsen *et al.*, 1984), predation on eggs and larvae (Murphy, 1961; Melle and Ellertsen, 1984), and physical factors acting directly on egg and larval populations (Garrod and Colebrook, 1978; Koslow, 1984; Sinclair *et al.*, 1985). At the active feeding stages of larvae, the variable contact rate between larvae and prey, induced by wind-mixing in the surface layer, may also be an important regulatory mechanism in the formation of year-class strength (Rothschild and Osborn, 1988; Sundby and Fossum, 1990). The relation between temperature conditions and the year-class variations of Arcto-Norwegian cod was examined by Sætersdal and Loeng (1987), who concluded that most of the year classes of high and medium abundance are associated with positive temperature anomalies in the early part of a warm period in the Barents Sea. The effect of temperature at the spawning ground on year-class strength has been studied by Ellertsen *et al.* (1987), who concluded that high temperature on the spawning ground is a necessary but not sufficient condition for the production of year classes of high abundance.

The present paper quantifies the effect of temperature conditions on the year-class strength – primarily of cod, secondarily of haddock and herring. In doing so, ratios between average values of recruitment indices within warmer and colder years are calculated. This is done for the 0-group back to 1965 and for the three-year-old fish

back to the 1943 year class for cod and 1947 year class for haddock. In order to differentiate between large-scale and more local variations, correlations are calculated between several time series of temperature as well as between the temperature series and recruitment series. The connection between 0-group abundance and modelled inflow of Atlantic water to the Barents Sea is also examined.

Material and methods

Indexes of 0-group abundance have been worked out from material gathered during the International Barents Sea 0-Group Surveys, which have taken place in late August to early September since 1965. We use the indexes for Arcto-Norwegian cod, haddock, and herring as published in the latest survey report (ICES, 1992a). There are two different indices for estimating the 0-group abundance. The *area index* is equal to the area of sparse occurrences plus 10 times the area of dense occurrences, while the *logarithmic index* is found by working out a logarithmic mean of the catches per nautical mile in a predefined stratification of the whole survey area. The methods of calculation of the indices are given in Haug and Nakken (1977) and Randa (1982, 1984).

A series on year-class abundance at age 3 is based on results of virtual population analysis (VPA). This series covers the 1943 to 1991 year classes for cod and the 1947 to 1991 year classes for haddock. The data are taken from the reports of the Arctic Fisheries Working Group (ICES, 1982, 1992b), except for the last three years which have kindly been provided by T. Jakobsen (pers. comm.). Calculations of the number of fish in the spawning stock and the total biomass of the spawning stock for 1966 to 1992 are also based on the same reports. A description of VPA can be found in ICES (1965).

Sætersdal and Loeng (1987) studied the temperature variations in the Barents Sea and classified the 1900 to 1983 years as periods of cold, medium, or warm climatic regime. From 1902 they also characterized the year-class abundance of cod as low, medium, or high. Both series have been prolonged to 1992. The average recruitment to the 0-group within each climatic period from 1965 has been estimated for cod, haddock, and herring. Within the same climatic periods, average survival indexes for cod have been calculated. These are defined as

$$I_{ssn} = \frac{1.0 \times 10^7 \times I_{log0}}{SSN}$$

and

$$I_{ssb} = \frac{1.0 \times 10^7 \times I_{log0}}{SSB}$$

where I_{log0} is the logarithmic 0-group index, SSN is the spawning-stock number, and SSB the spawning-stock biomass. To study the variation over a longer time span, the average recruitment at age 3 within climatic periods from 1943 (1947 for haddock) to 1991 is also calculated. This is done by using the VPA estimated recruitment and the climatic regime in the year of spawning.

We use time series of temperature from standard sections for the 0-group period (ICES, 1992a). The Kola and Cape Kanin (inner and outer) sections are shown in Figure 1. For the Kola section, in addition to the values from the period of the 0-group surveys (0–50 m interval), we have used annual averages for 0–200 m from 1921 to 1992 (Bochkov, 1982). The data from recent years have been provided by PINRO, Murmansk.

New temperature series for the period 1965 to 1992 are constructed by interpolating station data from the uppermost 60 m to yearly fields covering the Barents Sea. To secure a reasonable spatial coverage, stations for the period 15 August to 15 October are used. The grid resolution is 20 by 20 km horizontally and 5 m in the vertical. The interpolation scheme uses a combination of Laplace and spline fitting at each depth level and fills in linearly in the vertical (Ottersen, 1991). For further analysis we used time series of the arithmetic temperature mean at the 10 m and 60 m levels within the central 0-group area. In Figure 1 this area is seen together with an example of the hydrographic data coverage by Norwegian vessels for 16 August to 11 October 1991.

A proper statistical analysis of time series is complicated. Methods such as correlation analysis, *t*-tests, ANOVA, and linear regression all put assumptions on the data which are seldom met by time series. For non-parametric methods too, the true significance level of the test may deviate from the intended nominal level if the series in question are autocorrelated or non-stationary. For parts of our analysis we have chosen the first difference of the natural log transform of the recruitment series. The first difference of the temperature series is also used. This was done to get normally distributed, stationary series without autocorrelation. The appropriateness of such transformations is discussed later. The transformations do not, however, automatically yield series with the desirable properties. This necessitates an analysis of each series in question.

For detecting statistically significant autocorrelations we have studied plots of the estimated autocorrelation function and calculated the Durbin–Watson test statistic. For testing normality, the Shapiro–Wilk statistic, W, was used. The null hypothesis here is that the data are a random sample from a normal distribution. Stationarity was examined by means of the unit-root hypothesis test, which has the null hypothesis that the series is non-stationary. To determine the significance in difference of recruitment between warm and cold years we applied

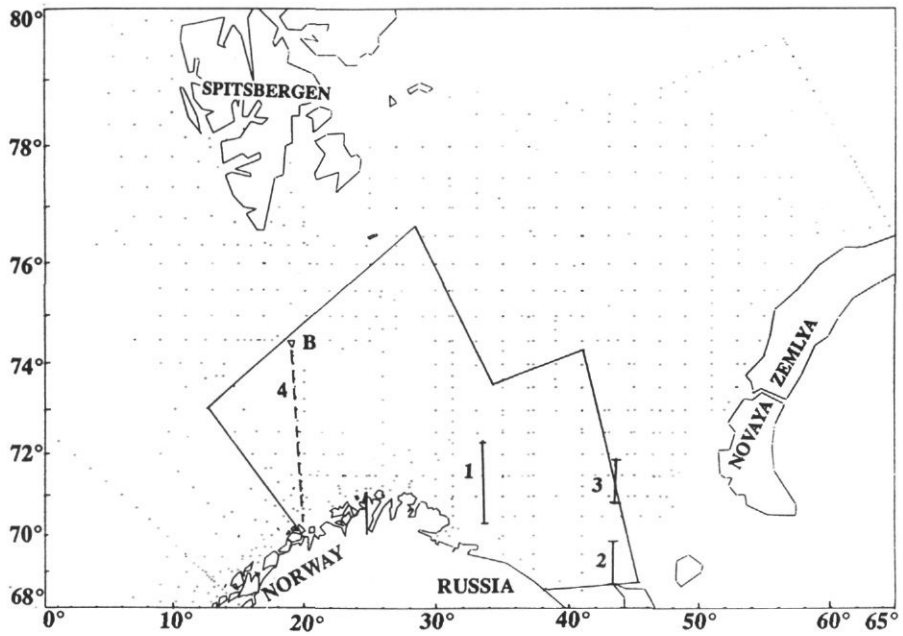


Figure 1. Locations of sections and stations. Temperature series from Kola (1), Cape Kanin, inner (2) and Cape Kanin, outer (3), flux through the Fugløya–Bjørnøya section (4) and surface air pressure at Bjørnøya (B) are used. The dots exemplify hydrographic data coverage from 16 August to 11 October 1991. Stations within the enclosed area, used for the integrated series, are observed mainly during the 0-group period.

the non-parametric Wilcoxon and median tests. These tests are likewise employed to find the difference in temperature between years with high and low 0-group abundance. For the analyses above and other computations we have used the SAS statistical package (SAS Institute, 1988a, 1988b, 1992).

Results

Statistical properties for six recruitment series are summarized in Table 1. The non-transformed series are positively autocorrelated and non-normal. Four of the series are also non-stationary. Taking the natural log transformation reduces the problem of non-stationarity and normalizes some of the series, but they are still significantly autocorrelated. The first order differenced series, however, have the properties desired.

Average recruitment within climatic periods is tabulated in Table 2 for cod, haddock, and herring. Figure 2 shows histograms for the 0-group cod and haddock and Figure 3 for the year-class strength of cod at age 3 from the VPA. The variability between the different periods is shown to be large for all the series. Since 1965 a distinct feature has been a higher recruitment in warmer than in colder periods. The fluctuations in the cod and haddock recruitment seem to be similar throughout the years studied. This impression is supported by the correlations calculated. The correlation between the log transformed logarithmic 0-group indices for cod and haddock for the 1966–1992 period was found to be 0.83 and that between their first-order differences 0.58. For the log-transformed VPA recruitment series the correlation between cod and haddock for 1947–1991 was 0.73 and for the differenced series 0.51. All correlations are significantly different from 0 at the 1% level.

The average recruitment to the 0-group and 3-group within all warm years and all cold years has been worked out excluding medium temperature years. These results are given in Table 3 together with the significance levels from the Wilcoxon and median tests used to determine whether the difference in average year-class strength is statistically significant. The null hypothesis is no difference, the alternative is a higher value in warmer years. The recruitment in warmer years for both 0-group series of cod and haddock, as well as the VPA series of cod from 1965, is 2.5–3.0 times as high as in colder years. As the herring stock was nearly depleted during the late 1960s and throughout the 1970s only data from the last 10 years have been used for this calculation. The picture is the same as for cod and haddock, only clearer. The recruitment is substantially higher in warmer years; for this series six times as high. For all the series, with the possible exception of the logarithmic 0-group index for haddock, the differences are statistically significant. For

Table 1. Statistical properties of the recruitment series, X(t), the natural log transform, ln (X(t)), and the first order difference of the log-transformed series, ∇ ln (X(t)). The autocorrelation of a series may be positive (POS.), negative (NEG.), not significant (NO) or the test may be indecisive (IND.). A series is regarded stationary if the test performed is significant at the 5% level and normal if the test is not significant at the 5% level.

	X(t)			ln (X(t))			∇ ln (X(t))		
Series	Significant autocorrelation	Stationary	Normal	Significant autocorrelation	Stationary	Normal	Significant autocorrelation	Stationary	Normal
0-Group cod Logarithmic index	POS.	NO	NO p = 0.00	POS.	NO	YES 0.10	NO	YES	YES p = 0.87
0-Group cod Area index	POS.	NO	NO p = 0.00	POS.	YES	NO 0.02	NEG.	YES	YES p = 0.86
0-Group haddock Logarithmic index	IND.	NO	NO p = 0.02	IND.	NO	NO 0.04	NO	YES	YES p = 0.48
0-Group haddock Area index	POS.	NO	NO p = 0.00	POS.	YES	NO 0.00	NEG.	YES	NO p = 0.01
VPA 3-year index cod	POS.	YES	NO p = 0.00	POS.	YES	YES p = 0.10	NO	YES	NO p = 0.03
VPA 3-year index haddock	POS.	YES	NO p = 0.00	POS.	YES	YES p = 0.14	NO	YES	YES p = 0.81

Table 2. Average recruitment for cod, haddock, and herring within periods of warm (W), medium (M), or cold (C) climatic regime as categorized by Sætersdal and Loeng (1987). The survival indexes, I_{ssn} and I_{ssb}, are defined in the text. Periods where the herring stock was nearly depleted are indicated by (*). The latest period for the VPA series is 1989–1991 indicated by (x).

Period	Temperature category	0-Group cod logarithmic index	0-Group cod area index	0-Group haddock logarithmic index	0-Group haddock area index	0-Group herring logarithmic index	VPA cod recruitment at age 3	VPA haddock recruitment at age 3	Survival index, I_{ssn}	Survival index, I_{ssb}
1943–1944	W						575			
1945–1949	M						780	227		
1950–1955	W						708	249		
1956–1958	C						797	225		
1959–1962	W						580	234		
1963	C						1 580	240		
1964	M						1 290	290		
1965–1969	C	0.08	32	0.09	28	(*)	380	263	10	2
1970–1976	W	0.89	289	0.40	102	(*)	680	121	135	23
1977–1982	C	0.32	100	0.20	70	(*)	255	52	58	11
1983–1984	W	1.62	436	0.56	220	1.05	550	276	193	55
1985–1988	C	1.08	353	0.21	119	0.14	193	27	184	52
1989–1992	W	1.71	648	0.70	281	0.79	900(x)	209(x)	102	33

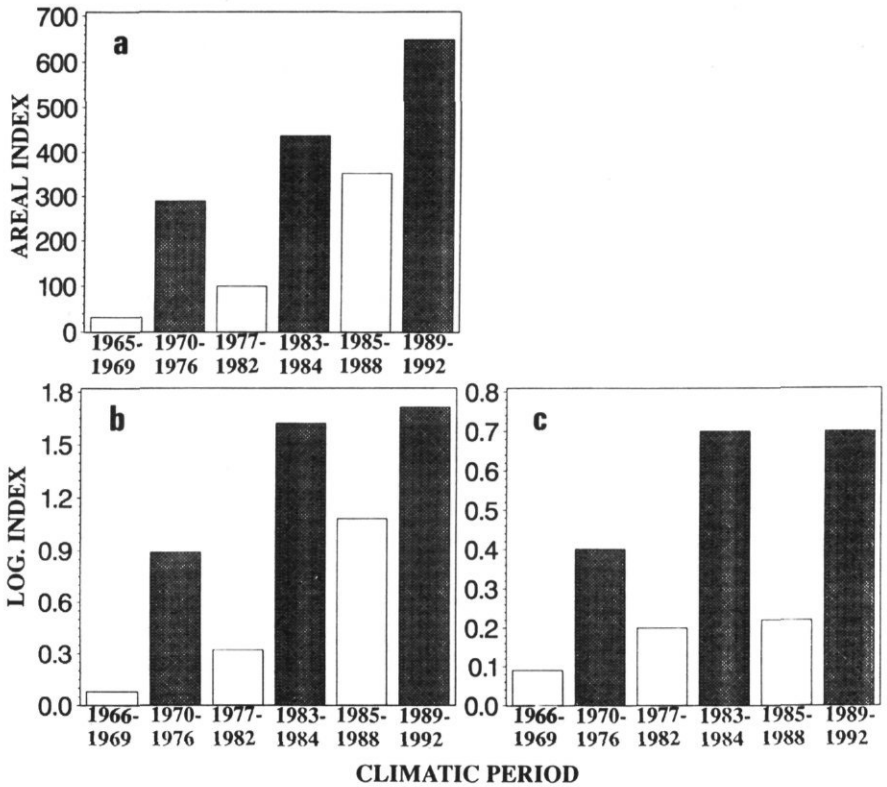


Figure 2. Average recruitment within climatic periods for 0-group cod, area index (a), logarithmic index (b) and haddock, logarithmic index (c). The double-hatched bars show warm periods, the open bars cold periods.

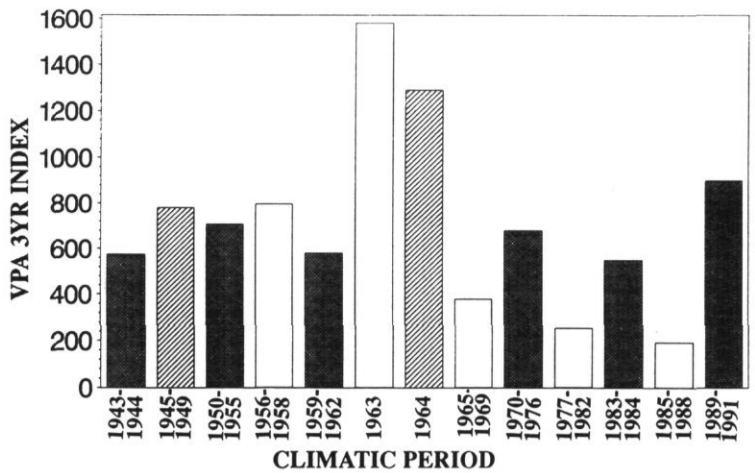


Figure 3. Average recruitment of cod at age 3 in millions from VPA within climatic periods from 1943 to 1991. The double-hatched bars show warm periods, the single-hatched bars periods of medium temperature, and the open bars cold periods.

Table 3. Average abundance within warm and cold years for different recruitment series, ratios between the averages, and probability levels of tests for difference in recruitment between the climatic regimes. The tests are applied to the natural log-transformed series. VPA in millions. The survival indices, I_{ssn} and I_{ssb}, are defined in the text. The asterisks indicate that the test was not performed as the herring series used covered only 10 years.

Species	Index	Period	Average index warm years (n)	Average index cold years (n)	Ratio warm/ cold	p-value Wilcoxon test	p-value median test
Cod	0-Group log	1966–1992	1.26 (13)	0.47 (14)	2.7	0.007	0.005
Cod	0-Group area	1965–1992	422 (13)	145 (15)	2.9	0.006	0.001
Haddock	0-Group log	1966–1992	0.54 (13)	0.18 (14)	3.0	0.002	0.054
Haddock	0-Group area	1965–1992	175 (13)	69 (15)	2.5	0.005	0.009
Herring	0-Group log	1983–1992	0.84 (6)	0.14 (4)	6.0	*	*
Cod	I_{ssn}	1966–1991	137 (12)	80 (14)	1.7	0.009	0.021
Cod	I_{ssb}	1966–1991	31 (12)	22 (14)	1.4	0.011	0.021
Cod	VPA 3-year	1943–1991	678 (24)	430 (19)	1.6	0.007	0.050
Cod	VPA 3-year	1965–1991	713 (12)	280 (15)	2.5	0.001	0.014
Haddock	VPA 3-year	1947–1991	203 (22)	140 (19)	1.5	0.014	0.160
Haddock	VPA 3-year	1965–1991	169 (12)	116 (15)	1.5	0.004	0.014

Table 4. Correlation among five different temperature series during early autumn and with the yearly mean temperature from the 0–200 m interval of the Kola section (1965–1992 period, above the diagonal), among the first-order differences of the temperature series (below the diagonal), and between the temperature series and the log-transformed logarithmic 0-group indices of cod and haddock (1966–1992 period, to the right of the thick vertical line). Correlations given in parentheses are not significantly different from zero at the 10% level.

	Temperature Cape Kanin inner part	Temperature Cape Kanin outer part	Temperature area average 10 m level	Temperature area average 60 m level	Temperature Kola section 0–50 m	Yearly mean temperature Kola sec. 0–200 m	Cod logarithmic ind.	Haddock logarithmic ind.
Temperature C. Kanin inner		0.85	0.35	0.76	0.67	0.83	0.28	0.47
Temperature C. Kanin outer	0.80		0.36	0.79	0.79	0.89	0.46	0.53
Temperature area av. 10 m	(0.17)	(0.21)		(0.31)	0.68	0.40	(0.20)	(0.09)
Temperature area av. 60 m	0.66	0.64	(0.15)		0.68	0.90	0.51	0.52
Temperature Kola sec. 0–50 m	0.51	0.71	0.61	0.51		0.73	0.41	0.42
Yearly mean temperature Kola sec. 0–200 m	0.38	0.53	(0.02)	(0.30)	(0.22)		0.57	0.69

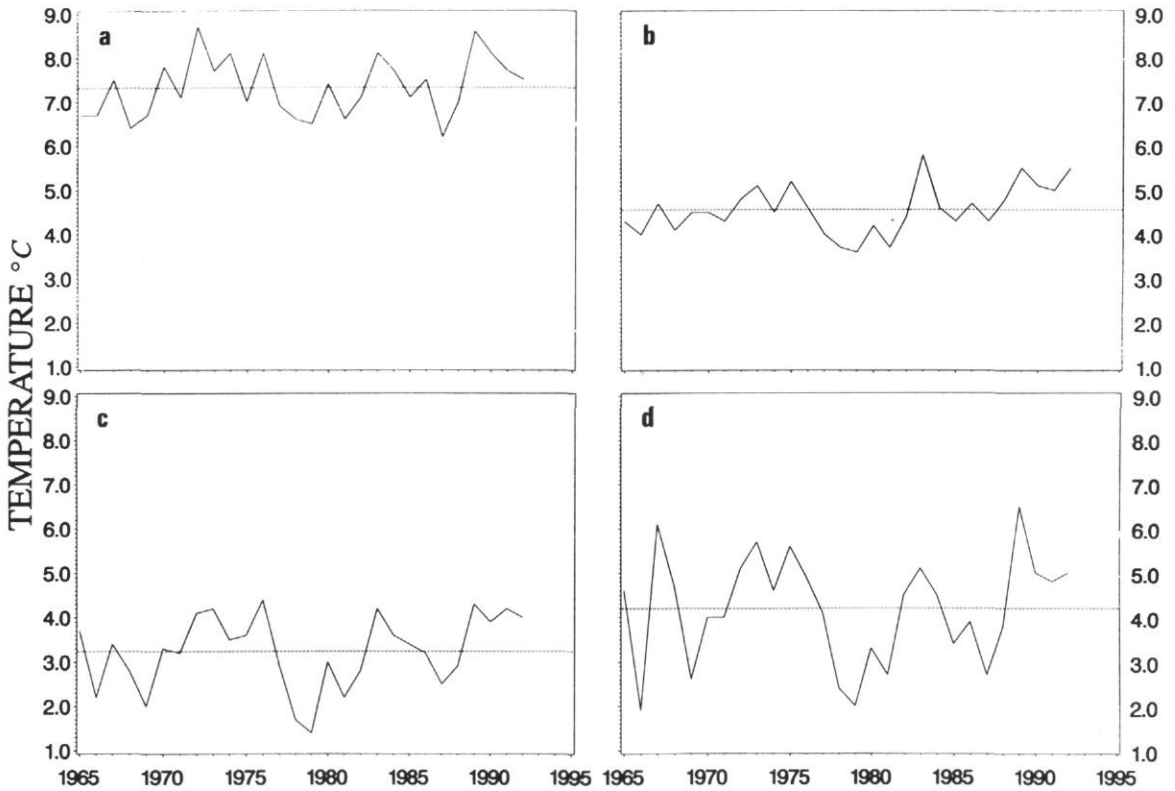


Figure 4. Temperature during early autumn in the Barents Sea for the period 1965–1992: (a) Kola section (0–50 m), (b) integrated at the 60 m level in the central area of 0-group cod, (c) Cape Kanin section, outer part (0-bottom), and (d) Cape Kanin section, inner part (0-bottom). The stippled lines represent average values of the series.

the full VPA series the ratios are reduced to about 1.5. The ratios of the survival indices, I_{ssn} and I_{ssb}, between warmer and colder periods are shown in Table 3 to be lower than the corresponding 0-group ratios for the same 1966–1992 period. This indicates that some of the recruitment variation can be explained by fluctuations in the spawning stock.

Figure 4 shows early autumn temperature during 1965–1992. The series all have a warm period during the first half of the 1970s, an overall minimum in 1979 and especially warm years in 1983 and 1989. The correlations among these series as well as with the temperature integrated from the early autumn stations at the 10 m level and the yearly mean temperature from the 0–200 m interval of the Kola section are given in Table 4. While there are no problems with significant autocorrelation for the first five temperature series in the table, the Kola 0–200 m series is autocorrelated. For this series, and for the integrated series at the 10 m and 60 m level, we cannot reject non-stationarity at the 10% level. The results given in Table 4 seem to support the visual impression of distinct similarities in the temperature fluctuations of the Kola and Cape Kanin sections, as well as in the integrated series from the 60 m level. The 10 m level integrated series stands out not just by having no statistically significant correlation with three of the other temperature series, but also by the lack of significant correlation with the recruitment series.

To determine whether the temperature on average is higher in years classified as having high or medium 0-group abundance than in years with low 0-group abundance, the Wilcoxon and median tests were applied to the six series given in Table 4. Four of the series showed a statistically significant difference: temperature interpolated at the 60 m level (p Wilcoxon = 0.00, p median = 0.02), yearly mean temperature from the Kola section 0–200 m level (p Wilcoxon = 0.00, p median = 0.02), temperature from the outer-most part of the Cape Kanin section (p Wilcoxon = 0.01, p median = 0.02), and temperature from the upper 50 m of the Kola section (p Wilcoxon = 0.04, p median = 0.04). The temperature interpolated at the 10 m level had no statistically significant difference (p Wilcoxon = 0.40, p median = 0.44). Using the abundance categorization as above and the

Table 5. Modelled wind-driven flux through the Fugløya–Bjørnøya section in June, the average air pressure at Bjørnøya in June and the year-class strength of 0-group cod for the 1970–1989 period. The flux is categorized as strong into the Barents Sea (IN), in, weak (w), out or strong out (OUT). The flow is strong if it is larger than 0.5 Sverdrup, weak if it is less than 0.1 Sverdrup. The air pressure is classified as being lower than average (L), average (A), or higher than average (H). The pressure is average if it differs by less than 1.5 standard errors from the mean for this period.

Year	Flux June	Air pressure June	0-Group index	Year	Flux June	Air pressure June	0-Group index
1970	IN	L	H	1980	out	A	L
1971	OUT	H	L	1981	IN	L	L
1972	OUT	H	L	1982	w	H	L
1973	in	L	M	1983	in	L	H
1974	out	H	L	1984	in	L	M
1975	in	L	M	1985	out	H	H
1976	out	H	L	1986	IN	L	M
1977	in	L	L	1987	out	H	L
1978	OUT	A	L	1988	w	A	L
1979	w	L	L	1989	w	L	L

yearly mean temperature from the 0–200 m interval of the Kola section back to 1921, the same tests were applied again. For the period from 1921 to 1992 both the Wilcoxon test and the median test gave a statistically significant difference in temperature between years with high, years with medium, and years with low year-class abundance of cod ($p = 0.02$ for both tests). However, there was no significant difference for the 1921–1964 period. For these years the p-values were 0.67 and 0.74 respectively. This indicates a lesser influence of temperature before 1965.

In Table 5 the relationship between two other time series and the year-class strength of 0-group cod is summarized. Wind-driven flux through the Fugløya–Bjørnøya section has been modelled for 1970 to 1989 (Ådlandsvik and Loeng, 1991; Loeng *et al.*, 1992), while monthly averages of atmospheric surface pressure at Bjørnøya were provided by the Norwegian Meteorological Institute. The results indicate that the fluctuations in 0-group abundance are related to meteorological conditions and inflow of Atlantic water during early summer. For the years 1970 to 1989, below average pressure over the western Barents Sea and increased inflow during June occurred in six of the seven years with an 0-group of high or medium abundance, while of 13 years with low abundance in the same period only 1977 and 1981 had an increased inflow in June. The correlation between the June flux and air-pressure series is high ($r = 0.79$, $p = 0.00$), but this is partly explained by the atmospheric data being one of the driving forces of the model.

Discussion

It is important not to ignore autocorrelation and non-stationarity when dealing with statistical analysis of environmental and recruitment time series. Thompson and Page (1989) point out two major ways to proceed. One method is to allow for autocorrelation when assessing the statistical significance of the correlation between series. The alternative method is to transform the series such that the autocorrelation is removed. One can then proceed using critical levels based on the assumption of serial independence. Classical time-series analysis as described by Box and Jenkins (1970) dealing in terms of auto-regressive (AR) and moving average (MA) processes are much used in other fields. However, Shepherd *et al.* (1984) point to the difficulties in getting meaningful results with few data, and Hoenig and Prager (1989) say these methods are unsatisfactory when the data reflect complex dynamics and are of short duration. This is usually the case with recruitment series.

In order to transform autocorrelated, non-normal, non-stationary recruitment series to a form where ordinary *t*-tests and regression methods could be applied, Cohen *et al.* (1986) took the first difference of the natural log transformed series. This method was also adopted by Thompson and Page (1989) for detecting possible synchrony of recruitment between several cod and haddock stocks. In agreement with Hennemuth *et al.* (1980) they argue for log transforming recruitment series by pointing to the frequency distribution of such series being approximately lognormal. Shepherd *et al.* (1984) recommended such an approach as a means of reducing the effect of extreme values in the series. Chatfield (1989) and SAS Institute (1992) suggest that in general this transformation is useful for making the variance constant. In the latter, differencing a series is put forth as a means of removing a trend in addition to reducing autocorrelation.

Several of our series are not normally distributed even after log-transformation. Since *t*-tests also are

prone to bias because of autocorrelation, the non-parametric Wilcoxon and median tests were chosen instead. These tests are not restricted to normally distributed data sets. They are, however, also influenced by autocorrelation and non-stationarity. Applying the test to the natural log transform of the series reduces the problem of non-stationarity, as given in Table 1, but not that of autocorrelation. Even if the calculation of correlations between positively autocorrelated and non-stationary series may lead to the significance levels found being lower than the true value, these figures are still of interest and are therefore included. Caution is shown when one of the two tests gives a significant p-value and not the other. For most of our series, significance or the lack of it is so clear that even a large adjustment of the significance level will not affect the conclusion.

We are well aware that correlation is a measurement of linear similarity in variation and that the influence of an environmental parameter on recruitment is seldom linear. Shepherd *et al.*y(1984) state that the response to environmental factors is unlikely to be monotonic (let alone linear), except for species at the extremes of their range. When considering cod and haddock in the Barents Sea we are dealing with species at the lower end of their temperature range, so we can justify using linear methods.

Classifying years as warm or cold and calculating averages may seem unnatural. However, such an approach is supported by the results of Ådlandsvik and Loeng (1991), who concluded that the climate of the Barents Sea oscillates between two states – one warm and one cold.

Our results seem to show beyond reasonable doubt that variation of ocean temperature does influence the level of recruitment of Barents Sea cod. Positive temperature anomalies affect several factors, which again act favourably on the cod recruits, and it is the sum of these effects which is detected through studying temperature–recruitment relations. Nakken and Raknes (1987) examined the link between temperature variation and the distribution and growth of adult cod, concluding that the connection between environmental changes and properties of the cod population was far more complex than a simple length–temperature relation. Loeng and Gjøsæter (1990) in studying the relationship between temperature conditions and growth in 0-group fish in the Barents Sea, stated that temperature effects linked to the availability of food might be just as important as direct temperature effects. Rey *et al.* (1987) concluded that climatic variations have a pronounced effect on the development in time of the Barents Sea spring bloom, the primary production available for zooplankton being larger in warmer years. Ellertsen *et al.* (1989) studied the influence of temperature on the feeding conditions for fish larvae, concluding that the temperature-dependent spawning of the copepod *Calanus finmarchicus* may be the most likely process causing variability in cod larval survival.

These results also give clear indications of temperature variations having a greater impact on fluctuations in the Arcto-Norwegian cod recruitment during the last 25–30 years than in the preceding decades. While the warmer periods from 1965 and onwards all have higher average VPA year-class strength than the corresponding colder periods, no such pattern can be seen for 1943–1964. Rather the contrary, Table 2 indicates that the average values are stable until 1962. The ratio of the number of recruits hatched in a warm year to those hatched in a cold year is 2.5 for the 1965 to 1991 period (Table 3), but only 1.6 for the 1943 to 1991 period. The test performed on the Kola section temperature series for 1921 to 1964 showed no statistically significant difference between years with low recruitment of cod and years with high or medium year-class size.

One explanation for this development is the large change in the structure of the Arcto-Norwegian cod stock over the past 40 years. The fished stock has declined by approximately 75% from the early 1950s to the late 1980s (Jørgensen, 1990). The influence of temperature on recruitment seems to be more pronounced when the spawning stock is small. The variability in recruitment from a small herring stock (Table 3) supports this hypothesis. The composition of the spawning stock has also changed. From the VPA estimates for the last 25–30 years (ICES, 1982, 1992b), it can be seen that the spawning stock depends to a large degree on one or only a few dominating year classes. Borisov (1978) expressed concern about the rejuvenation of the spawning population. The abundance of cod older than 10 years is at present less than 1% of that in the late 1940s (Nilssen *et al.*, 1994). Younger fish tend to have a shorter spawning period than older fish (O. Kjesbu, pers. comm.). Recruit spawners also produce eggs which have a narrower range of vertical distribution than repeat spawners, thus causing less horizontal spreading (Kjesbu *et al.*, 1992). We believe that these changed properties of the stock cause an additional sensibility to environmental fluctuations resulting in the greater difference in recruitment between warmer and colder periods described above.

The correlations between the 0-group indices of Arcto-Norwegian cod and haddock and the hydrographic series given in Table 4 show similar patterns. Also, the relatively high correlations both among the recruitment series and their first-order differences seem to reflect a close relationship between year-class strength of the two stocks, especially at the 0-group stage. Shepherd *et al.* (1984) found the correlation

between log-transformed recruitment series of Arcto-Norwegian cod and haddock from 1962 to 1976 to be statistically significant at the 1% level. We regard this as an indication of large-scale temporal environmental variation having an influence common to the early stages of both species. Also, the similarity in ratios between average 0-group abundance within warm and cold years suggests such a common source of variation. Dragesund (1971) and Sætersdal and Loeng (1987) found several cases of favourable recruitment coinciding for cod, haddock, and herring stocks in the Barents Sea. Loeng *et al.* (in press) indicate that the same close relationship exists for larval growth. The favourable physical conditions in the Barents Sea seem to be related to increased heat transport by the warm Atlantic Current (Mukhina *et al.*, 1987; Sætersdal and Loeng, 1987). The correlation structure shown in Table 4 and test results support this view. The series we expect to be the most representative of Atlantic water masses are those which explain most of the variation in the recruitment series. The 10 m area integrated temperature series is not respresentative of what the fish larvae have experienced. This temperature depends mainly on atmospheric heating during summer, while the other series better reflect the large-scale variability in the oceanographic conditions. The most representative temperature series seem to be the yearly averages from 0–200 m in the Kola section and the 60 m autumn area average.

The one year with high or medium 0-group cod abundance that does not fit into the pattern of increased early summer inflow is 1985, a year which was special in many ways. While the temperature was high for the first two–three months, it decreased to below normal during the following months. Even so, both 0-group indices for cod are unusually high that year, the logarithmic index is only higher for 1992. The 1985 value is five times as high as the average over the 14 cold years (including 1985) during the 1966–1992 period. Actually, if we had considered 1985 as a warm year due to the positive anomaly of the early months, the average logarithmic index within cold years would be reduced to 0.32 and the ratio between warm and cold years would rise to 4.2 (see Table 3). Loeng (1989) pointed out that 1963 and 1985 were the only year classes since 1930 not fitting the pattern of high recruitment with a regime of increasing temperature or positive temperature anomalies. Loeng *et al.* (in press) found that 1985 was an outstanding year also when considering growth from the early juvenile to the 0-group stage. The cold year of 1985 had one of the highest growth rates for cod as well as haddock and herring. This has been explained by the strong inflow of Atlantic water until April (Loeng *et al.*, in press) leading to a high concentration of zooplankton during April/May, as reported by Nestrova (1990).

Acknowledgment

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Growth, maturation, and longevity of maturation cohorts of Northeast Arctic cod

R. J. H. Beverton, A. Hylen and O. J. Ostvedt

Beverton, R. J. H., Hylen, A., and Ostvedt, O. J. 1994. Growth, maturation, and longevity of maturation cohorts of Northeast Arctic cod. – ICES mar. Sci. Symp., 198: 482–501.

Prior to 1955, before fishing intensified, a year class of Northeast cod matured over ages from 6 to 14. The Bergen database records both the age at maturation and the maximum age of each fish sampled in the Lofoten spawning fishery from 1932 onwards, thus enabling each year class to be subdivided into its constituent maturation cohorts. This article reports on an exploratory analysis of these individual maturation cohorts, using the Norwegian long-line c.p.u.e. data from the Lofoten fishery to ascertain whether their subsequent (adult) mortality, growth and longevity depend on the age at which they matured. The youngest fish to mature, at 6 and 7 years of age, had the poorest performance and shortest adult lifespan, but a conclusive answer from the older maturation cohorts was not possible from the present analysis owing to the relatively high and variable incidence of fishing mortality over the period covered by the data. However, so far as can be judged, cohorts maturing at 8 years and upwards had essentially the same growth and adult lifespans. The highest natural mortality rate (M) for these older maturing cohorts consistent with the data is 0.15; on that basis M for cohorts maturing at 6 and 7 years would have been about 0.25 and 0.17, respectively. Some implications of these findings are discussed.

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1. Introduction

1.1. Age and size at maturity in relation to longevity and ultimate size, with the associated implications for natural mortality and growth rate, are fundamental elements in the concept of reproductive strategy (e.g. Williams, 1957; Stearns and Crandall, R. E. 1984; Roff, 1984). Clear patterns emerge when these growth, maturity, and longevity parameters (GML matrices: Beverton, 1992) are compared across different animal groups (Beverton and Holt, 1959; Charnov, 1993) and between separate populations of the same species in different habitats (Beverton, 1987; Jennings and Beverton, 1991).

1.2. These GML matrices have presumably become established over long if not evolutionary timescales and constitute what may be thought of as the demographic *statics* of reproductive strategy. As such, they quantify the well-known phenomenon of individuals growing more slowly to a greater size, maturing at an older age, and living longer at the northern than at the southern end of the species range. However, the age and size at maturation in fishes is known from both field and experimental studies (e.g. Alm, 1959; McKenzie *et al.*, 1983; Beverton, 1987) to be readily modified by environmental conditions, in particular by temperature (Godø and Moksness, 1987). Furthermore, depletion of a population by fishing is usually followed by a decrease in the average age (and sometimes size) at maturity of the stock as a whole. In the Northeast Arctic cod, for example, the average age at maturation has fallen in the last few decades from between 10 and 11 years to around 6 years (Jørgensen, 1990). These are the *dynamics* of reproductive strategy and, as Jakobsen (1992) has shown, can have a profound influence when the response of the stock to fishing is being assessed.

1.3. Several questions therefore arise. How much, in a particular case, are these GML dynamics symptomatic of real biological changes due either to environmental factors or to density-dependent growth enhancement in the depleted stock; or how much are they purely "structural", caused by preferential fishing-out of the slowest growing and oldest maturing fish in the population?

Whatever their cause, are they associated with the changes in natural mortality and longevity that would be expected by analogy with the static GML patterns derived from inter-population and inter-specific comparisons? If the causes are removed, are the maturation changes reversed, and how fast?

1.4. To attempt to answer these questions when the demographic data cover a period of high or increasing fishing pressure (as is usually the case) is virtually impossible because the population structure in these circumstances is dominated by the large fishing mortality. This applies particularly to natural mortality and longevity, estimation of which is difficult enough in the best of circumstances. There is, however, another approach to analysing these dynamics of maturation. At the end of the 1920s Lea (1929) showed that a structural change at maturity could be detected in the scale of the Norwegian spring-spawning herring, and a little later Rollefsen (1934) discovered that the onset of maturity in Northeast Arctic cod was associated with a similar change in the ring structure of the otolith. After an individual fish of these two populations has reached maturity and spawned for the first time, it is therefore "marked" with a natural mark which it retains throughout its life.

1.5. Recording of both the actual age of the fish when caught and the age at which it matured, together with confirmation of maturity from the gonads, was thereafter included as a regular part of the age-reading procedures by the Bergen Institute of Marine Research in sampling the spawning cod fishery at Lofoten and the spring-spawning herring fishery off the southwest coast of Norway. This information makes it possible to trace the survival and growth of each maturation cohort (MC) of each year class throughout its adult life after spawning for the first time and to relate it to the age at which the cohort matured. Such data provide an extra dimension in the analysis of maturation dynamics. Thus, Rollesfsen (1935, 1954) and Østvedt (1963) used this additional age-at-maturation data to good effect in stock prognosis by re-organizing the conventional year-class data into "spawning classes", i.e. distinguishing all fish spawning for the first, second, etc., time in a given year. Law and Grey (1989) developed a simulation model for the Northeast Arctic cod distinguishing what, in effect, are maturation cohorts; but at that time the possible trade-offs between growth and mortality among the maturation cohorts, which could cause the behaviour of such a model to differ from that of a conventional yield/fishing rate model incorporating a stock–recruitment relationship (e.g. Beverton and Holt, 1957), were unknown.

1.6. This article reports the results of an exploratory analysis of the dynamics of maturation cohorts in Northeast Arctic cod, with the aim of seeing whether their subsequent growth, maturation, and longevity depend on the age at which the cohort matured. A companion article on the Norwegian spring–spawning herring was presented to the ICES Statutory Meeting in Dublin (Beverton *et al.*, 1993) and is in preparation for publication.

2. Total mortality rate of maturation cohorts

Material and methods

2.1. Since a central aim of this study is to try to detect whether the post-maturation (adult) natural mortality rate is influenced by the age at maturation (a possibility suggested by Østvedt, 1958, for herring), it is desirable to use data for a period when the stock was as little influenced by fishing as possible. Otoliths were first used systematically for determining both the total age and the age at maturity of Northeast Arctic cod in 1932 (Rollefsen, 1934), which in principle enables the post-maturation age compositions of each maturation cohort (MC) to be compiled for year classes as far back as 1920. For this article we accept the identification of the first spawning zone in the Bergen database as essentially correct. However, the early post-maturation ages of MC-6, MC-7, and MC-8 of year classes in 1920–1923 were necessarily absent from the data set, so these MCs are therefore excluded from subsequent mortality analysis of year classes 1920–1923. Furthermore, sample numbers were small in these early years and there is reason to believe that the ages of the oldest fish were underestimated (see 3.7 and 5.7); results for the year classes of 1920–1923 are presented here but must be interpreted with due regard to these uncertainties. At the other end of the data series, escalation of fishing and changes in fishing gear after the mid-1950s made it necessary to terminate analysis with the 1935 year class.

2.2. Since VPA requires a prior estimate of the natural mortality rate it is inappropriate – at least for this exploratory analysis. In any event, catch statistics of mature fish on a maturation cohort basis for the period in question are available only for the Lofoten fishery, which again makes VPA inapplicable. Age compositions have instead been expressed in terms of the c.p.u.e. (catch/man/day) of the Lofoten long-line fishery, which Rollefsen (1953) has shown to be a consistent index of abundance back to the middle of the last century. The vessels, methods, and gears in this fishery, which is conducted on the cod–spawning grounds among the skerries of the Lofoten Islands from January to April, have remained virtually unchanged until the introduction of synthetic fibres in fishing gears in the mid-1950s; but the reliability of long-line c.p.u.e. data as indices of abundance of individual MCs, especially as regards size-specific selection, must first be considered.

Long-line selectivity

2.3. The limited published data on long-line selectivity are not easy to interpret (Rollefsen, 1953; Sætersdal, 1963; Kenchington, 1992; Lokkeborg and Bjørdal, 1992; Johannessen *et al.* 1993). However, Hylen (1962) compared the length compositions of long-line and purse-seine net catches of cod in the 1950s when both were in use together at Lofoten, the seines presumed to be unselective; but the result is still ambiguous (Fig. 1). Thus, in the early and late 1950s the purse-seine catches had many more larger fish compared with the long-line, whereas in the five middle years 1954–1958 the length compositions were virtually identical.

2.4. Two main hypotheses concerning long-line selectivity have therefore been adopted in this article. The first, *Hypotheses (A)*, starts from the presumption that this near-perfect match for five consecutive years is not coincidental, and that in the conditions applying in those years the long-lines were therefore intrinsically unselective. Noting that both gears indicate that there were in fact more large fish in the spawning stock at the beginning and end of the decade, Hyp (A) postulates that the seine-netters were able in those circumstances to concentrate their activities where the larger fish were locally abundant and which therefore became over-represented in their catches. On Hyp (A) the long-line c.p.u.e. data are therefore taken as valid indices of abundance as they stand, without adjustment.

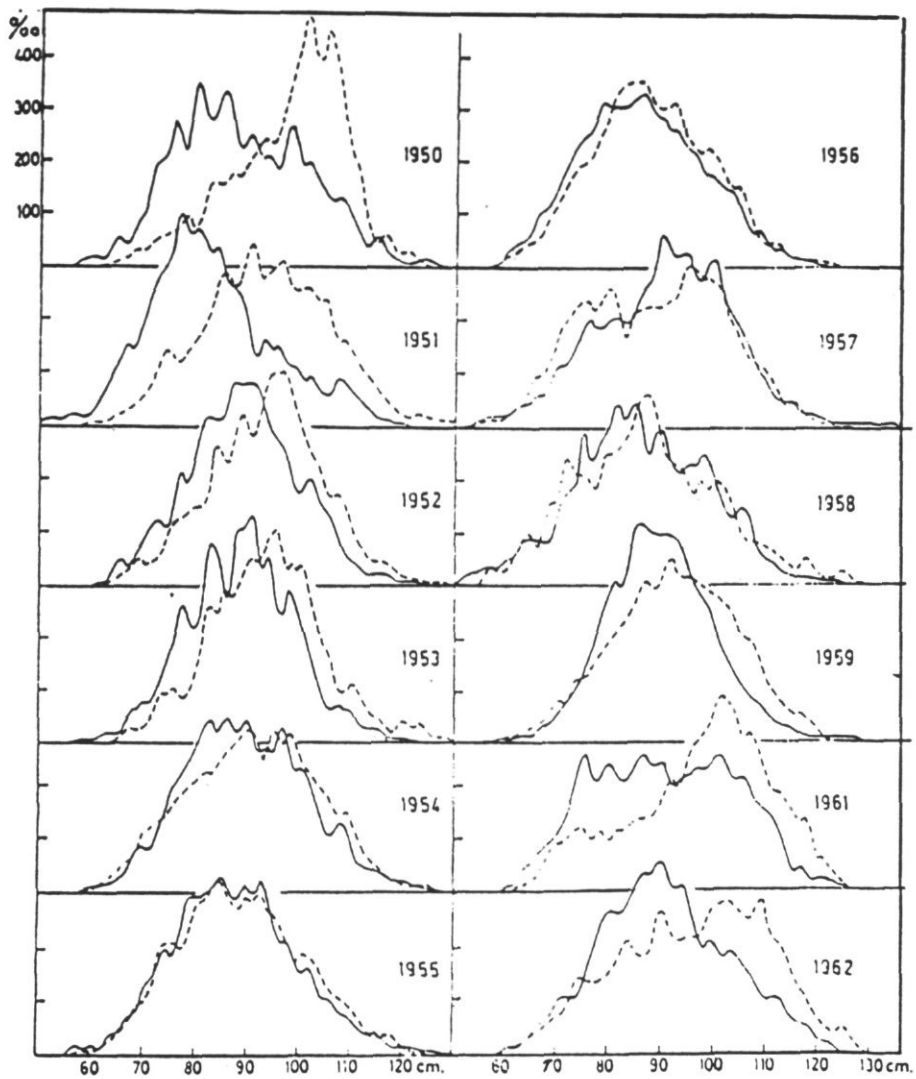


Figure 1. Length compositions of purse-seine (——) and long-line (– – – –) catches of Northeast Arctic cod at Lofoten (from Hylen, 1962).

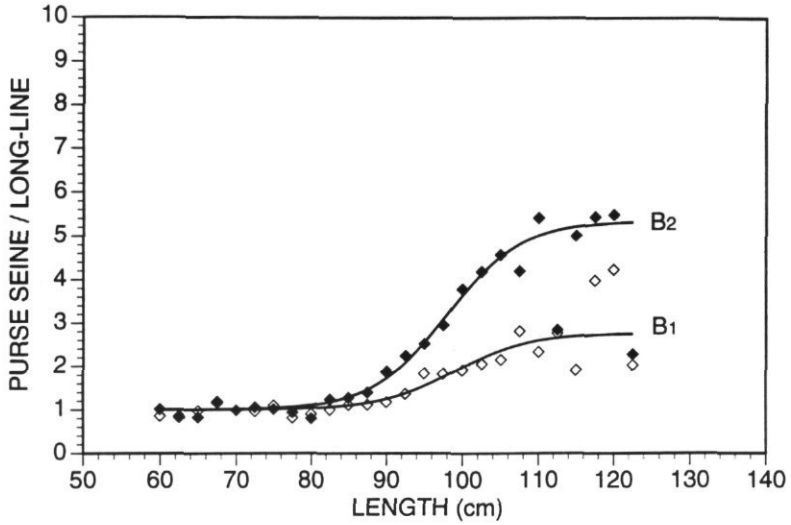


Figure 2. Derived selection ogives (purse-seine/long-line) for selection hypothesis (B).

2.5. *Hypothesis (B)* takes the opposite interpretation, namely that when large fish were abundant the seine-net catches remained representative but the long-lines became to varying degrees "saturated", their catching power for the larger fish diminished. On Hyp (B), therefore, the long-line c.p.u.e. data are adjusted according to the ratio of purse-seine to long-line catches at each length, depending on the relative contemporary abundance of large fish.

2.6. The resulting seine/long-line ogives for Hyp (B) are shown in Figure 2 by curve B_2 for periods when large fish are exceptionally abundant (i.e. calculated as the mean ogive over the years 1950, 1951, 1961, and 1962) and by curve B_1 when only moderately abundant (calculated from the years 1952, 1953, and 1959); no adjustment is made in years when the length compositions approximated to those in the years 1954–1958. The annual c.p.u.e. data have therefore been adjusted (upwards) on Hyp (B) by the appropriate ogive as judged by comparing the Lofoten length compositions back to 1920 (Rollefsen (1954) with those in Figure 1. Table 1 gives the resulting schedule of adjustment.

Table 1. Application of ogives of Fig. 2 to calendar years to adjust long-line selectivity according to Hyp B.

	No adjustment	Ogive B_1	Ogive B_2
	1937–1938	1935–1936	1932–1934
	1944–1946	1939–1941	1942–1943
	1955–1956	1947	1948–1950
	1958	1951–1954	1960
		1957	
		1959	
		1962	
Total years	8	13	9

2.7. As a further check, having in mind that ranking of pre-1950 size compositions has to rely on long-line data, the extreme assumption was also made that the most pronounced difference observed between purse-seine and long-line compositions (in 1950, see Fig. 1) should be applied to all years. This simply decreased the Hyp (B) mortality estimates by small amounts without causing substantial changes and so is not taken further in this article.

2.8. When the selectivity adjustments have a detectable effect it is almost always in the direction of *decreasing* the slope (Z) of the ln c.p.u.e. trajectories (by up to a maximum of 0.2). This is because the c.p.u.e.s of larger and hence older fish after adjusting for selectivity are increased more than those of the smaller fish. The precision of the estimates of slope is, however, usually less with Hyp (B) than with Hyp (A), because of the discontinuities introduced when changing from one adjustment schedule to another in successive years.

2.9. In addition to size selectivity, Angelsen and Olsen (1987) have shown that the general within-season catchability of the long-line effort as deployed in the Lofoten fishery is affected inversely by the spatial concentration of the gear units and also by the stock abundance. Whether the between-season long-line catchability is similarly affected by year-to-year changes in total stock, which are much smaller than the within-season changes, has yet to be examined, and we have not attempted to correct the c.p.u.e. data explicitly in this respect in this article. However, to the extent that the

adjustment for size selectivity by means of Hyp (B) is strongest when the stock is most abundant, it takes some account of the stock-dependent catchability effect.

Treatment of the c.p.u.e. data

2.10. Typically, in the interwar period, a very small proportion of each year class matured at 6 and 7 years, the majority between 8 and 12 years, and the remainder at 13 and 14 years (Rollefsen, 1954), although in no single year class were both the youngest maturation cohorts (MC-6) and oldest (MC-14) represented in the samples. The slopes of the ln c.p.u.e. trajectories (with or without adjustment, as appropriate) are interpreted as estimates of the total mortality rate (Z) of each maturation cohort of each year class, and will be referred to as such henceforth.

2.11. So far as can be judged (see e.g. Fig. 3) the trajectories are effectively linear throughout life, but the precision with which Z can be estimated for individual cohorts varies greatly. This is partly due to the fact that maturation cohort analysis involves a nine-fold subdivision of the year-class data but also because the two youngest (MC-6 and MC-7) and the two oldest (MC-13 and MC-14) maturation cohorts are always much less abundant than the main cohorts (MC-8 to MC-12) and are sometimes absent altogether.

2.12. Two precautionary criteria have therefore been adopted:

- a cohort is excluded for mortality rate estimation unless it is represented by at least four data points (i.e. 4 years of adult life)
- when calculating mean slopes and standard deviations (e.g. across the MCs for a given year class, or for a given MC across a set of adjacent year classes), the individual cohort Z estimates are weighted by the reciprocal of their variance.

Results: estimates of total mortality rate (Z) by year class and maturation cohort

2.12. Table 2 gives the estimates of adult (i.e. post-maturation) total mortality rates Z and their s.d. for each maturation cohort of each year class from 1920 to 1935 and for selection Hypotheses (A) and (B). An example of the ln c.p.u.e. age trajectories for the individual maturation cohorts comprising a single year class is shown in Figure 3 for the 1933 year class (with MC-11 omitted for clarity).

2.13. In this year class there is little difference between the slopes of the constituent cohorts, so there is no trend when MC-Z is plotted against cohort maturation age, as in Figure 4. In some other year classes, however, there is a marked trend (usually downwards) in Z with MC age, as shown for the 1927 year class in Figure 4. Weighted mean values of Z over all year classes combined (1920–1935) are given at the base of Table 2 and plotted against MC age for each selection hypothesis in Figure 5. With unadjusted c.p.u.e. data (Hyp A) there is a steady decrease of overall mean Z with MC age (in effect, with age at maturity); with adjusted c.p.u.e.s

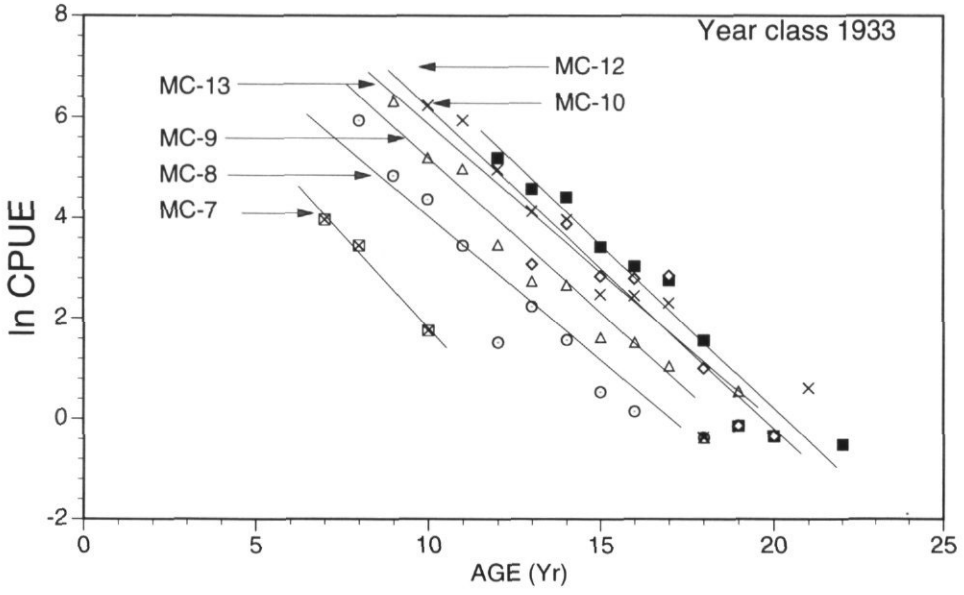


Figure 3. 1933 year class. ln c.p.u.e. vs age for individual maturation cohorts. Selection hypothesis (A).

Table 2. Total mortality rates (Z) and standard deviations (s.d.) of individual maturation cohorts of year classes 1920–1935.

Year class	MC-7 Z	s.d. (Z)	MC-8 Z	s.d. (Z)	MC-9 Z	s.d. (Z)	MC-10 Z	s.d. (Z)	MC-11 Z	s.d. (Z)	MC-12 Z	s.d. (Z)	MC-13 Z	s.d. (Z)
A: Unadjusted c.p.u.e. data (Hyp A)														
1920	0.274	0.241	0.392	0.222	0.411	0.130	0.399	0.116	0.560	0.120	0.472	0.110	0.321	0.252
1921	*	*	0.369	0.147	1.060	0.271	0.526	0.102	0.458	0.106	0.620	0.168	0.963	0.322
1922	*	*	0.573	0.195	0.549	0.176	0.673	0.121	0.636	0.112	0.506	0.141	0.506	0.141
1923	*	*	0.349	0.128	0.594	0.149	0.744	0.161	0.660	0.073	0.764	0.158	*	*
1924	*	*	0.606	0.161	0.329	0.181	0.595	0.100	0.823	0.197	0.093	0.157	*	*
1925	*	*	0.452	0.173	0.724	0.148	0.545	0.062	0.277	0.055	0.280	0.033	*	*
1926	0.549	0.149	0.845	0.131	0.586	0.105	0.613	0.092	0.319	0.037	*	*	*	*
1927	0.908	0.055	0.587	0.129	0.754	0.131	0.642	0.146	0.454	0.106	0.195	0.101	*	*
1928	0.693	0.134	0.723	0.130	0.767	0.049	0.511	0.061	0.353	0.060	*	*	*	*
1929	0.521	0.436	0.973	0.130	0.516	0.069	0.605	0.051	0.569	0.085	0.498	0.051	0.298	0.074
1930	1.020	0.358	0.845	0.122	0.649	0.102	0.682	0.084	0.599	0.059	0.573	0.071	0.480	0.131
1931	*	*	0.764	0.486	0.498	0.092	0.666	0.065	0.495	0.077	0.627	0.135	0.543	0.080
1932	*	*	0.629	0.121	0.668	0.055	0.608	0.028	0.603	0.124	0.607	0.061	0.513	0.089
1933	*	*	0.575	0.060	0.617	0.050	0.635	0.062	0.625	0.059	0.650	0.055	0.589	0.113
1934	0.622	0.260	0.837	0.156	0.751	0.056	0.578	0.068	0.708	0.032	0.711	0.060	0.586	0.101
1935	0.524	0.107	0.787	0.114	0.785	0.054	0.756	0.067	0.566	0.042	0.472	0.083	0.448	0.107
wt.mean Z & SE (Z)	0.768 0.042		0.644 0.032		0.671 0.020		0.608 0.016		0.527 0.015		0.473 0.018		0.481 0.034	
B: C.p.u.e. data adjusted for selectivity (Hyp B)														
1920	0.349	0.233	0.421	0.213	0.527	0.093	0.428	0.154	0.710	0.112	0.537	0.146	0.366	0.304
1921	*	*	0.348	0.149	0.941	0.304	0.510	0.104	0.448	0.109	0.724	0.174	1.360	0.364
1922	*	*	0.552	0.171	0.496	0.186	0.686	0.124	0.681	0.152	0.698	0.225	0.958	0.288
1923	*	*	0.299	0.126	0.529	0.171	0.862	0.146	0.733	0.140	1.070	0.188	*	*
1924	*	*	0.612	0.161	0.203	0.226	0.597	0.157	0.814	0.064	0.060	0.130	*	*
1925	*	*	0.464	0.178	0.639	0.201	0.407	0.059	0.033	0.079	0.012	0.092	*	*
1926	0.557	0.150	0.735	0.160	0.415	0.120	0.400	0.075	0.127	0.220	*	*	*	*
1927	0.902	0.056	0.373	0.131	0.597	0.093	0.362	0.062	0.337	0.128	0.189	0.221	*	*
1928	0.557	0.110	0.588	0.071	0.629	0.041	0.399	0.092	0.287	0.079	*	*	*	*
1929	0.487	0.413	0.661	0.108	0.398	0.053	0.572	0.087	0.502	0.133	0.444	0.102	0.240	0.165
1930	0.983	0.467	0.589	0.110	0.547	0.140	0.560	0.138	0.506	0.107	0.459	0.127	0.353	0.205
1931	*	*	0.624	0.443	0.400	0.113	0.542	0.102	0.399	0.114	0.457	0.207	0.312	0.141
1932	*	*	0.468	0.164	0.489	0.083	0.465	0.052	0.362	0.137	0.366	0.105	0.350	0.138
1933	*	*	0.542	0.070	0.477	0.066	0.540	0.078	0.514	0.099	0.602	0.089	0.474	0.183
1934	0.627	0.253	0.627	0.253	0.590	0.067	0.532	0.065	0.580	0.078	0.622	0.110	0.580	0.121
1935	0.529	0.103	0.685	0.150	0.565	0.071	0.580	0.095	0.413	0.117	0.531	0.069	0.597	0.125
wt.mean Z & SE (Z)	0.741 0.041		0.521 0.032		0.531 0.021		0.485 0.021		0.484 0.026		0.447 0.031		0.476 0.053	

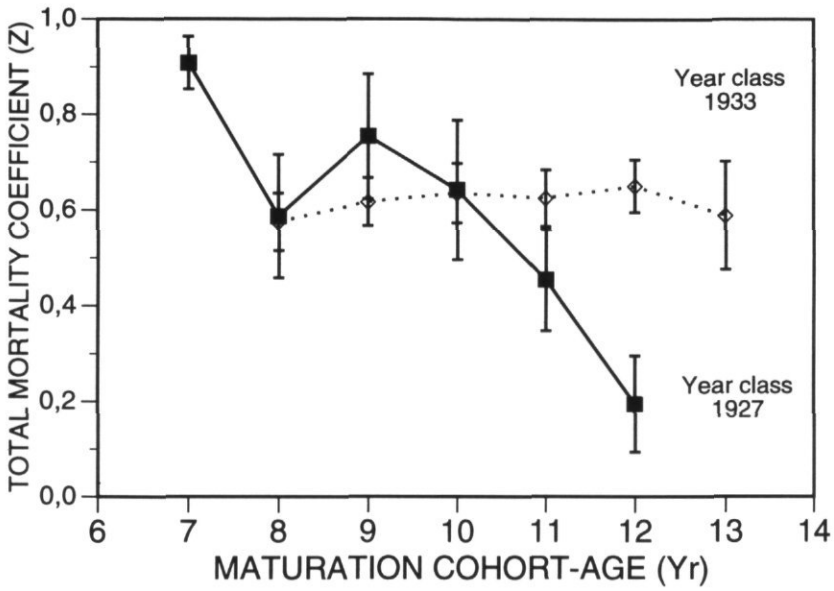


Figure 4. Cohort Z with ±2 s.e. vs cohort maturation age, 1927 and 1933 year classes. Selection hypothesis (A).

(Hyp B), this trend is still present but much weaker (except for MC-7).

2.14. More detailed analysis showed that the trend of Z with MC age varied systematically over the year-class series. This is seen in Figure 6a and b, where the regressions of Z on MC age are drawn from MC-7 to MC-13 for each year class sequentially. The slopes of Z on MC age for the first four year classes (1920–1923) are somewhat erratic (probably owing to the limitations of these early data; see para 2.1) but predominantly positive (i.e. Z increasing with MC age). In contrast, for year classes 1924–1929, the slopes are strongly and consistently negative for both selection hypotheses. Finally, for year classes 1930–1935, the trajectories of Z on cohort age become weakly negative or effectively horizontal.

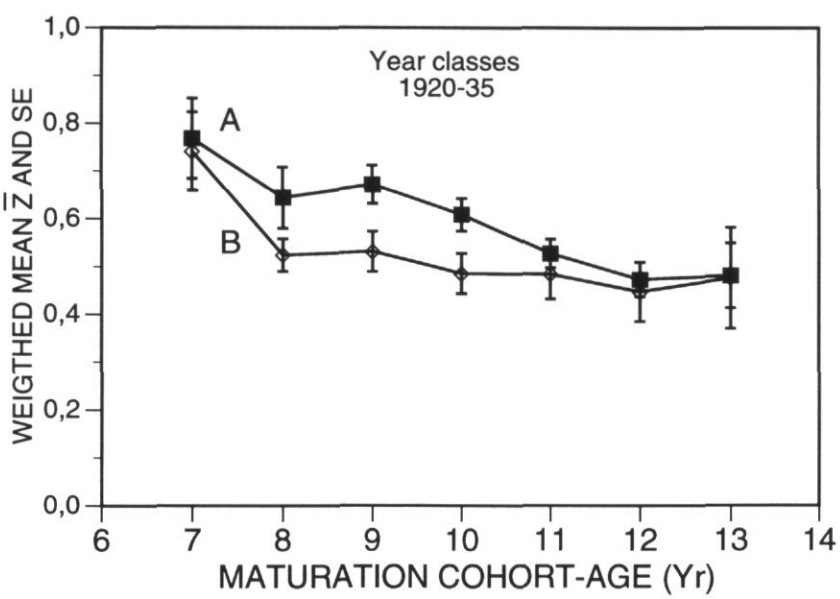


Figure 5. Weighted means with ±2 s.e. vs cohort maturation age, 1920 to 1935 year classes. Selection hypotheses (A) and (B).

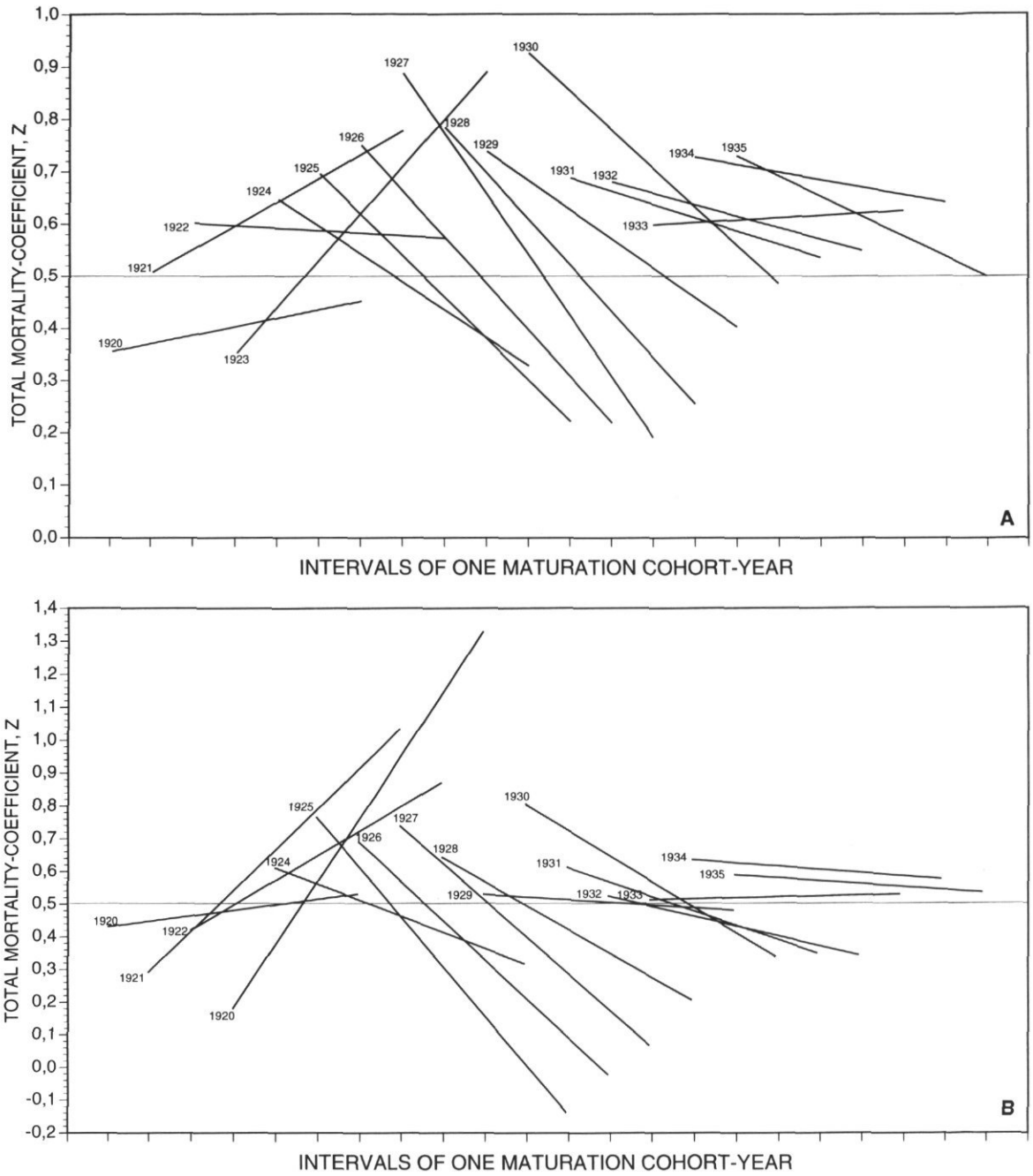


Figure 6A. Regressions of Z on cohort maturation age for individual 1920 to 1935 year classes. Selection hypothesis (A). B. Regressions of Z on cohort maturation age for individual 1920 to 1935 year classes. Selection hypotheses (B).

2.15. Possible explanations of these trends are given in sect. 5 (Discussion). For further analysis of these and other data (longevity and growth) the pattern of Figure 6a and b suggests that a division into three groups of year classes would be appropriate, as follows: Group I 1920–1923 (4), Group II 1924–1929 (6), Group III 1930–1935 (6). The weighted mean Z for each maturation cohort in the above year-class Groups I, II, and III are tabulated in Table 3 and plotted in Figure 7 against cohort maturation age, with bars indicating ±2 s.e. of the means.

Table 3. Weighted mean total mortality rates ($\bar{Z}$) and standard error (s.e.) of maturation cohorts for year class Groups I (1920–1923), II (1924–1929), and III (1930–1935).

Year class	MC-7 $\bar{Z}$	SE ($\bar{Z}$)	MC-8 $\bar{Z}$	SE ($\bar{Z}$)	MC-9 $\bar{Z}$	SE ($\bar{Z}$)	MC-10 $\bar{Z}$	SE ($\bar{Z}$)	MC-11 $\bar{Z}$	SE ($\bar{Z}$)	MC-12 $\bar{Z}$	SE ($\bar{Z}$)	MC-13 $\bar{Z}$	SE ($\bar{Z}$)
A: Hypothesis (A)														
I-(1920–1923)	*	*	*	*	0.554	0.079	0.558	0.059	0.597	0.047	0.562	0.068	0.526	0.108
II-(1924–1929)	0.839	0.04	0.724	0.057	0.667	0.031	0.572	0.028	0.353	0.022	0.328	0.023	0.298	*
III-(1930–1935)	0.573	0.084	0.668	0.038	0.683	0.024	0.635	0.020	0.640	0.019	0.621	0.027	0.530	0.040
B: Hypothesis (B)														
I-(1920–1923)	*	*	*	*	0.546	0.067	0.610	0.063	0.624	0.062	0.728	0.088	0.848	0.180
II-(1924–1929)	0.800	0.030	0.581	0.044	0.536	0.025	0.422	0.030	0.430	0.035	0.175	0.046	0.240	*
III-(1930–1935)	0.561	0.080	0.518	0.044	0.522	0.032	0.517	0.030	0.488	0.042	0.523	0.039	0.466	0.058

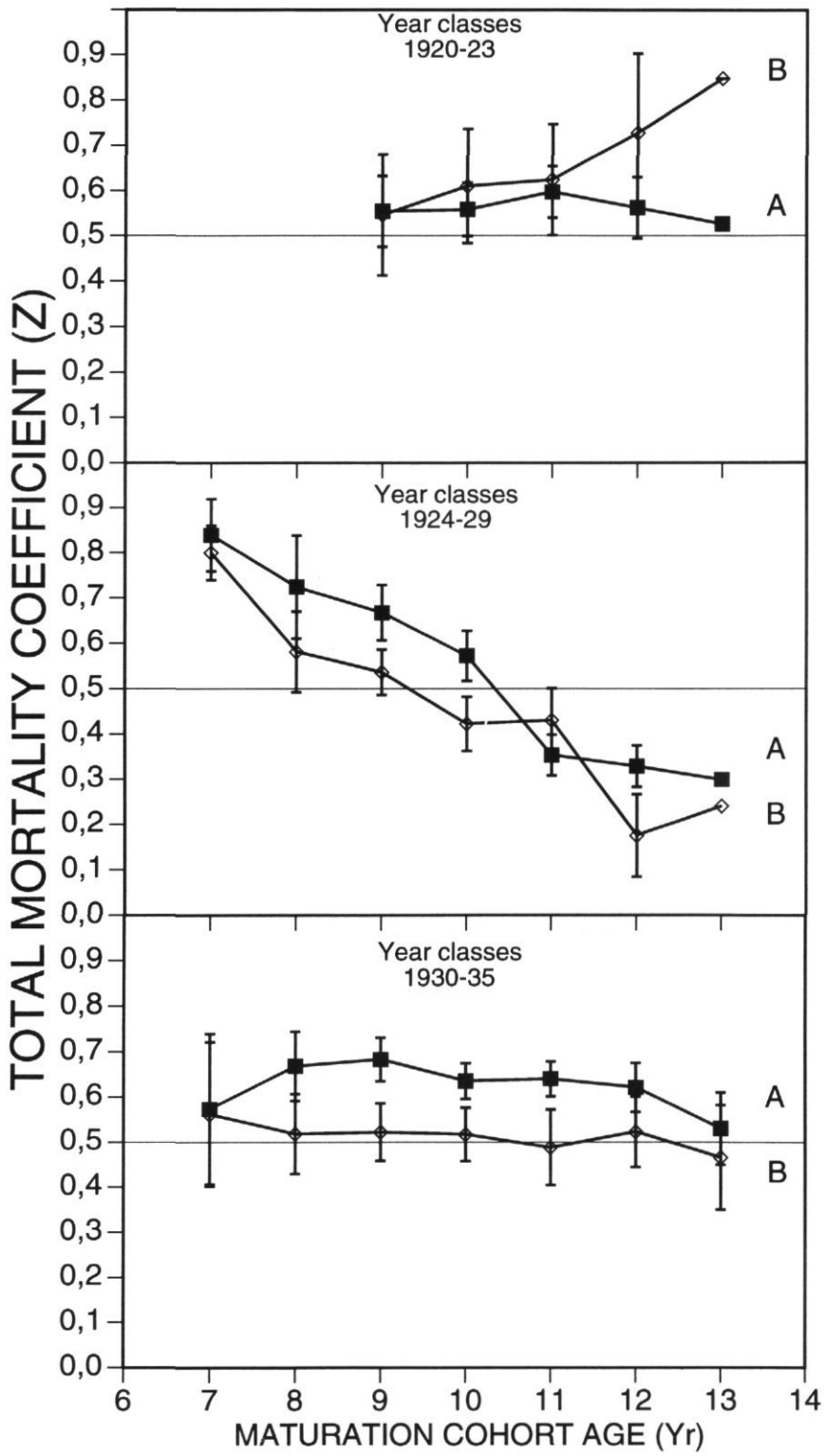


Figure 7. Trends of Z vs MC age for each year-class group. Selection hyoptheses (A) and (B).

Separate trajectories are shown for each selectivity hypothesis (A) and (B).

2.16. The outcome can be summarized as follows. In year classes of Group I, Z increases sharply for MC-12 and MC-13 with Hyp (B), but these two estimates have a high variance and overall there is no significant trend of Z with MC age. In Group II year classes, however, Z decreases significantly ($p < 0.001$) with MC age at about 0.1 per additional year to maturity. Finally, in Group III year classes, the downward trend effectively disappears and Z becomes almost the same for all cohorts, at much the same level as in Group I. These general trends are similar irrespective of which selectivity hypothesis is used, the main effect of which being to lower Z throughout, especially in the middle cohorts (MC-8 to MC-12) which cover the greatest span of length.

3. Longevity of maturation cohorts

3.1. Life expectancy is a fundamental demographic parameter of a species and its living conditions. Provided age determination is reasonably reliable, maximum age data (T_{max}) can give some idea of the effective adult mortality rate even when direct mortality estimates are unavailable or suspect, especially (as in this case) on a comparative inter-cohort basis.

Material and methods

3.2. Every age reading in the Bergen cod database is recorded individually and includes maximum age data for the youngest (MC-6) and oldest (MC-14) cohorts which are too sparse to meet the criteria for mortality estimation set out in para 2.11. However, the observed T_{max} in an age-composition sample depends on the sample size as well as the starting age and the mortality rate. Since sample size necessarily varies greatly between cohorts (being smallest for the youngest and oldest cohorts), observed T_{max} values must be normalized to a standard sample size for comparison between cohorts.

3.3. With an age-independent mortality rate, T_{max} varies linearly with $\ln[2 \times \text{sample size} + 1]$ (Hoenig, 1983), the constant term being the age at maturity (T_m). Put another way, for a given overall mortality rate the observed *Maximum Adult Lifespan* ($T_{ad} = T_{max} - T_m$) should increase proportionately with $\ln[2 \times \text{sample size} + 1]$. Adult lifespans were therefore computed for each MC and regressed against $\ln[2 \times \text{sample size} + 1]$. All MCs were combined for year-class Group I (1920–1923) where samples were rather small, but MCs 6–9 and MCs 10–14 were treated separately in year-class Groups II (1924–1929) and III (1930–1935). The regression slope for Group I (0.572) was significant ($p=0.02$), but highly significant regressions ($p<0.001$) were obtained in all the other four data sets, as in Table 4.

Table 4. Slopes (and s.e.) of regressions of adult life-span. $T_{ad} = (T_{max} - T_m)$ on $\ln [2 \times \text{sample size} + 1]$.

Maturation cohorts	Year-class group		
	I-(1920–1923)	II-(1924–1929)	III-(1930–1935)
6–9	0.572 (0.232)	0.916 (0.222)	1.423 (0.275)
6–14			
10–14		1.058 (0.260)	1.292 (0.225)

3.4. There is no significant difference in the between-MC slopes of year-class Groups II and III, but the between-group slopes of both MC regressions are different at the 0.01% level. For illustration, all MCs in year-class Groups II and III have been combined in Figure 8, although for normalization the individual slopes in Table 2 have been used. For normalization in Group I the mean of the slopes for that Group and for Group II is used, i.e. 0.849. Observed values of T_{max} have been normalized to the approximate average size of the best sampled cohorts (400 fish) by the equation:

$$T_{max}\,(\text{norm.}) = T_{max}\,(\text{obs.}) + Q \times \ln \frac{2 \times 400 + 1}{2n + 1}$$

where Q is the appropriate slope from Table 4.

Results: Maximum age (T_{max}) and adult lifespan (T_{ad}) of maturation cohorts

3.5. Individual and mean observed (○) and normalized (●) T_{max} are plotted against MC age in Figure 9, using the year-class Group II data for illustration. Normalization lifts the observed trend at both ends (where sample numbers are small) and makes it nearly straight, though not quite proportional. Consequently, adult life-expectancy increases only slowly with age at maturation (Fig. 10).

3.6. The normalized adult lifespans of MC-8 to MC-14 in year-class Group III (1930–1935) shown in Figure 11 are effectively the same and some 2–3 years longer than in Group II year classes, but those of the three youngest cohorts are appreciably shorter. In the 1920–1923 year classes of Group I, however, the trend is in the opposite direction, T_{ad} decreasing sharply for MCs older than MC-8. This result and certain of the other trends of Figure 11 which are not in accordance with the corresponding mortality rates could be explained if the precision with which the age of the oldest fish could be determined improved with experience over the years covered by this study.

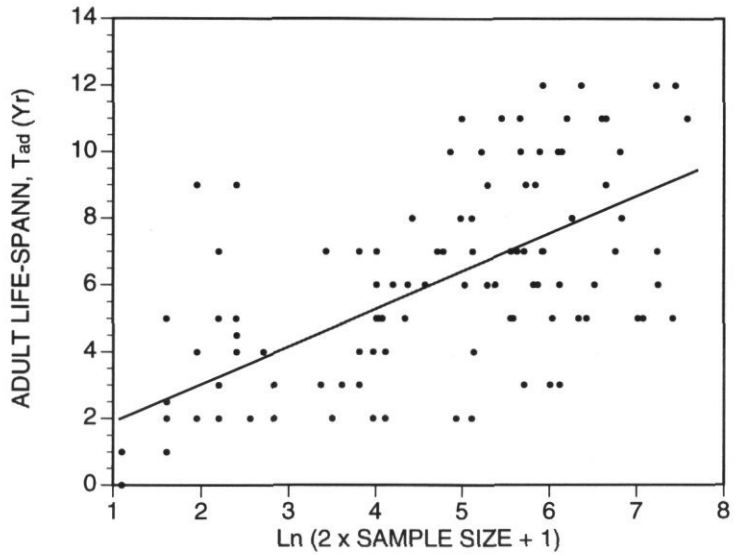


Figure 8. Adult life-span $T_{ad} = (T_{max} - T_m)$ vs ln [2 × sample size +1]. Combined data for year-class Groups II and III.

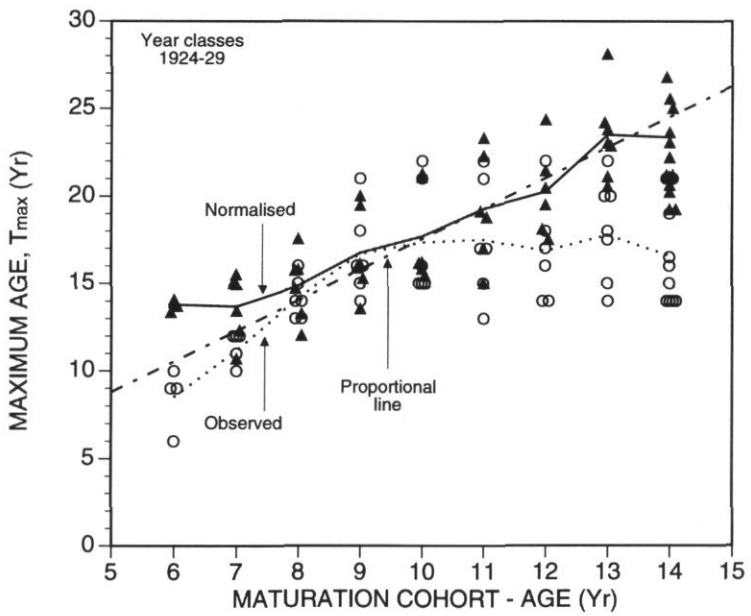


Figure 9. Observed and normalized T_{max} vs MC age for year-class Group II.

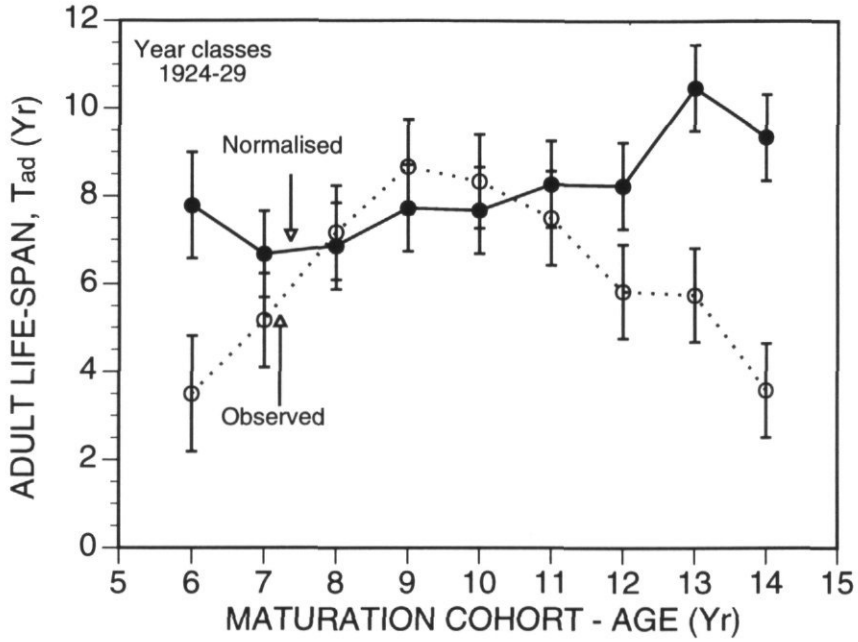


Figure 10. Observed and normalized T_{ad} with ± s.e. vs MC age for year-class Group II.

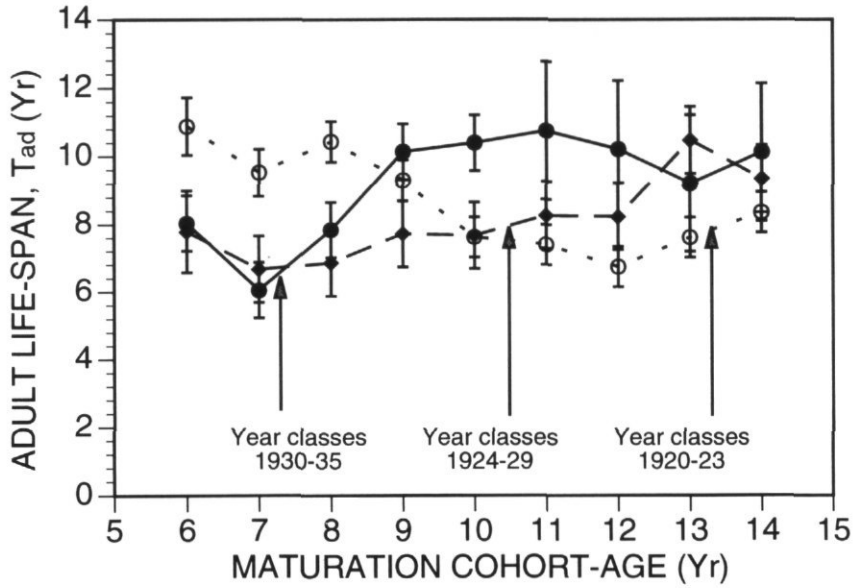


Figure 11. Normalized T_{ad} with ± s.e. vs cohort maturation age for year-class Groups I, II, and III.

4. Length-at-maturity and adult growth of maturation cohorts

4.1 The Bergen cod database is a rich source of information on growth and many articles have been published over the years (e.g. Rollefsen, 1954; Jørgensen, 1992), but the growth of individual maturation cohorts has not hitherto been studied. Analysis is limited here to examining (a) whether, and if so how, the adult growth of a maturation cohort depends on the age at which it matured, and (b) whether the cohort growth patterns changed appreciably between the three groups of year classes, as the total mortality rates appear to have done.

4.2. Von Bertalanffy coefficients K and L_{inf} for each maturation cohort of each year class were estimated by non-linear regression. Because the length-at-age trajectories are only slightly curved and start at relatively high ages far from the origin, allowing t_o to vary freely when using the non-linear regression package resulted in a high correlated variance between t_o and K and an appreciable proportion of "no fit possible" results. For the present purposes, K and L_{inf} were therefore estimated with t_o held constant at zero, but a check showed that the trends in both parameters with MC age and between year-class groups were similar with both methods. It may also be noted that fitting to immature length-at-age data from research vessel samples from the Barents Sea in the years 1980–1987 gave a mean t_o = 0.08 and K = 0.10, the former being not significantly different from zero. Examples of the fit to three individual cohorts using the mean lengths-at-age of year-class Group II (1924–1929) are shown in Figure 12. Estimates of K and L_{inf} are plotted against MC age for each year-class Group in Figures 13 and 14, respectively. There is little change of K and L_{inf} across the cohorts, i.e., with age at maturation, except for MC-6 and MC-7, where K is larger and L_{inf} smaller than for later maturing cohorts.

4.3. There is, however, a small but distinct difference in the level of the trajectories of K and (to a lesser degree) L_{inf} between year-class Groups II and III, K being about 0.03 lower and L_{inf} about 5 cm higher in Group III than in Group II. These differences reflect the fact that growth was a little faster in the Group II year classes, as can be seen from the fact that all cohorts except the youngest (MC-6) and oldest (MC-13 and MC-14) matured at about 5 cm longer compared with those of Group III (Fig. 15).

4.4. The similarity in values of K and L_{inf} for all maturation cohorts (except MC-6 and MC-7) indicates that the individual growth curves of all cohorts would be much the same. This is seen in Figure 16, which shows the maturation cohort growth curves for year classes of Group II (for illustration) calculated from the fitted

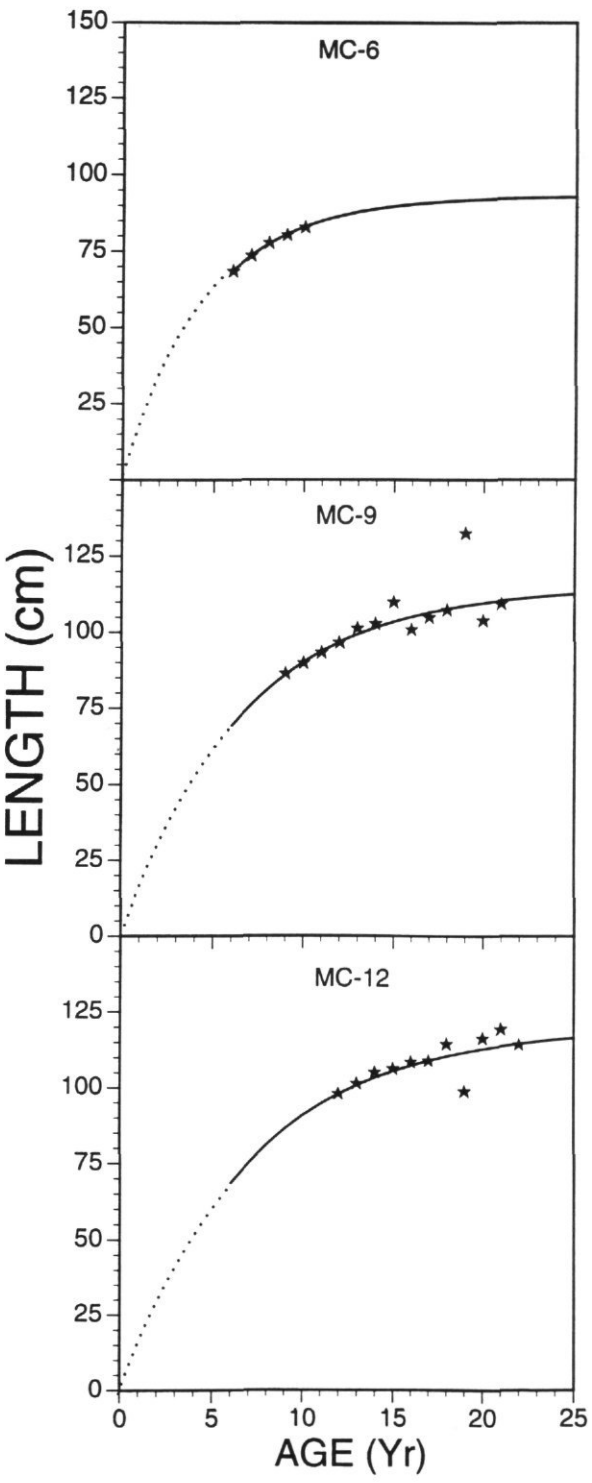


Figure 12. Examples of fit of von Bertalanffy growth equation to MCs-6, 9, and 12 of year-class Group III.

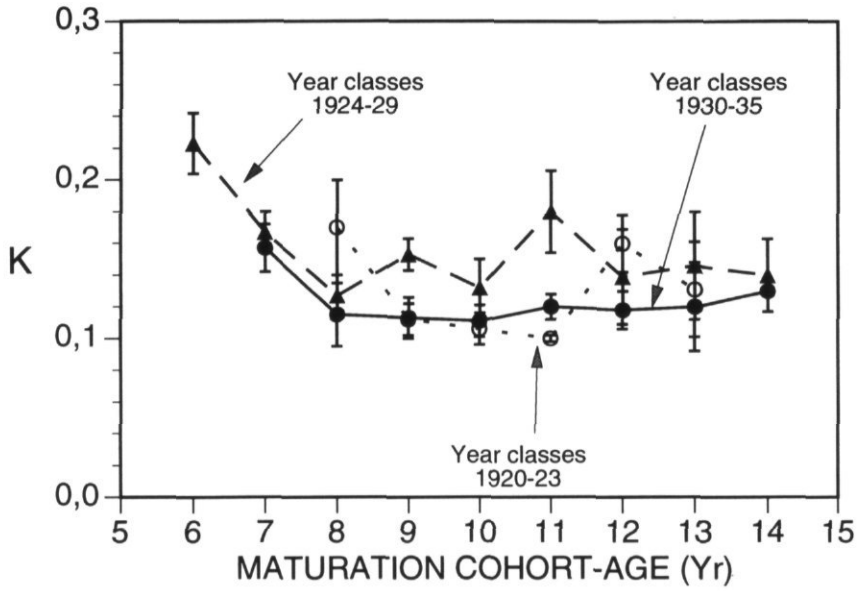


Figure 13. K with ± 2 s.e. vs MC age for each year-class group.

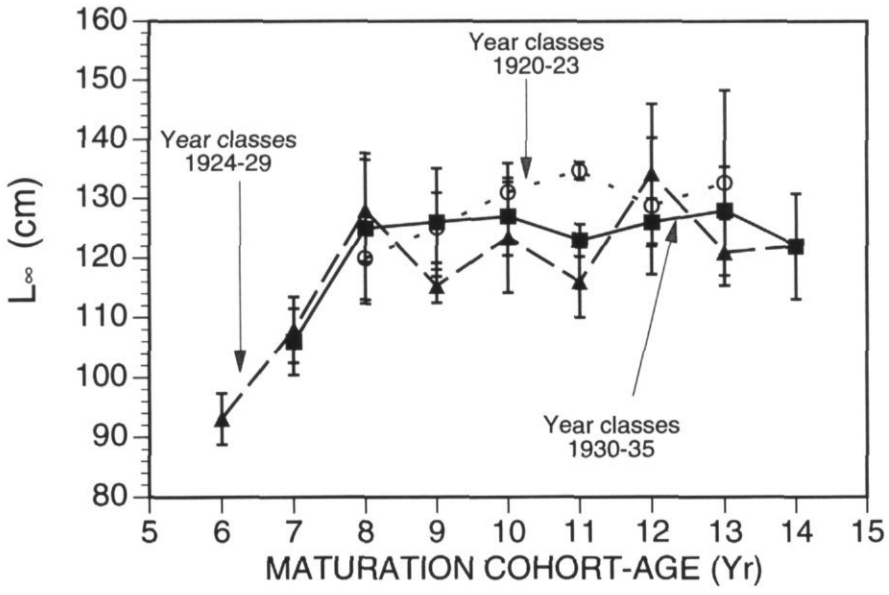


Figure 14. L_{inf} with ± 2 s.e. vs MC age for each year-class group.

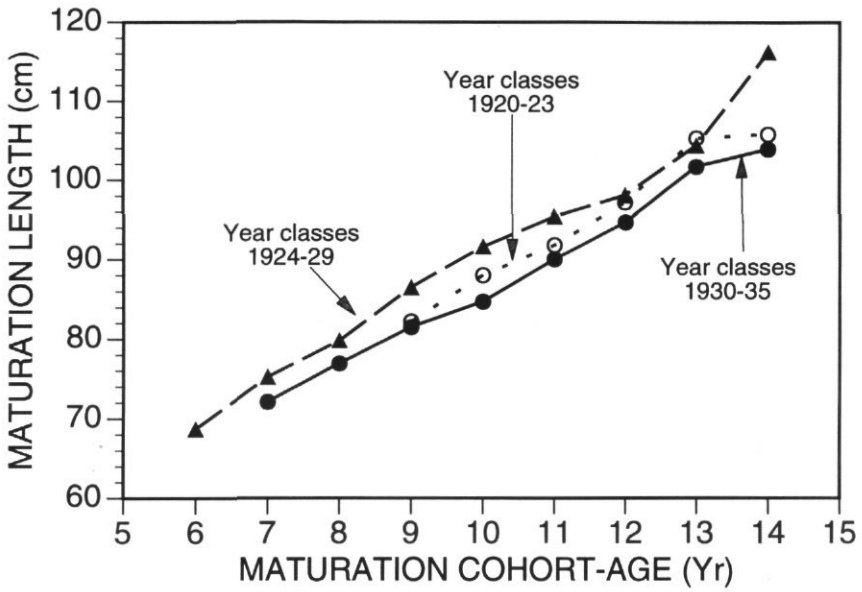


Figure 15. Length at maturity vs MC age for each year-class group.

values of K and L_{inf}, the observed mean lengths-at-age for the individual cohorts being shown in the inset panel. The lengths at which each cohort reached maturity are indicated by the solid diamonds on the calculated curves.

5. Discussion

5.1. Here we return to the central question of the present paper: are the GML matrices of individual maturation cohorts dependent on the age at which the cohort matured? The three sets of maturation cohort-specific parameters bearing on this are Z, T_{max}, and $K - L_{inf}$.

Evidence from the cohort age-composition data

5.1. It is first necessary to clarify the question of adjustment of the c.p.u.e. data for selectivity. The main features of the c.p.u.e. trends persist irrespective of whether and how the c.p.u.e data are adjusted for selectivity; but in our judgement, on present information, the best interpretation lies closer to Hyp (B) than to Hyp (A), and in what follows we take estimates of Z from Hyp (B) as the nearest approximation to true mortality rates. These "Best Judgement" estimates of trends of Z with maturation age for each or the three year-class groups are shown in Figure 17, and will be used as the basis for further discussion.

5.2. It is theoretically possible for these differences in slope of Z with MC age between the year classes to be due to changes in the natural mortality rate (M). However, even if results for the four year classes comprising Group I (1920–1923) are set aside, Z on the oldest cohorts still decreased by about 0.3 between year-class Groups II and III and increased in the youngest cohorts by 0.2 – an overall shift of around 0.5. Such dramatic changes in M seem highly improbable, and a more plausible explanation is that fishing mortality was not uniform across the cohorts over the period covered by the data.

5.3. In this connection it has to be recalled that the fishing mortality component of the Z values was not generated solely by the short but intensive spawning fishery of Lofoten. Substantial (and at present unquantifiable) amounts of mature cod were caught during the rest of the year on the feeding grounds and migration routes all through the 1920s and 1930s by trawlers from a number of countries, particularly the UK, Germany, the USSR, and France. This fishing was halted by the onset of the World War II in 1939 and resumed again towards the end of 1945, although at a reduced level for a time. However, Norwegian fishing inside the skerries at Lofoten continued during the war with only minor restrictions (Rollefsen, 1954).

5.4. Year classes in the prewar period matured at an average age of about 10 years and had an adult life of a further ten years. The oldest survivors of the late-maturing cohorts of year classes from 1925 onwards were therefore beginning to be affected by what must have been a considerable reduction in overall fishing

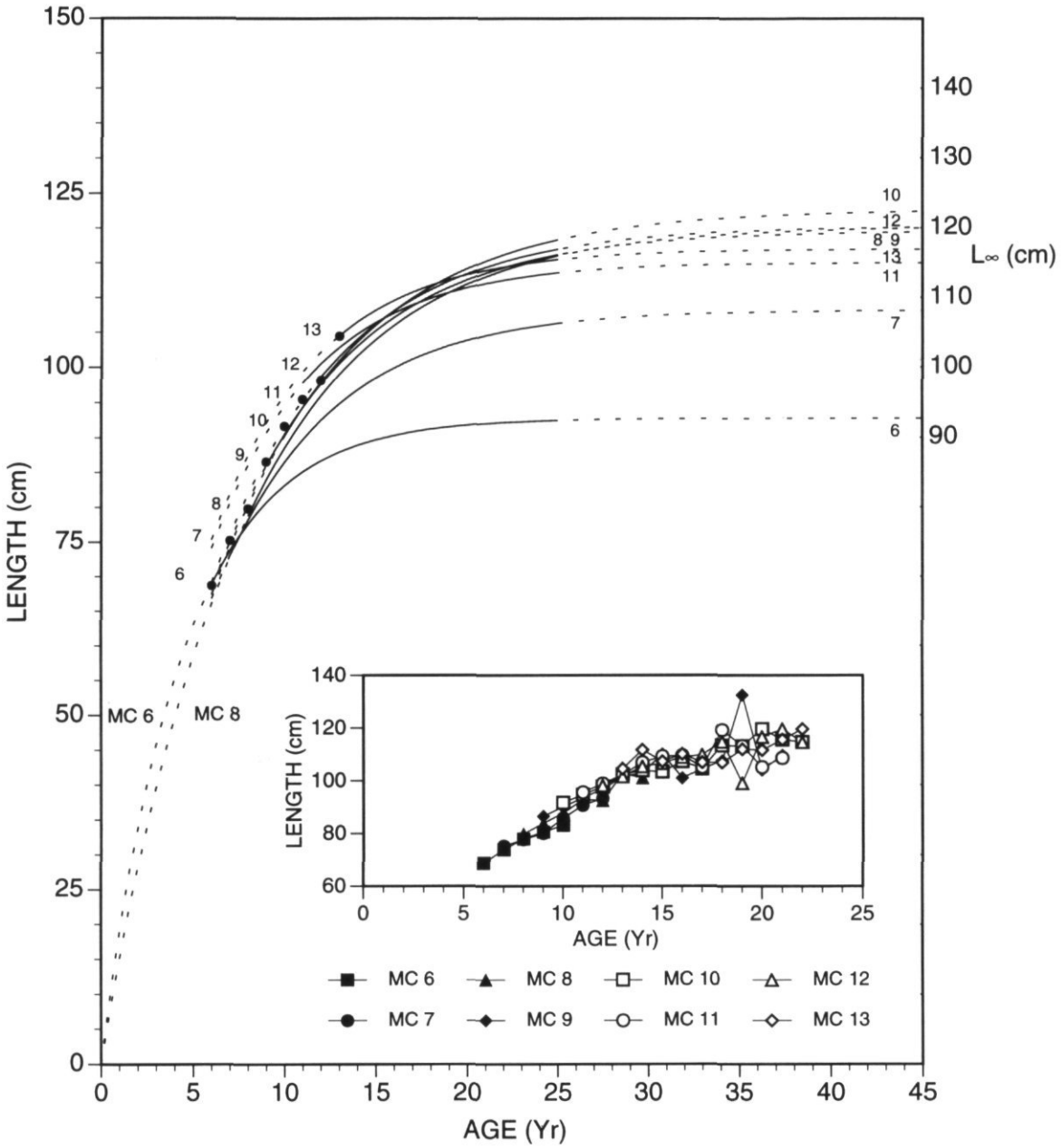


Figure 16. Calculated growth in length of year-class Group II with observed data and lengths at maturity.

pressure during the war period. Conversely, the younger maturation cohorts of year classes born in the early 1930s would have had the full benefit of the war-time relaxation of fishing whilst the older cohorts would only have started entering the Lofoten fishery towards the end of the war and so would have been depleted by the renewed postwar trawling.

5.5. The time sequence of trends of Z with MC age in Figure 6 broadly matches this sequence of events. Z for the oldest cohorts starts falling with the 1924 year class and rises by the 1930 year class, when Z of the youngest cohorts begins to decline. It therefore seems reasonable to conclude that differential shifts in fishing pressure on the younger compared with the older maturation

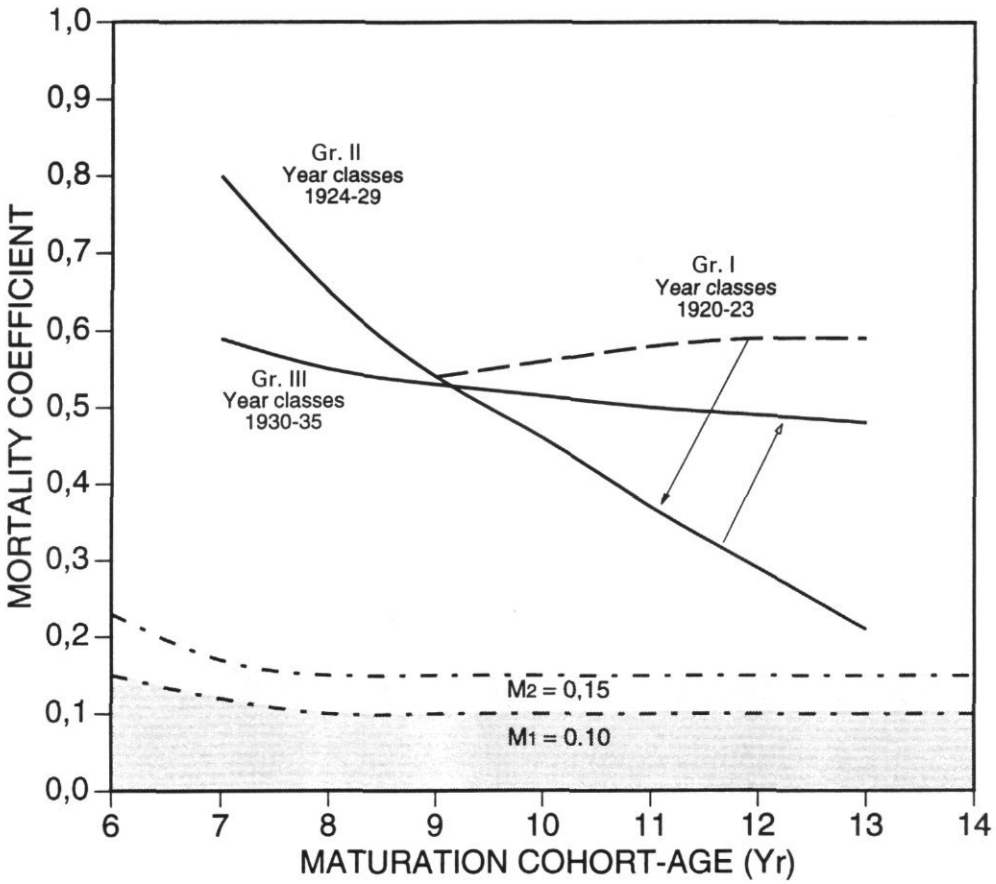


Figure 17. "Best judgement" estimates of trends of Z with cohort maturation age for each year-class group with possible trajectories of M.

cohorts over the period were the main cause of the changes in slope of the relationship between Z and CM age.

5.6. While a systematic linkage between natural mortality rate and age at maturation cannot be ruled out, the analysis so far does not point to any marked change of M with cohort age except in the youngest cohorts MC-6 and MC-7. Nevertheless, some bounds can be set for M. Thus, since there must have been some fishing on the oldest maturation cohorts even when Z for them was at its lowest (about 0.2 for the Group II year classes), M on these cohorts could scarcely be greater than 0.15 and it could easily have been nearer 0.1.

Evidence from the maximum age data

5.7. Normalized adult lifespan is dimensionally related to the reciprocal of mortality rate, so the T_{ad} data of Figure 11 are plotted against 1/MC-Z in Figure 18, the cohorts being identified by numbers. Adult lifespan increases with 1/Z in both year-class groups as expected, both regressions being significant at the $p=0.001$ level, but the slope of the Group II regression does not fully reflect the sharp decrease in Z with MC age in this group of year classes. Again, this may be due to underestimation of the age of the oldest fish in these earlier year classes (see 3.6). In the Group III year classes, although Z is nearly constant, T_{ad} tracks what little movement in Z there is.

5.8. Where the maximum age data offer valuable guidance is at the extremes of the cohort range, where numbers are too small for reliable mortality estimation. Thus, referring back to Figure 11, and discounting Group I for the reasons already mentioned, there is a strong indication that the adult lifespans of MC-6, MC-7, and possibly MC-8 (in which T_{max} is less than 15 years and not subject to the uncertainty of the very high ages) are shorter than those of later maturing cohorts. By contrast, there is no suggestion that the adult lifespan of the oldest maturation cohort (MC-14) is other than a

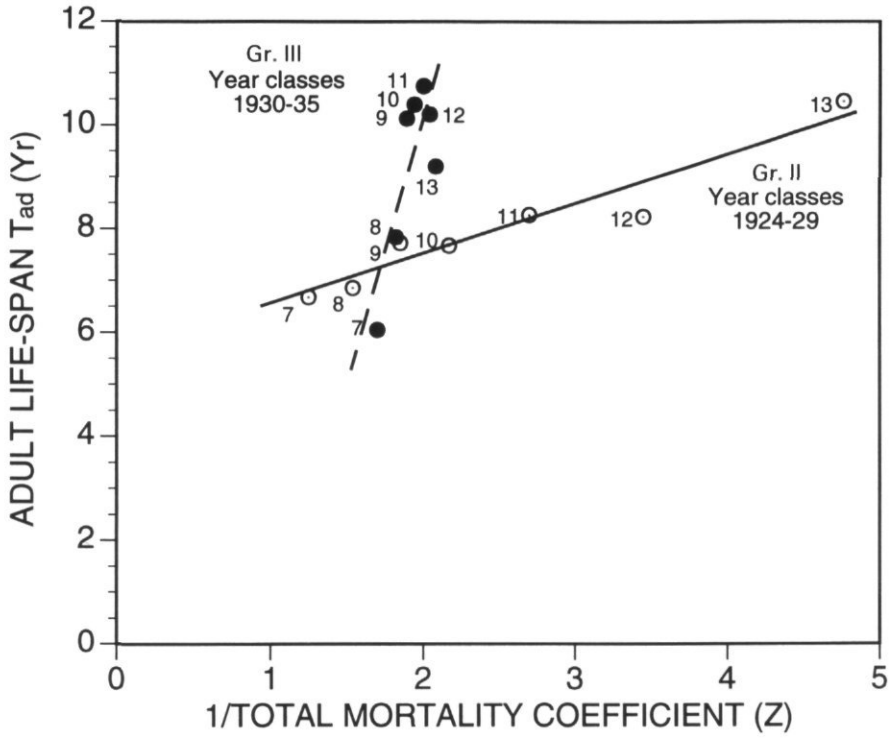


Figure 18. Normalized adult life-span (T_{ad}) vs 1/Z for year-class Groups II and III.

continuation of whatever trend (or lack of trend) is shown by the preceding cohorts.

Evidence from growth data

5.9. This is the most straightforward. K is highest and L_{inf} lowest in the two youngest maturation cohorts (MC-6 and MC-7; Figs. 13 and 14). Thereafter, both parameters become effectively constant and independent of age at maturation. Within the limits of the data, this conclusion holds for all three year-class groups.

6. Concluding remarks

6.1. The uncertainty concerning the interpretation of the changes of Z with cohort maturation age over the sequence of year classes investigated unfortunately precludes a clear-cut answer at this stage from investigation as to whether age at maturation affects adult natural mortality rate. If, however, it is assumed that the changes in Z were caused mainly or wholly by changes in F as the year classes moved through the war period, then the maturation cohort GML matrices are consistent with the conclusion that only for the youngest cohorts MC-6 and MC-7 is there evidence of a reduced growth performance and natural life expectancy compared with older maturing cohorts.

6.2. Recalling the conclusion of par. 5.6 that M for the late maturing cohorts could hardly have been above 0.15, this conclusion implies that possible envelopes defining M as a function of age in maturation are as shown by the broken lines of Figure 17; these reach values of M between 0.17 and 0.25 for MC-6 . Remembering that under increasing fishing pressure for several decades following the period of this investigation the average age at maturity of the whole Northeast Arctic cod stock has fallen to between 6 and 7 years, the implications to the reproductive performance of the present stock are considerable.

6.3. Several questions arise from this exploratory study, perhaps the most immediate being the need to resolve if possible the present uncertainty concerning the interpretation of the c.p.u.e. data and hence the estimation of the natural mortality of maturation cohorts. One approach is to estimate total mortality rates between each pair of calendar years across all cohorts and year classes instead of following each year class through its life (i.e. a Eulerian instead of Lagrangian approach, to borrow from the fluid dynamicists). A "smoother" application of selection Hypothesis (B) and possible additional corrections for stock-dependent

catchability could then be introduced. If some idea can be obtained of the catches of mature fish other than during the spawning fishery at Lofoten, a form of maturation cohort VPA may be feasible. Other investigations could include checking of maturation age reading using modern techniques of otolith examination; cohort-based fecundity measurements to establish whether specific fecundity is dependent on maturation age; and back-calculation of immature growth of known maturation cohorts.

6.4. In later articles, using the results presented here, it is hoped to develop further the potential of maturation cohort analysis for discriminating between biological and structural changes in mean population size and age at first maturity, and for examining questions relating to evolution and stock assessment.

7. Acknowledgments

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Thermal Increase Enhancement: a possible link between recruitment and climate in high latitude environments

K. S. Tande, T. Rasmussen, and G. Pedersen

Tande, K. S., Rasmussen, T., and Pedersen, G. 1994. Thermal Increase Enhancement: a possible link between recruitment and climate in high latitude environments. – ICES mar. Sci. Symp., 198: 502–509.

Recent studies on the zoea larval phase of *Pandalus borealis* showed that mortality was dramatically lowered in environments with continuously increasing temperature, compared with mortality at a constant higher temperature. If, for instance, larvae of the northern shrimp fed *ad libitum* experienced a temperature increase over 60 days from 2.5 to 4.9°C, then survival increases by a factor of 3.5 compared with larvae raised at 4.3°C. The effect of this temperature increment is enhanced survival at low and intermediate temperature ranges in boreal waters. We call this Thermal Increase Enhancement (TIE) for marine larvae. In light of the TIE, we contend that our perception of how temperature affects larval survival has basically been wrong. An exploratory study of the effect of long-term climatic changes on variation in population abundance of northern shrimp in temperate waters is performed. In the Gulf of Maine, strong year classes were formed only during periods of downward trends in water temperatures. The most likely explanations for this has been given to fecundity and factors which maximize egg production. The increased fecundity and survival of embryo and larvae would create an effect large enough to increase population abundance during periods of low temperature. These ideas are applied on the physical setting during the winter and spring period in Arctic-boreal waters. Thermal Increase Enhancement for larval shrimp is examined in relation to the different prevailing temperature scenarios in Arctic-boreal waters.

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Introduction

There is increasing evidence that in marine environments, temperature is a key factor for determining the rates of processes, both within the food web (Kemp and Boynton, 1981) and for groups of animals (Huntley and Lopez, 1992). Data on both natural mortality and predation, are essential in order to determine the actual levels of these rates, but comparatively few systematic studies on mortality schedules in crustaceans are at hand (see for instance Miller and Tande, 1993). The prevailing way to assess the effect of temperature on vital rates, has been to measure the actual rate of a component (for instance mortality) under controlled temperature conditions in the laboratory at several constant temperatures for a certain period of time.

This might not be the most precise way to describe the effect of temperature on larval survival. In the present paper, we try to look at this problem in more detail, and will focus on how mortality of lower trophic level animals might be linked to temperature. A hypothesis stating that during the main annual growth period *Calanus finmarchicus* is sensitive to a temperature decrease, and that also a certain increase in temperature is a prerequisite for successful growth and survival from copepodite stage I to copepodite stage IV and V was put forward by Tande (1988). We report some recent progress in testing this hypothesis under laboratory conditions, and we further review the literature on how these new results fit into our current knowledge of how recruitment relates to temperature. In doing so we have performed an exploratory analysis of the link between climate and fluctuations in population abundance of *Pandalus borealis* in the Gulf of Maine. The discussion of the results above are also extended to the recruitment problem in fishery research.

The background for the hypothesis

Zooplankton ecological studies in north Norwegian fjords have been in progress since the middle of the

1970s, and the new information obtained on copepods has recently been reviewed by Tande (1991). Although the first years were more of a descriptive nature, a stronger emphasis has been given later to quantitative and experimental studies. This was encouraged by an effort to develop and refine a quantitative model for estimating *Calanus* productivity in Arctic-boreal waters (i.e. Slagsted 1981). The shift in emphasis materialised in a series of population and bioenergetic studies. Some experiments were set up to establish temperature-rate functions for growth and development for copepodite stages of *C. finmarchicus* at the lower end of its temperature range.

In the early 1980s growth and development data for marine copepods from Arctic-boreal water were scarce, and in order to obtain ecologically relevant data for *C. finmarchicus* from these waters, experiments were performed in the temperature range from 0.5 to 6°C. At that time the prevailing technique for cultivating marine copepods from temperate waters was to produce a large experimental cohort of copepodite stage I from eggs obtained from ovigerous females (Paffenhöfer and Harris, 1979; Vidal, 1980a,b).

Environmental conditions

The data reported here stem from experiments on *C. finmarchicus* and *P. borealis* obtained from Balsfjorden, Grøtsund and Malangen (Fig. 1), fjords or basins at approximately 69°N in northern Norway.

In coastal and fjord areas north of Lofoten *C. finmarchicus* have an annual reproduction and recruitment period from April until mid June (Tande 1982). Spawning in April takes place at minimum temperatures, which vary from year to year and among different localities. The intensive growth of *C. finmarchicus* during May and June coincides with the yearly build up of a thermocline. Information about food availability in these waters indicates particulate organic carbon content > ca 350 μg C l^{-1} and cell concentrations in general > 3 × 10^5 cells l^{-1} during the same period (Tande, 1988).

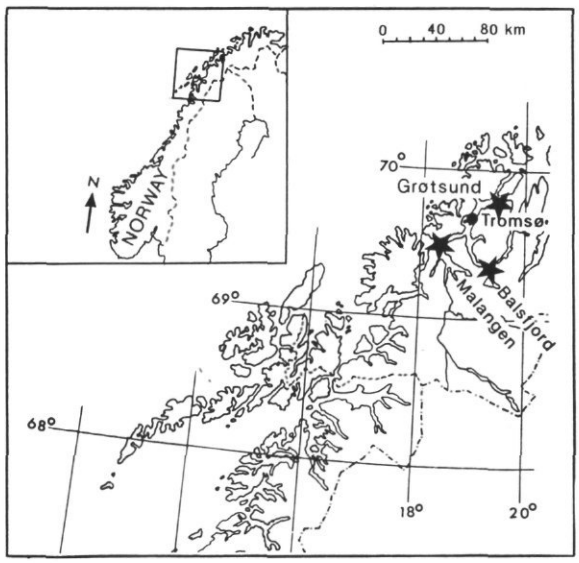


Figure 1. Map showing the study sites in Balsfjorden, Grøtsund, and Malangen, northern Norway.

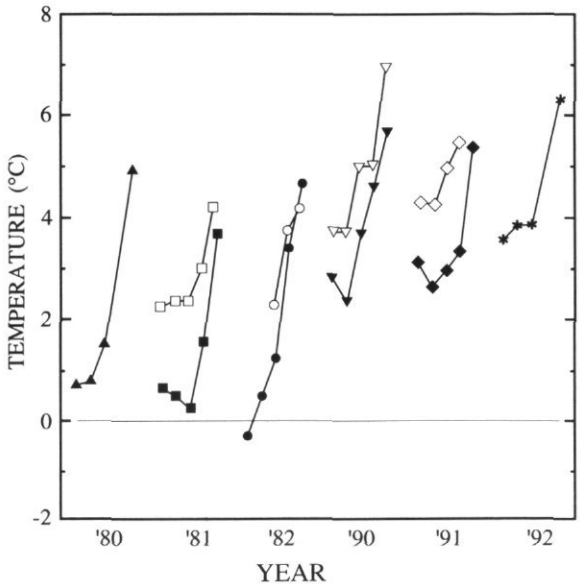


Figure 2. The monthly temperature at 20 m of depth from February to June in Balsfjord (Svartnes) and Malangen (Ytre Malangen) for some of the years in the period from 1980 to 1992. Note that some of the months are missing. Open symbols are Malangen, filled symbols are Balsfjord. Temperature data for Malangen in 1992 are missing.

In order to highlight the prevailing temperature conditions in north Norwegian fjords during the larval period of *C. finmarchicus* and *P. borealis*, the mean monthly temperature at 20 m of depth is plotted from January to June for Balsfjorden and Malangen (Fig. 2). Balsfjorden has been described as the coldest of north Norwegian fjords (Eilertsen *et al.*, 1981), and this is clearly seen in the data. These two fjords have almost the same pattern of temperature increase at 20 m during spring. Malangen, however, is more influenced by oceanic water conditions. The deep water is more saline and generally warmer than in Balsfjorden.

Mortality in copepods under constant temperature conditions

The results stem from 1981 and 1982 when *C. finmarchicus* was cultivated following the techniques described by

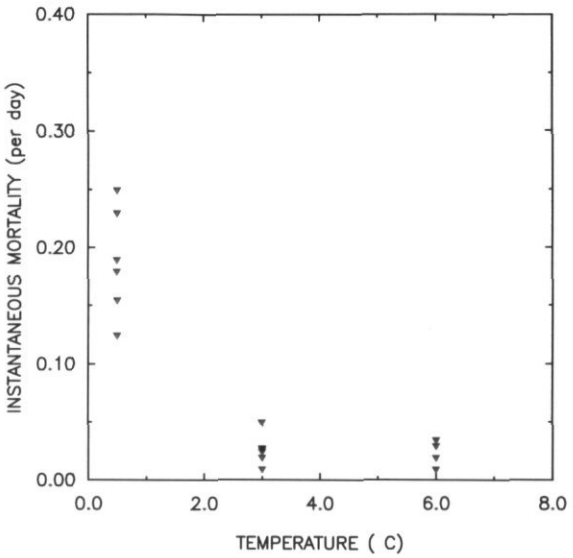


Figure 3. *Calanus finmarchicus*. Instantaneous mortality rates for copepodites cultivated at different temperatures (after Tande, 1988).

Tande (1988). The nauplii were kept at a constant temperature at 2°C, and approximately one month thereafter, populations of CI were established and transferred to 0.5, 3 and 6°C in a gradient of algal food concentration from 50 to 600 μg C l^{-1}. The different cohorts progressed through several copepodite stages only at the two highest temperatures (see Tande 1988). Instantaneous mortality was highest for those populations experiencing the lowest temperature (0.5°C), which suffered virtually mass mortality during the first two weeks of incubation (see Fig. 3). Mortalities at 3 and 6°C were not significantly different. This experiment was not specifically designed to study the effect of temperature on mortality, part of it was run at the lower end of the species thermal range, which might have influenced the quality of the data. All these aspects are discussed in more detail in conjunction with the specific hypothesis formulated in Tande (1988).

Testing the hypothesis

Mortality in copepods at constant vs continuous increasing temperatures

In order to pursue the hypothesis raised by Tande (1988), another experiment was designed to study the effect of different thermal conditions on mortality in copepodite stages of *C. finmarchicus* (Pedersen and Tande, 1992). In this study we designed a variable thermal regime based on the temperature increase which is found in these latitudes during the spring and early summer (Fig. 2). Thus, eggs and nauplii were held at 2°C until completion of the naupliar phase, then programmable temperature control baths held one group at 2°C, warmed another at 0.1°C d^{-1}, and warmed a third at 0.2°C d^{-1}. The rate of temperature increase was designed to cover the observed increase in surface waters both in Balsfjorden and in Malangen which takes place when the cohort of *C. finmarchicus* progress from CI to CV in May and June.

Eight beakers of 200 late nauplii approximately day 40 after hatching were introduced to each of three different thermal regimes. At each 6th day during the following 24 days, two populations from each series were taken out for abundance and stage determinations. Plotting the results on a three dimensional scale (Fig. 4), shows that the mortality rate was highest at the constant temperature during the 24 days period. There was also a tendency for mortality to increase progressively with time, more so for the two lower thermal regimes. The naupliar developmental rates at 2°C obtained in 1980 (Tande 1988) were definitely higher than those obtained for

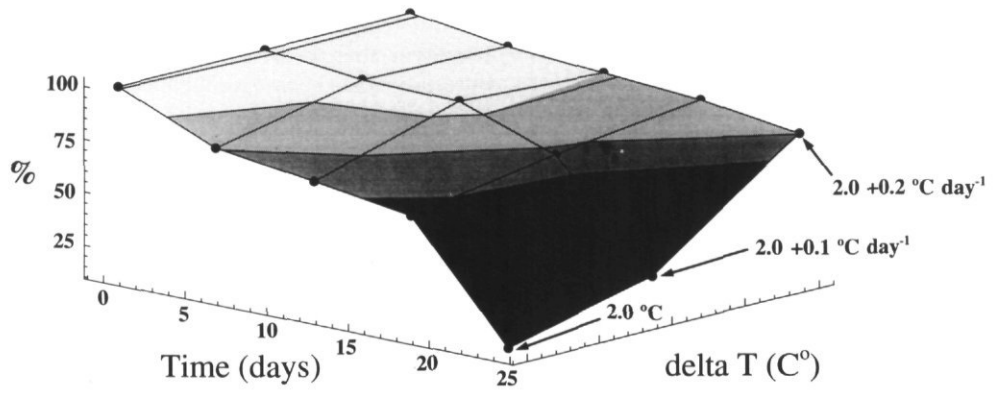


Figure 4. *Calanus finmarchicus*. Relative changes in population abundance at three temperature series during a period of 24 days. Modified from Pedersen and Tande (1992).

1989 (Pedersen and Tande, 1992). The overwintering temperature, which female *C. finmarchicus* experienced, differed markedly between 1980 and 1989. Possibly different overwintering temperatures experienced by adults could shift the temperature tolerance of the offspring. Possible other reasons for this have been discussed in Pedersen and Tande (1992).

Mortality in pandalid larvae

Since the above data indicated that the thermal history of both the maternal stock and the progeny could impose differences in mortality among marine larvae, we had to consider this in further work. This type of information is in general difficult to obtain for holoplanktonic forms, and we therefore chose to continue working on the larval stages of the northern shrimp *P. borealis*. This species is found in boreal waters in the North Atlantic Ocean and in the Barents Sea (Shumway *et al.*, 1985). In some areas, it co-occurs with *C. finmarchicus*, but, as a semibenthic species, should be more confined to specific thermal ranges and therefore have a more traceable thermal history.

We chose to test the effect of constant and continuously increasing temperature on survival of larvae of *P. borealis*. The field collection of females and the experimental procedure are detailed in Rasmussen and Tande (*in subm.*). Based on experience from a long term and an ongoing monitoring of *P. borealis*, two spawning areas, in Balsfjorden and Malangen, respectively, were selected as sites for obtaining egg bearing females for the larval experiments.

The temperature conditions at 20–50 m in the two regions in 1991 were used as the basis for designing the temperature conditions for the larvae (Fig. 2). Basically, the females were kept at *in situ* temperatures recorded from the bottom at the two sites, from the time of sampling in January until hatching at the end of March. Then, newly hatched larvae were kept individually in glass containers at superabundant food concentrations, and held in programmable temperature control baths for 60 days. From the Balsfjorden stock, two series of each 200 larvae were transferred to 2.5°C, then one was held at 2.5°C and the other warmed at 0.04°C d^{-1}. From the Malangen stock, two series of each 200 larvae were transferred to 4.3°C, where one was held while the other was warmed at 0.03°C d^{-1}. The rate of temperature increase was designed to cover the observed increase in surface waters in Balsfjorden and Malangen in April and May.

The mortality was highest at constant temperatures (Fig. 5), more severe at the lower temperature in Balsfjorden than in Malangen. Both series, provided a temperature increase, had lower mortality than the other two. Based on the present data, the rate of temperature increase tend to have a stronger positive influence on survival than does the particular developmental temperature (i.e. Malangen constant vs Balsfjorden increasing). Given two sites with different overwintering temperatures, as in Balsfjorden and Malangen, survival rates in larvae of *P. borealis* are likely to be enhanced when exposed to low initial temperature and a slightly elevated rate of temperature increase.

The experiments reported for *C. finmarchicus* and *P. borealis* demonstrate that a thermal increase enhanced survival of copepodites and zoea larvae at low and intermediate temperature ranges in boreal waters. We call this Thermal Increase Enhancement (TIE) for marine larvae. In light of the TIE, we contend that our perception of how temperature affects larval survival has basically been wrong.

We have highlighted a possible link between temperature and crustacean larval mortality in the laboratory. Therefore we decided to undertake an explanatory study of how and to what extent this mechanism can

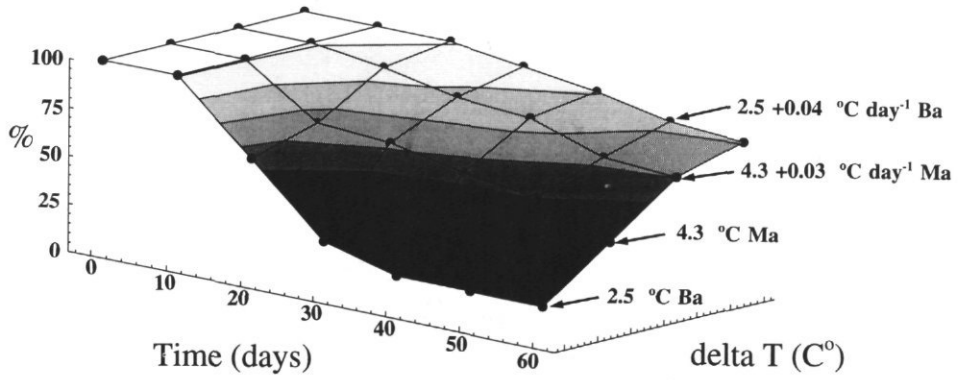


Figure 5. *Pandalus borealis*. Relative changes in larval population abundance at four temperature series during a period of 60 days. Modified from Rasmussen and Tande (submitted).

explain observed fluctuations in population abundance of northern shrimp in one well defined location. So, we ask the following question:

Do natural populations respond to change in habitat temperature?

To our knowledge, the best long term data on northern shrimp are from the Gulf of Maine. A resource management program including the biology and ecology of this species was undertaken in 1966 (Dow, 1981a). Some of the results have been made available by Schumway *et al.* (1985) and Apollonio *et al.* (1986), which form the basis for the following outline.

The Gulf of Maine is the southern limit of the northern shrimp in the Northwest Atlantic. Records of sea water temperature, c.p.u.e. and landings of *P. borealis* are available from 1962 to 1977 (Apollonio *et al.*, 1986). A rapid increase in population size (as inferred from c.p.u.e. data) from 1964 culminated in 1971 (Fig. 6). Although delayed by approximately three years, the same pattern was seen in the recorded landings. This coincided with a decrease in sea water temperature lasting from late in the 1950s and ending in 1969. The trend in the sea water temperature was then reversed, but the relation of these three variables after 1969 is not quite so clear. Apollonio *et al.* (1986) contend that both fishing pressure and temperature changes may have affected population size. The importance of temperature as a strong regulator of population abundance has already been shown by earlier studies on *P. borealis* in the Gulf of Maine (Dow, 1981a). Near extinction of the fishery during warm periods, underlines that the species is at its most southern range of distribution, so that its success is likely governed by temperature rather than by any biological factor (Dow, 1981b).

How is the relationship between variability in population size and temperature explained for the Gulf of Maine? Apollonio *et al.* (1986) state: "As a working hypothesis, we propose that the mechanism controlling long-term variations in fecundity and, perhaps, changes in population size, is water temperature, or, more specifically, the magnitude of the temperature differences encountered by maturing female shrimp during diurnal vertical migration." The most weight should be given to fecundity and factors which maximise egg production.

Firstly, the fecundity was found to vary inversely with temperature in the Gulf of Maine, and this has also been supported by experimental results on shrimp from Alaskan waters (Nunes, 1984). Secondly, it has been shown

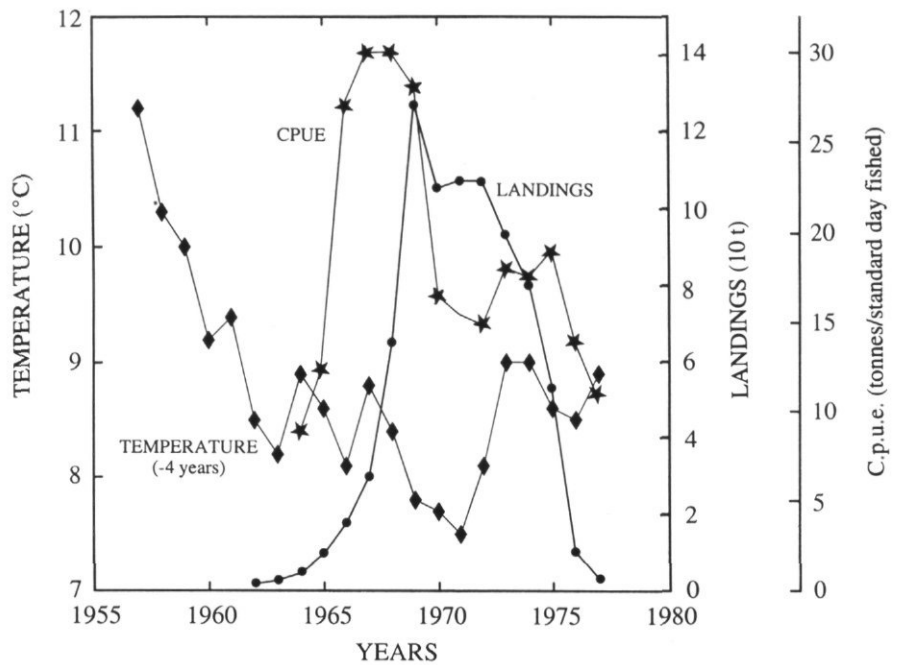


Figure 6. Mean annual sea-surface temperatures (lagged 4 years) at Boothbay Harbor, Maine, total catch and catch-per-unit-effort (c.p.u.e.) data estimated from commercial landings of 34–50 GT vessels in Gloucester and Portland for which shrimp accounted for 50% or more of the catch (after Apollonio *et al.*, 1986). The temperature was lagged by 4 years in order to match the ambient temperature with the spawning of the mature 4-year-old female year class.

that *P. borealis* in the Gulf of Maine tend to segregate into separate areas according to age: larvae and juveniles are mostly found inshore, separating them from the adults further offshore (Scattergood, 1952, Apollonio and Dunton, 1969; Shumway *et al.*, 1985; Apollonio *et al.*, 1986). Inshore female migrations during autumn and early winter are likely to bring the egg bearing females to lower habitat temperatures, and will also ensure that the embryos are kept at low temperature until hatching. This ontogenic, horizontal, inshore–offshore migration pattern has been observed off Norway (Wollebæk, 1908; Hjort and Ruud, 1938), and off West Greenland (Hornsted and Smidt, 1956).

Detailed information on possible long term trends in the timing, progression and variations in productivity of phytoplankton and zooplankton are not available from the Gulf of Maine. Neither data on larval abundances of *P. borealis*. Therefore, we cannot assess the possible effects from biological factors on potential variation of food conditions on the recruitment of shrimp to the juvenile stock. The general circulation pattern, long term temperature data, population abundance fluctuations, together with laboratory derived mortality schedules from north Norwegian fjords, allow us to be more specific in spelling out possible links between climate and recruitment mechanisms of *P. borealis* in the Gulf of Maine.

In the winter, a vertically homogenous water column is found inshore in the Gulf of Maine (Townsend *et al.*, 1992) with temperatures varying from 1.5 to 3°C (Apollonio *et al.*, 1986). There is a tendency to find the largest interannual differences in water temperature near the bottom (Colton, 1968). Temperature increases in surface waters from February and March at rates of 0.02 and 0.06°C in cold and warm periods, respectively (Colton, 1968, his Fig. 4). This is comparable to the temperature increase found from April to May in north Norwegian fjords, and simulated in laboratory experiments. During April and May surface waters in the Gulf of Maine heat up at a much higher rate compared to north Norwegian waters (0.083 and 0.13°C). This thermal increase did not differ between the warm period from 1955–60 and the cold period from 1961–66 in the Gulf of Maine (see Colton, 1968).

If *P. borealis* consistently seeks a decrease in the temperature during the egg bearing period, it must have evolved as a consequence of strong selective forces for increased fecundity and larval survival. Data in Appollonio *et al.* (1986) showed that decreasing temperature favoured survival of embryos due to reduced infestation of parasites and bacteria during the incubation period. Experimentally derived results fit well into the inshore migrations of berried females prior to spawning. Larvae of *P. borealis* from Alaskan waters, when raised on satiating diet, were shown to survive better at 9°C, than at 3 or 6°C. But offspring from females kept at low temperatures survived better at lower temperatures during later larval rearing (Nunes, 1984). Thus, a decline in the temperature during egg development tends also to favour an upward shift in subsequent survival of larvae developing at low temperatures.

Larval hatching – transition to different temperature conditions

In order to clarify the different thermal conditions which *P. borealis* larvae are likely to meet when hatching, we have reformulated a diagram developed by Schumway *et al.* (1985) from Gulf of Maine. Three different thermal scenarios for newly hatched and developing larvae are suggested to prevail throughout its area of distribution (Fig. 7). The first situation, will be where cold deep (bottom) water is overlain by warmer intermediate or surface water masses. Here, larvae will be introduced to an abrupt increase in temperature. The condition is likely to occur later in the spring and late-hatched larvae are likely to be exposed to quick warming on ascent.

Hatching larvae could also experience a decrease in temperature, leaving a warm near-bottom layer and enter a cold surface one. That situation could be found in several fjords in north Norway, winter cooling of surface layers and convection is too weak to establish a vertically homogenous temperature down to the bottom. This condition prevails in fjords in Norway which is highly influenced of oceanic conditions as seen in Malangen (cf. Fig. 2). In Polar Front areas in the Barents Sea, even larger temperature differences between Atlantic bottom

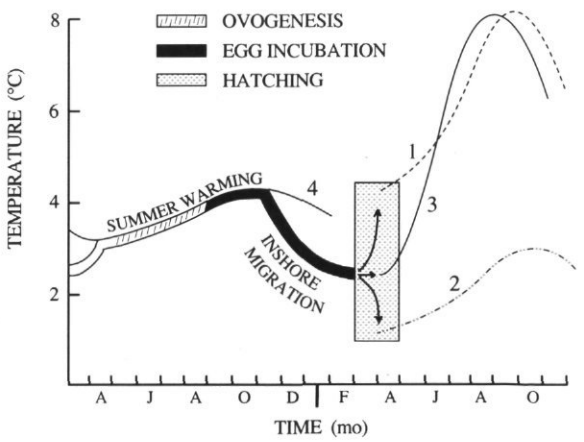


Figure 7. *Pandalus borealis*. Diagram showing the temperature conditions which ovigerous females and larval are subjected to in boreal waters (redrawn from Shumway *et al.*, 1985). Symbols: 1–3 represent different thermal scenarios for newly hatched and developing larvae; 4 is a generalized temperature curve representative of ovigerous females.

water and overlying Arctic surface waters during spring and early summer are found (Loeng, 1991). Areas like these are known as productive grounds for deep-water prawn, but we do not know to what extent the larvae liberated into these surface water masses are recruited to the same stocks.

The third situation occurs where the water column is homogenous down to the bottom, which often occurs in more hydrographically isolated fjords as Balsfjorden. Substantial areas in the Atlantic part of the Barents Sea and some fjords around Svalbard would also fit into this winter–spring thermal condition (Loeng, 1991; Støle-Hansen and Slagstad, 1991). In hatch scenarios one and three, the timing of larval hatching relative to the spring warm-up of surface water determines the survival rates of crustacean larvae. The temperature in surface waters is likely to show a high, but variable rate of temperature increase during the period when the larvae are subjected to surface waters. Inshore waters in the Gulf of Maine are likely to fall into the third category (Colton, 1968; Apollonio *et al.*, 1986).

The temperature dependent mortality in northern shrimp is predicted to be very different in the three above described hatching scenarios. The laboratory results on larvae do indicate that the mortality rate is lowered then the temperature is gradually increased as opposed to constant temperatures during the larval period. The instantaneous mortality rate (m) could be considered a function of three variables

$$m = f(T_a, \Delta T, T)$$

where T_a is temperature at which the progeny is acclimated prior to hatching, ΔT is the rate of temperature increase and T is the actual temperature at hatching. Given that there is no effect on m from temperature acclimation, within the temperature range normally experienced by the species, T_a could be neglected. Mortality will then depend on only two variables.

Is this relevant to larval cod?

It is our contention that mortality rates obtained during limited time periods at several constant temperatures are a pitfall for understanding how the temperature influences larval mortality during spring and early summer. The impact of sea climate on larval mortality is more precisely described when the relationship between mortality and temperature is established in a continuously changing temperature regime. It is premature, on the other hand, to assess how acclimation to various temperatures, prior to hatching, might interact or modify the effect of TIE on larval survival in northern shrimp. The Thermal Increase Enhancement demonstrated in *C. finmarchicus* might ultimately modify the prey availability for fish larvae and juveniles given a low temperature increase during the spring and early summer.

The apparent failures of linking, for instance recruitment and climate in fish populations, might be that a definite understanding of the underlying mechanisms have not been established. Promising results (Frank and Leggett, 1982; Johannesen and Tveite, 1989) have recently reinforced arguments for studying larval mortality and recruitment problems on more confined local scales (Pepin, 1992).

If cod larvae have the same mortality pattern as shown for the above two crustacean species, remains so far unanswered. But Nilssen *et al.* (1993) found a high degree of similarity in pattern between temperature along the Kola meridian and recruitment of 0-group cod to the stock in the Barents Sea. Recruitment pulses of strong year classes tended to coincide either with temperature peaks or with increasing temperatures. Poor year classes tend to coincide with decreasing or low temperatures (cf. Nilssen *et al.*, 1993, Fig. 1). The Thermal Increase Enhancement could also operate in cod, and might be included as an important underlaying mechanism for understanding how the sea climate adds to recruitment variability in cod stocks.

Acknowledgment

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Vertebrae numbers as an indicator for the recruitment mechanism of coastal cod of northern Norway

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Løken, S., Pedersen, T., and Berg, E. 1994. Vertebrae numbers as an indicator for the recruitment mechanism of coastal cod of northern Norway. – ICES mar. Sci. Symp., 198: 510–519.

Cod (*Gadus morhua* L.) in northern Norway are divided into two main groups (coastal cod and Northeast Arctic cod), but both groups are managed as a single stock. The coastal cod inhabit coastal and fjord regions and differ from Northeast Arctic cod with respect to growth pattern, age and size at maturity, and migration and spawning areas. Cod from the coastal and Northeast Arctic groups have been distinguished on the basis of meristic characters (average number of vertebrae), otolith type, and habitat selection during different life stages. We investigated whether the coastal cod are self-recruiting, or whether this group also contains vagrants from the larger group of Northeast Arctic cod. Cod juveniles in coastal areas segregate vertically during the settling process, and the juveniles that settle in shallow-water sites have morphometric characteristics similar to those of adult coastal cod. The effects of topography and depth that influence separation are discussed. It is concluded that coastal and Northeast Arctic cod recruits have different early life histories.

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Introduction

Cod (*Gadus morhua* L.) in northern Norway are divided into two main groups: Northeast Arctic cod (NA) and coastal cod (CC) (Rollefsen, 1934, 1954). CC inhabit coastal and fjord areas and undertake only short-range migrations. The larger NA stock, however, migrates from the feeding areas in the Barents Sea and near Svalbard to spawning areas along the Norwegian coast (Hylen, 1964a, b; Godø, 1986; Jakobsen, 1987; Bergstad *et al.*, 1987). CC spawn in several fjords along the coast (Rollefsen, 1954; Jakobsen, 1987), and large numbers of them spawn in the most important NA spawning area in Lofoten–Vestfjorden (Hylen, 1964a). The larval and juvenile drift from the NA spawning grounds on the Norwegian coast towards the NA juvenile habitat in the Barents Sea and near Svalbard have been well described (Sundby *et al.*, 1989). In contrast, there is very little information on larval and juvenile drift from the CC spawning in fjords and it is uncertain whether the CC group is mainly self-recruited or recruited by vagrants from the NA spawning. The separation of cod into CC and NA is based on differences in the sizes and shapes of otolith zones (Rollefsen, 1934), which are influenced by environmental factors (Godø and Moksness, 1987). The CC also differ from NA with respect to growth pattern and age and size at sexual maturity (Rollefsen, 1934, 1954; Hylen, 1964a). Jakobsen (1987) points out that the crucial question of whether CC and NA should be regarded as separate stocks is dependent upon "whether fry from some of the main spawning grounds of Northeast Arctic cod drift to nursery areas on the coast or in the fjords and acquire the characteristics of coastal cod from the environment". In order to identify whether vagrant juveniles originating from NA spawning areas inhabit the CC habitat in fjords and along the coast, an identifying marker for NA juveniles is needed.

Meristic characters have frequently been used in investigations of the structure of cod stocks in the western Atlantic (Templeman, 1981, 1983; Lear *et al.*, 1981; Lear and Wells, 1984). Vertebrae number in fish is fixed during the early part of the embryonic period (Fahy, 1976), and differences in the average number of vertebrae (AV) between the groups of cod have been attributed to differences in temperature during the embryonic period (Dannevig, 1947; Brander, 1979; Lear *et al.*, 1981). In support of this, Brander (1979) found a negative correlation between field data on temperature during the spawning period and AV in cod stocks.

Investigations carried out in northern Norway during

the 1920s and 1930s indicate that NA cod have higher AV than CC (Schmidt, 1930; Rollefsen, 1934, 1954). The biological significance of the differences in AV found in adult NA and CC are uncertain. The aim of this study is to investigate whether AV could be used as a natural mark to trace cod juveniles settling to the bottom in the CC habitat. After settlement, the group identity (CC or NA) could be determined by the otolith structure. Vertebrae numbers were measured to assess the variability in vertebral numbers of CC and NA in their feeding and spawning areas.

Materials and methods

Spawning cod were collected on the spawning grounds in Lofoten and Malangen in March and April during the years 1991–1993 (Fig. 1). Cod were fished with a pelagic trawl at a depth of 70 m in Lofoten, and using a bottom trawl in Malangen.

Pelagic juveniles collected from the Norwegian coast and Barents Sea during July and August/September in 1991–1992 were obtained from the Institute of Marine Research, Bergen. Juveniles were also collected at these times at locations along the coast and in the fjords of Troms and Finnmark. All pelagic cod were taken in pelagic trawls at 0 to 60 m depth, in hauls lasting one half to one hour.

Bottom-settled cod juveniles were caught in Malangen, Sørfjorden, and other localities around Tromsø in September and October 1992 (Fig. 1). Bottom trawling was used to obtain samples from deep water (>55 m), and beach seining was employed in shallow water (0–6 m). Cod juveniles collected by beach seine in Finnmark during 1992 were obtained from Finnmarksforskning, Hammerfest, and six samples taken by Danish seine on the coast of Finnmark in 1990 were provided by the Institute of Marine Research in Bergen.

Young cod (age 1+) were sampled from various locations ranging from the inner parts of fjords to the outer coast of Nordland, Troms, and Finnmark in 1991–1993 (Fig. 1). Samples were taken with bottom trawling, and with Danish seine, at various depths.

In the laboratory, fish length, weight, and sex were recorded and then flesh was cleaned off the bones to facilitate counting the number of vertebrae. 0-group cod were examined under a binocular microscope. All vertebral counts include the urostylar half-vertebrae. Otoliths were used for age determination and for characterizing the fish as either coastal cod or Northeast Arctic cod based on the growth pattern criteria described by Rollefsen (1933, 1934). If available, 30 fish were analysed in each sample of 0-group fish.

Analysis of variance (ANOVA) was used to test for effects of group identity, year class, and year of sampling on vertebrae number for cod sampled on the spawning

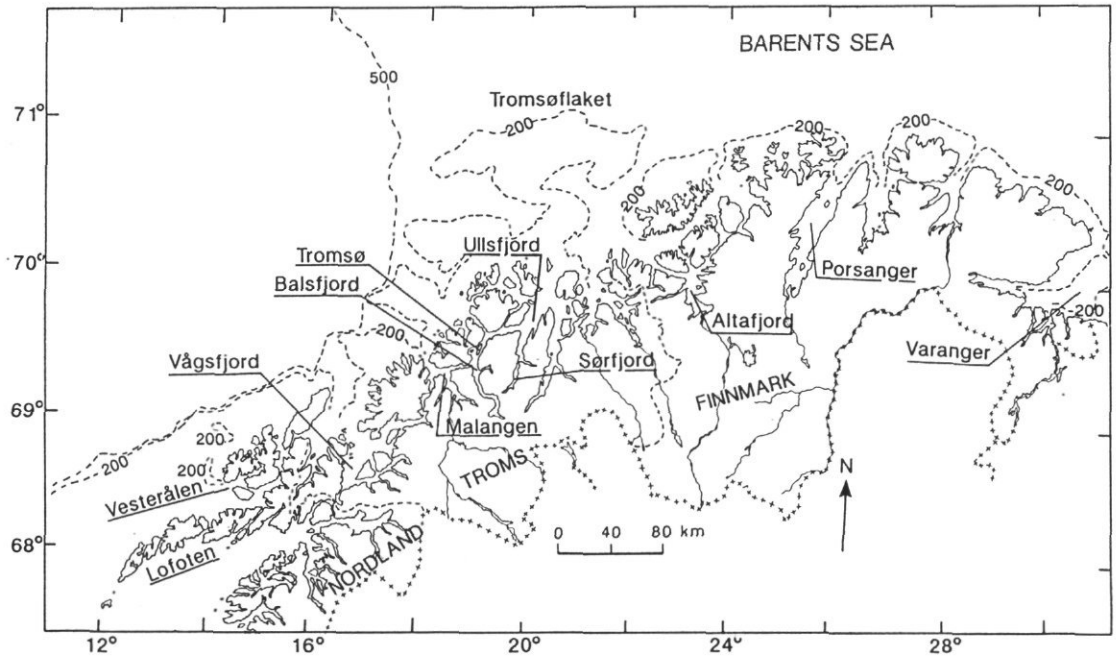


Figure 1. Overview of the area sampled.

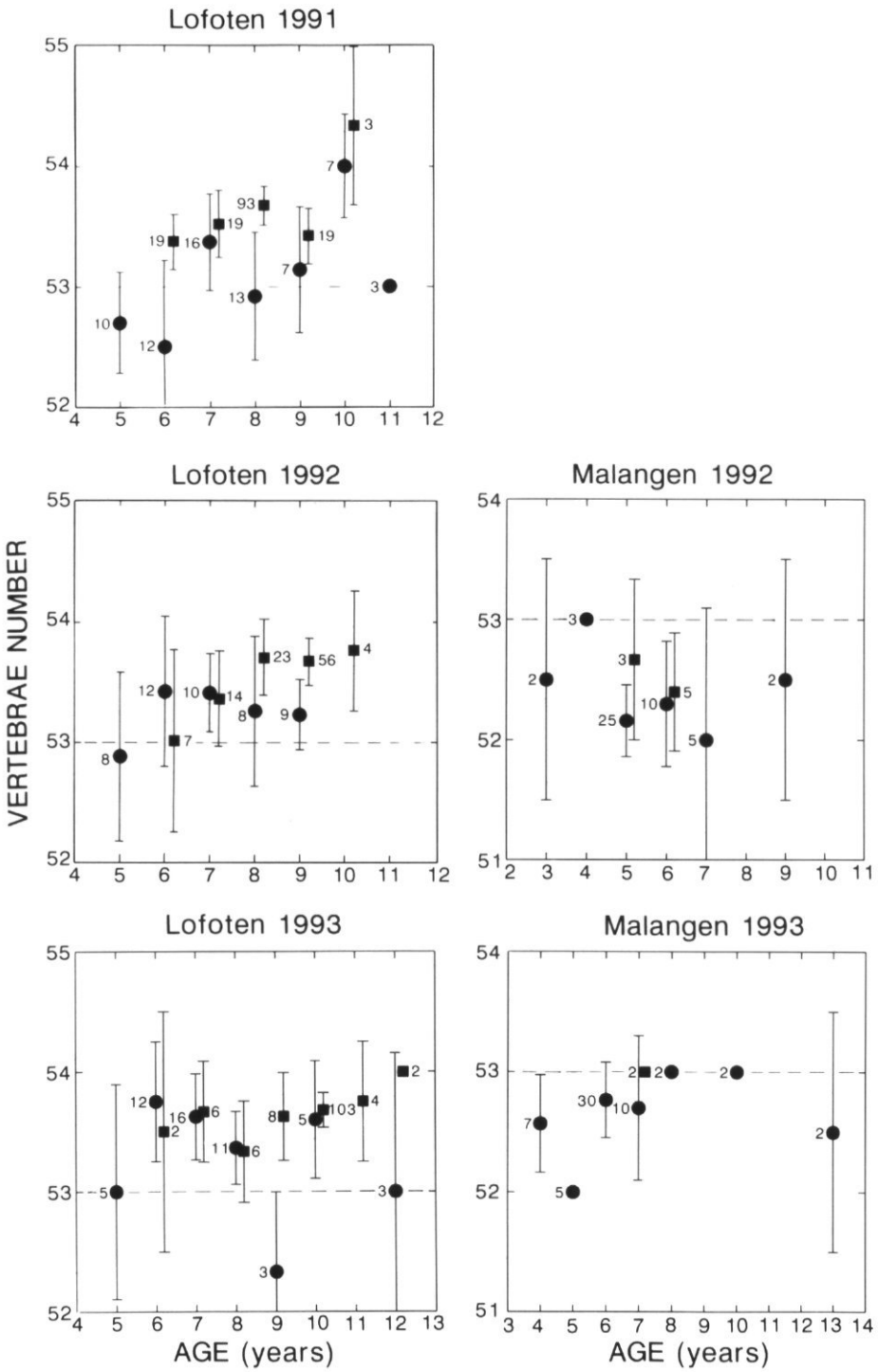


Figure 2. Comparison of number of vertebrae (average vertebrae number AV ± 2 × SE(AV)) in different year classes of coastal cod (CC) (circles) and Northeast Arctic cod (NA) (squares) sampled on the spawning grounds in Lofoten 1991–1993 and Malangen 1992–1993. Sample sizes are given.

grounds. Because of the unbalanced data set it was necessary to restrict the ANOVA to year classes that were present in all sampling years. A probability level of 5% was taken as indicating statistical significance. All statistical tests were performed using SYSTAT (Wilkinson, 1990).

Results

Cod sampled on the spawning grounds

In cod sampled on the spawning grounds in Lofoten and Malangen, there was no statistical significant difference in vertebrae number between female and male fish for either NA or CC (ANOVA).

ANOVA on the material from Lofoten was restricted to the year classes 1983, 1984, and 1985. The ANOVA revealed that there was a highly significant effect of group identity ($p < 0.001$), a just significant effect of year class ($p = 0.044$), but no significant effect of sampling year in the material from Lofoten (Table 1). To investigate whether vertebrae number differed between spawning locality, years of sampling, and year classes, an ANOVA was performed on the CC year classes 1987 and 1988 sampled in Malangen and Lofoten. This analysis was restricted to CC because in the samples from Malangen in 1992 and 1993, 83 and 95% of the cod were characterized as CC. The ANOVA revealed a significant effect of sampling year ($p = 0.008$) (cod sampled in 1992 had lower value than those sampled in 1993), and sampling locality ($p < 0.001$) (CC sampled in Malangen had lower vertebrae counts than those sampled in Lofoten) (Table 2, Fig. 2).

Pelagic and bottom settled 0-group juveniles

The juveniles that drifted towards the Barents Sea and Svalbard area had relatively homogeneous AV values both in 1991 and 1992, compared with the cod juveniles sampled in the fjords and coastal areas (Fig. 3A and 3B).

Table 1. Analysis of variance testing the effects of year class (1983–1985), group identity (CC or NA), and sampling year (1991, 1992, and 1993) on vertebrae number in cod sampled on the spawning grounds in Lofoten. SS = sum of squares, DF = degrees of freedom, MS = mean square, F = Fisher ratio, p = significance level, n = 429.

Source	SS	DF	MS	F	p
Year class	3.513	2	1.757	3.138	0.044
Group identity	10.768	1	10.768	19.235	<0.001
Sampling year	0.732	2	0.366	0.654	0.521
Error	236.813	423	0.560		

Table 2. Analysis of variance testing the effects of year class (1986–1987), sampling year (1992 and 1993) and sampling locality on vertebrae number in coastal cod (CC) sampled at the spawning grounds in Lofoten and Malangen. SS = sum of squares, DF = degrees of freedom, MS = mean square, F = Fisher ratio, p = significance level, n = 103.

Source	SS	DF	MS	F	p
Year class	0.002	1	0.002	0.003	0.959
Sampling year	5.938	1	5.938	7.419	0.008
Sampling locality	20.512	1	20.512	25.629	<0.001
Error	79.234	99	0.701		

The cod juveniles sampled along the coast of Finnmark in 1990 at depths of 15–30 m had AV values ranging from 52.6 to 53.0. Samples of settled cod juveniles that were taken at intermediate water depths (26–110 m) in autumn 1991 had AV values ranging from 52.9 to 53.3. These values increased with increasing depth.

Cod taken in northern Norwegian fjords showed consistent variations between the AV seen in different sampling gears (Fig. 4). Cod taken in beach seine samples in shallow water in 1992 had consistently lower AV than those caught by bottom trawling in deeper water (Fig. 4). In Sørfjorden, the AV of pelagic juveniles in July was intermediate between that of bottom-settled juveniles sampled in the sublittoral by beach seine, and the AV of juveniles sampled by bottom trawling in deep water during August–September at depths greater than 60 m (Fig. 4).

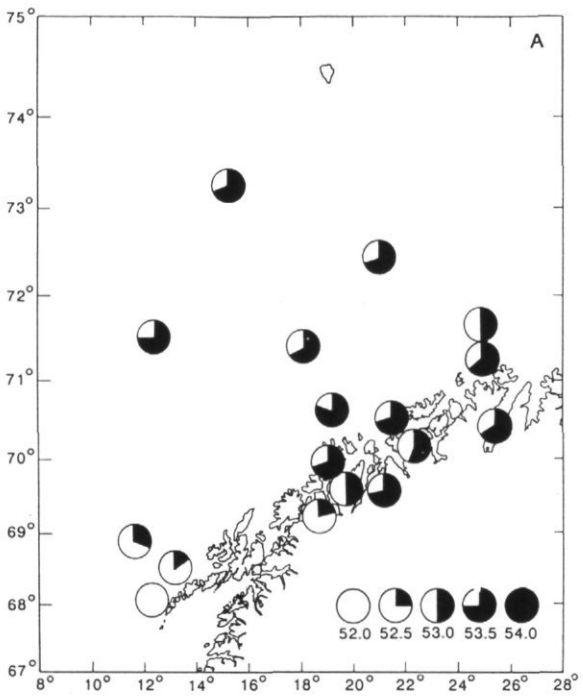
Cod (age 1+) on the feeding grounds

In most samples taken in various areas and depths, AV was below 53.0 (Fig. 5). In Malangen, Altafjord, and in samples taken along a depth gradient from the Finnmark coast to the Barents Sea, there was a positive trend between AV and depth (Fig. 5).

Discussion

Our results for AV of CC and NA are similar to those reported earlier for cod in northern Norway (Schmidt, 1930; Rollefsen, 1934, 1954), indicating a relative stability in the observed AV values in CC and NA over a long time period. The AV values found in CC in northern Norway are similar to or slightly higher than those of cod in western and mid-Norway (Schmidt, 1930).

The differences in vertebrae number between spawning CC and NA caught in Lofoten and between spawning CC caught in Lofoten and Malangen (Fig. 2, Tables 1 and 2) suggest that the fish may have had a different prehistory. NA in Lofoten had higher vertebrae num-



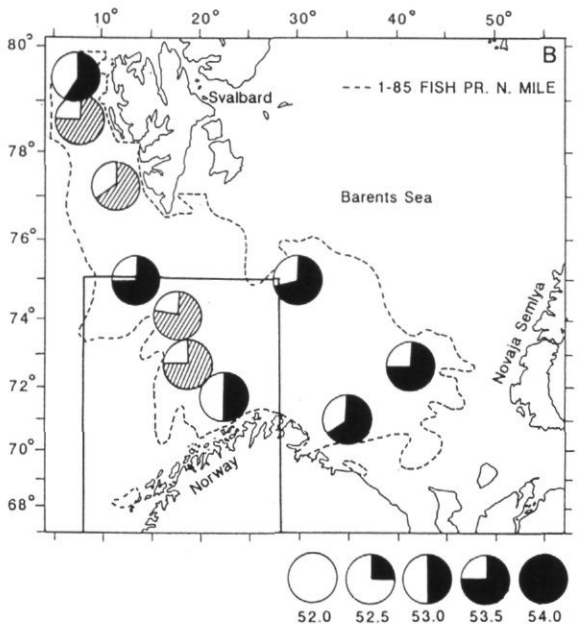


Figure 3. Horizontal distribution of average number of vertebrae (AV) in samples of pelagic juveniles in 1991 and 1992: (A) juveniles sampled in June–July, (B) juveniles sampled in August–September. The main concentration of pelagic juveniles in August–September 1991 is indicated by a stippled line (ICES, 1991). Samples taken in 1992 are hatched.

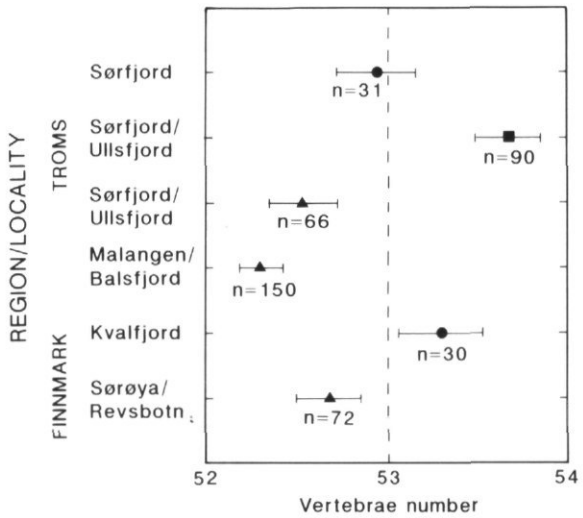


Figure 4. Vertebrae numbers (average number of vertebrae (AV) ± 2 × SE(AV)) of pelagic juveniles caught in July 1992 (circles), bottom-settled juveniles caught by beach seine in shallow water (triangles), and juveniles caught by bottom trawl in deep water (squares).

bers than CC caught in Lofoten, and CC in Malangen had lower values than CC in Lofoten. It is known that exposure to low temperatures during embryonic development induces high vertebrae numbers (Brander, 1979; Løken and Pedersen, unpubl.). However, water temperatures at the CC spawning grounds in fjords tend to be lower in April than those recorded on the NA spawning grounds (Sundby and Bratland, 1987). The data that exist on the timing of spawning by CC in fjords indicate that the CC spawn during the same time period (March–April) as cod in Lofoten (Skreslet and Danes, 1978; Falk-Pedersen, 1982; Kjørsvik *et al.*, 1984). Since low temperatures during egg development induce high vertebrae numbers, it could be expected that CC would have higher AV than NA, if the juveniles that recruit to the CC group are mainly a result of CC spawning in the fjords in March–April. Contrary to this expectation, the lowest AV values were found in samples of pelagic juveniles taken near the coast and in the fjords (Fig. 6), and it is unlikely that differences in water temperature during embryonic development have induced the differences in AV between CC and NA.

Some samples of pelagic juveniles in the fjords and at the coast were characteristic of NA (high AV), some were intermediate, indicating mixing, and some were characteristic of CC (low AV) (Figs. 3 and 6). NA spawn in several localities from the Møre area (ca. 63°N) in the south to Sørøya in Finnmark (ca. 70°30′N) in the north (Godø, 1986; Sundby and Bratland, 1987), and the northward drift of eggs, larvae, and small juveniles

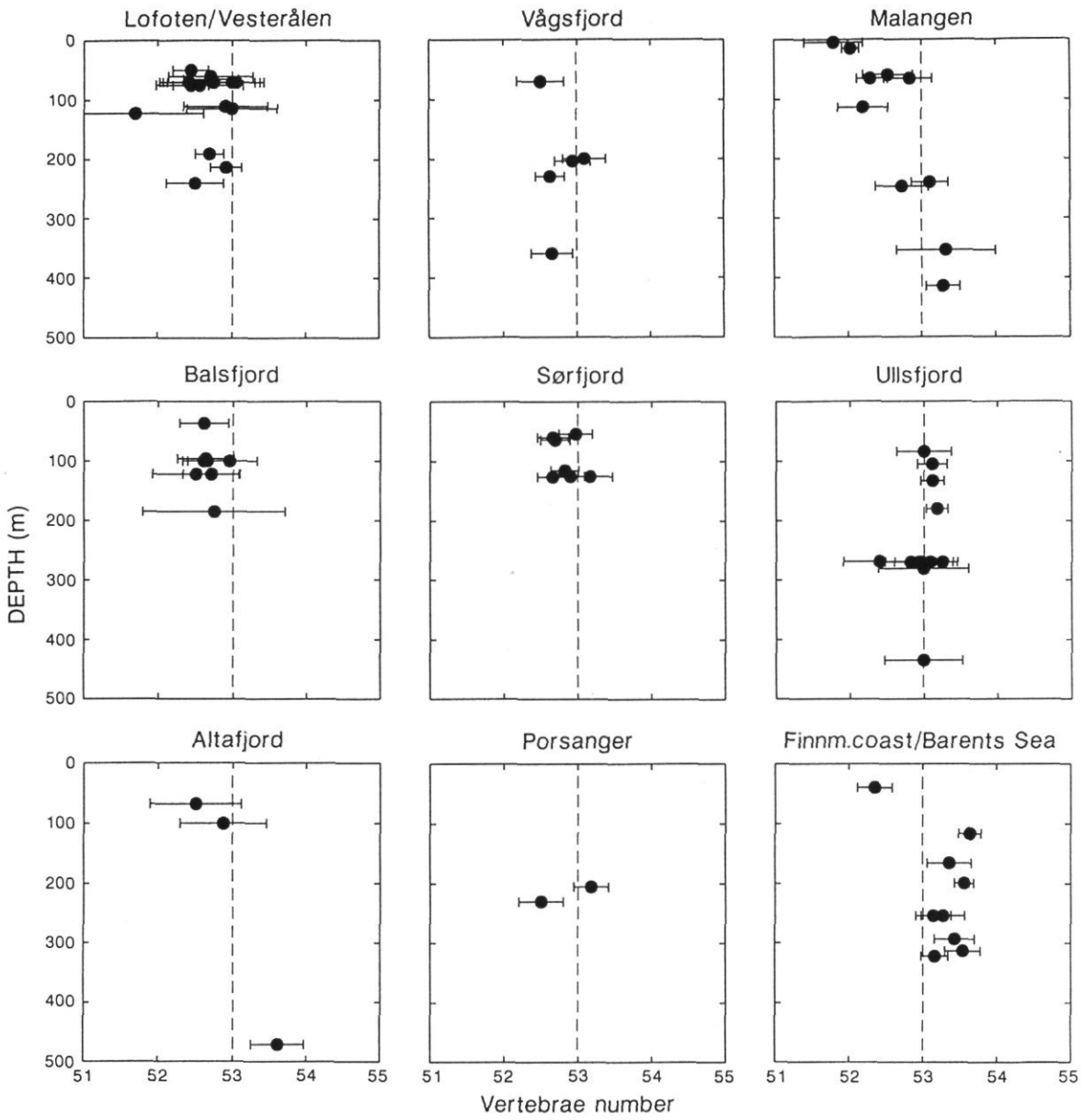


Figure 5. Distribution of average vertebrae number (AV) in age 1+ cod with increasing depth in different geographical regions (average number of vertebrae AV ± 2 × SE(AV) are shown).

covers a large area that often continues into the fjords in northern Norway (Sundby *et al.*, 1989). Eggs spawned on CC spawning grounds in the fjords may partly be advected out of the fjords during the egg stage (Skreslet and Danes, 1978), and are likely to mix with offspring from the NA spawning grounds. The difference in vertebrae numbers between mature CC caught in Lofoten and CC caught in Malangen, as well as the difference between sampling years, suggest that the CC group is a heterogeneous group with regard to vertebrae number.

AV values in samples of pelagic juveniles in July 1992 were intermediate to the low AV values for cod sampled in beach seine and the high AV recorded in samples from bottom trawling (Fig. 4). Thus, juveniles with low and high vertebrae numbers appear to segregate during the bottom settling process, probably reflecting different settling strategies in juveniles with low and high vertebrae numbers. A vertical segregation of low and high AV 0-group cod was maintained in larger cod (age 1+) in some deep fjords (Fig. 5). High AV cod were

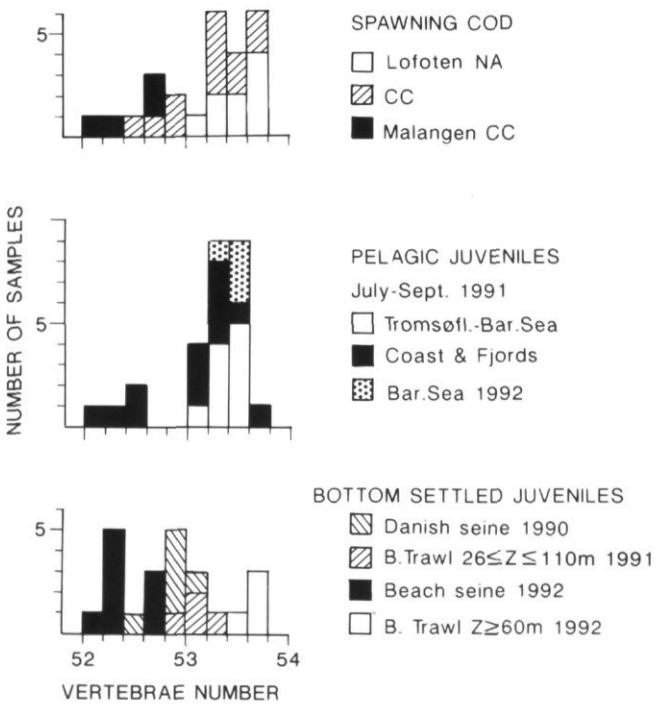


Figure 6. Overview of average number of vertebrae (AV) from samples of cod from the spawning grounds in Lofoten and Malangen, and samples of pelagic and bottom-settled 0-group juveniles. For spawning cod, each value represents a year class sampled in a particular year. For juveniles, each AV-value represents one sample. The bottom-settled juveniles were caught off the coast of Troms and Finnmark. Samples with less than 10 individuals are not included.

found deeper than ca. 300 m in some fjord areas. In these fjords, there is a gradual decrease in AV towards shallow depths, which indicates a mixture of juveniles with low and high vertebrae numbers at intermediate depths (150–300 m). The results and interpretation of AV distribution with depth and age of cod are summarized in Figures 6 and 7. In the Barents Sea, most of the area inhabited by the NA have depths between 150 and 400 m (Nakken and Raknes, 1987), while at the coast and in the fjords, cod inhabit depths between 0 and 500 m (Fig. 5).

We suggest that in the fjords and at the coast it may be advantageous (i.e. maximum fitness obtained) for an individual to settle in the sublittoral while in the Barents Sea it may be advantageous to settle far to the east and north in the Barents Sea, where the density of large potential cannibalistic cod is low (Nakken and Raknes, 1987; Mehl, 1989). In late August–early September, juveniles (ca. 4–8 cm length) in the fjords had settled at shallow depths and were caught with beach seine samples (Fig. 4), while the juveniles in the Barents Sea were still pelagic (Olsen and Soldal, 1989; Sundby *et al.*, 1989). The macroalgae belt in the sublittoral may provide hiding places for small cod juveniles (Gjøsæther, 1987a, b, 1990; Keats *et al.*, 1987), and the predation risk may be maximal at intermediate depths, where the bulk of the large cannibalistic CC live (Bax and Eliassen, 1990). Settlement at shallow depths similar to CC in northern Norway is observed in the North Sea (Riley and Parnell, 1984), off the Skagerrak coast (Tveite, 1971, 1984), and in western Norway (Godø *et al.*, 1989). This shallow water settling strategy is very different from that found in NA juveniles in the Barents Sea, but it is uncertain whether this inter-stock difference in settling strategy is due to genetic differences between stocks.

Haemoglobin allele frequencies (HbI^1) found in cod juveniles settled in deep and shallow water in northern Norway resembled HbI^1 allele frequencies in larger juveniles and adult NA and CC, respectively (Møller, 1966, 1968, 1969). Other polymorph proteins and mitochondrial DNA reveal small and, rarely, statistical differences between samples from CC and NA (Jørstad, 1984, Mork *et al.*, 1985; Jørstad and Nævdal, 1989; Johansen *et al.*, 1990; Dahle, 1991), and the scale of genetic differentiation in cod in northern Norway is disputed (Mork *et al.*, 1985). The degree to which vertebrae number, depth preference, and other life history characteristics in NA and CC are genetically

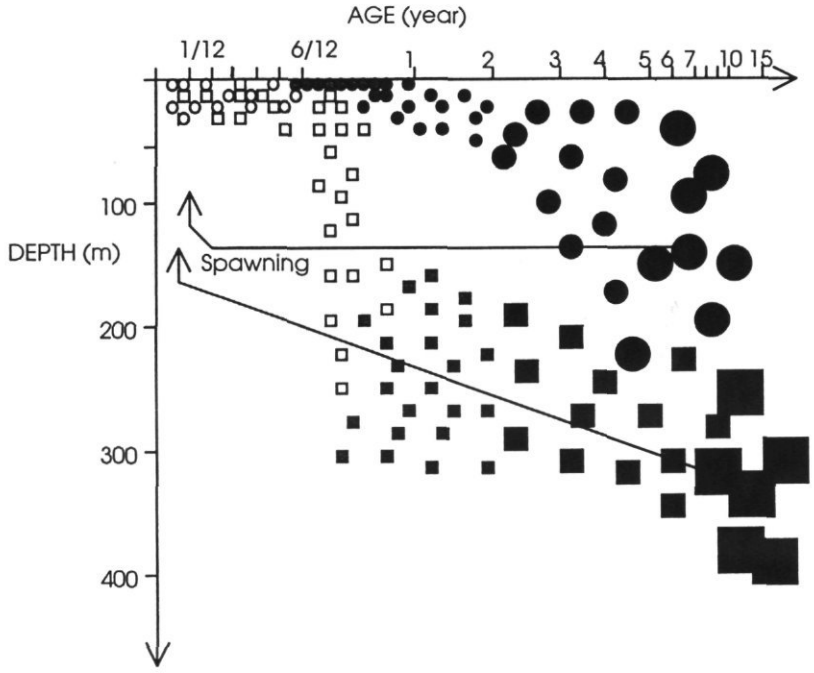


Figure 7. Conceptual model of CC recruitment mechanism. The interpreted relation between age, vertebrae number, otolith type, stock group (CC and NA), and depth distribution. ○ Coastal cod (low AV), immature; ● coastal cod (sexually mature); □ NA cod (high AV), immature; ■ NA cod (sexually mature). Unfilled symbols denote pelagic individuals. Grey-filled symbols denote bottom-settled individuals. AV = average vertebrae number.

determined is unknown. The influence of parental group on vertebrae number in offspring can be tested experimentally by comparing AV in offspring from CC and NA reared under identical environmental conditions during the embryonic period, and is the target of further studies by the authors.

Age distributions at the spawning areas in Lofoten (Hylen, 1964a) and fjords in Finnmark (Jakobsen, 1987) indicate a different mechanism in the recruitment of NA and CC. In NA, year-class strength (measured as recruits at age 3 years) is largely determined during the early pelagic phase (Sundby *et al.*, 1989). Recruitment in NA is variable and strongly influenced by climatic variability, with high temperature during spring being a prerequisite for the production of strong year classes (Sætersdal and Loeng, 1987; Ellertsen *et al.*, 1989; Nilssen *et al.*, 1994). Current data are too scarce to assess the long-term variability of CC recruitment, but the influence of climatic variability on recruitment could be expected to be different in NA and CC because of different habitats and life histories from the egg stage onwards.

It is concluded that cod recruiting to the coastal cod group in northern Norway have a different early life history than those cod recruiting to the Northeast Arctic cod group. The juvenile segregation into CC and NA appears to be due to different bottom settling strategies in juveniles recruiting to these two groups.

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Physical effects on recruitment of Faroe Plateau cod

Bogi Hansen, Eilif Gaard, and Jákup Reinert

Hansen, B., Gaard, E., and Reinert, J. 1994. Physical effects on recruitment of Faroe Plateau cod. – ICES mar. Sci. Symp., 198: 520–528.

The cod stock on the Faroe Plateau has traditionally been considered as relatively stable, with fairly constant recruitment levels. In the late 1980s this situation changed dramatically when recruitment levels dropped by one or two orders of magnitude below what appears to have been the norm during most of this century. Much of the change seems to have been due to processes operating during the first three months of the life history. Combining the available biological information on this stock with results from investigations on zooplankton and hydrography, it is argued that survival during these first months is critically dependent upon the advection of spawning products from the spawning grounds to the shallow parts of the shelf, and upon the production and advection of *Calanus finmarchicus* from the Faroe Bank Channel to the shelf. Evidence is presented that during the period of recruitment collapse spring winds were abnormally strong from the southwest, increasing the probability of the transport of cod eggs and larvae and copepods off the shelf and possibly also affecting primary production and hence production of copepod nauplii. In addition, the Faroe Plateau seems to have been less dominated by Atlantic waters with weaker copepod import and less stable advection paths as conceivable consequences.

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Introduction

The Faroe Plateau is separated from other shallow areas by depths exceeding 500 m in all directions and is dominated by Atlantic waters from the North Atlantic Current (Fig. 1a). This area supports the Faroe Plateau cod stock, which appears to be a fairly self-sustained stock unit (see Jákupsstovu and Reinert (1994) for details on stock status, biology, assessments, and fishery). Despite very high fisheries intensities during most of this century, annual landings have been fairly stable throughout most of the period, indicating that recruitment levels must have been fairly stable in the period as well. This is confirmed in Figure 2, where year-class strengths, calculated from three different data sets (Jákupsstovu and Reinert, 1994), are depicted for the period 1961–1992.

Figure 2 shows fairly stable fluctuations for most of the period, but it also shows exceptionally small year classes at the end of the period. This development has

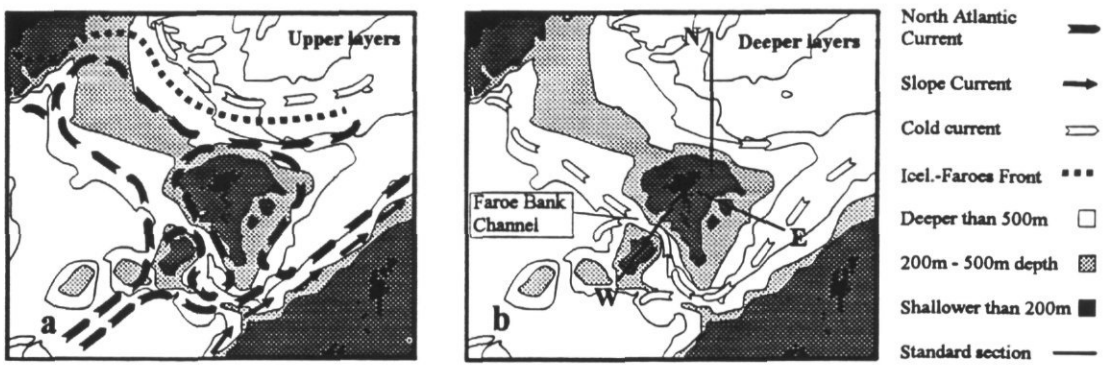


Figure 1. Bottom topography and main features of the flow field around the Faroes in the upper layers (a) and deeper than about 500 m (b). The three standard sections regularly operated by the Faroese Fisheries Laboratory are shown in (b).

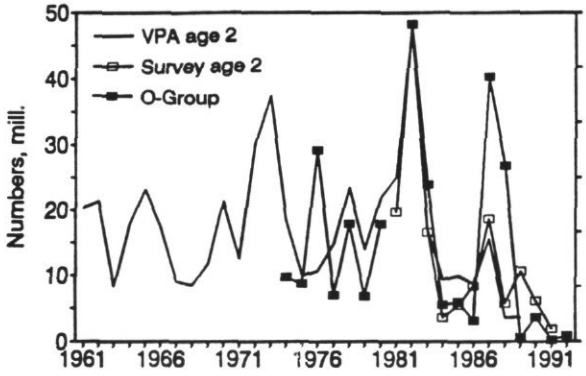


Figure 2. Estimates of year-class strength of the Faroe Plateau cod in the period 1961–1992, based on VPA, on groundfish surveys, and 0-group surveys (Jákupsstovu and Reinert, 1994). The vertical scale refers to the VPA estimates. The other two indices are in relative scales.

been so pronounced that it indicates a major change rather than random variation from the norm, and some factor or combination of factors must have caused it. These factors may be strictly biotic or they may be related to the high fisheries intensity, but a change in the abiotic environment is also likely and it is the aim of this article to explore that possibility. A more comprehensive discussion, including the effect of other factors, can be found in Jákupsstovu and Reinert (1994).

The Faroe Plateau cod spawns in the second half of March, while the 0-group index is derived from surveys carried out some 3 months after this. In Figure 2 it can be seen that despite discrepancies in occasional years, for most years there is good agreement between the 0-group index and the year-class sizes of two-year-old fish, calculated from groundfish surveys and from VPA. This indicates that processes during the first 3 months in most years determine year-class strength; we have chosen to focus on this period.

Many physical parameters may, a priori, affect cod recruitment. In other regions temperature has been considered important, but with the available data we have not been able to establish any direct links between temperature and recruitment. We have instead focused on winds and advection by currents, since these are the parameters considered most likely to influence the conditions of the cod eggs and larvae in the first 3 months.

On the shallow parts of the shelf, advection seems to be controlled largely by tidal effects (Hansen, 1992), but although the tides have variations on annual and decadal scales, an evaluation of these indicates that they are too small to explain the dramatic changes in cod recruitment. In deeper water the advection is dominated by the large-scale flow past the Faroe Plateau (Fig. 1a). Unfortunately, direct measurements of flow off the shelf are much too scarce for any indication to be derived of long-term changes. A discussion on flow variations therefore has to be based on the more indirect evidence of hydrographic parameters, especially temperature and salinity.

Material and methods

Wind data

Wind observations are often seriously biased in some way. Therefore three different data sets were originally investigated: synoptic data from two sites in the Faroe Islands (Tórshavn and Akrabyrgi) and data from a grid point due northeast of the Faroes (62°20′N 5°49′W) in the Norwegian Meteorological Institute Hindcast data set. Intercomparisons between these three series showed fairly large discrepancies between the two synoptic series and analysis indicated that relocation of the wind recorder in Tórshavn to a slightly different site in 1979 was the main reason for the difference. The Akrabyrgi and the Hindcast data compared very favourably, however, and as the Akrabyrgi series extends two years longer, this was the one used.

Four wind indices were derived from the wind observations from Akrabyrgi for the period 1962–1992: *storm frequency,* defined as the frequency of observations with windspeeds above certain values (15 m s^{-1} and 20 m s^{-1}); mean *wind energy input* to the sea, defined as mean windspeed cubed; and two components of the *wind-stress*, computed as the windspeed squared and decomposed along the east and north axes using the wind direction. All four indices were computed as averages for the period March to May during cod spawning and the planktonic stages.

Hydrographic data

The main hydrographic data set used is a collection of about 4000 CTD profiles obtained by the Faroese Fisheries Laboratory from 1976 to August 1993 (Hansen and Kristiansen, in prep.). The CTD data have been augmented by the inclusion of data from Nansen casts obtained from the ICES Oceanographic Data Centre. The salinities from these stations are of variable quality, but the constancy of the salinity in the deep water of the Norwegian Sea has been used to screen the data. Three time series were constructed from this data set.

To describe the dominance of Atlantic water off the spawning grounds we defined an index, termed the *width of Atlantic water north of the Faroes*. It was based on temperature and salinity observations from all available occupations of standard section N (Fig. 1b). For each station the vertically averaged content of Atlantic water was computed from 25 m depth down to the bottom at the shallow stations and down to 500 m depth at the

deeper ones, assuming the water to be a mixture of Atlantic water, water from the East Icelandic Current ($t = 4°C$, $s = 34.80$), and from the deep Norwegian Sea ($t = -0.5°C$, $s = 34.91$). Atlantic water was defined as the average between 25 and 100 m depth for the station on the section, which had the highest average salinity in this depth range. To exclude small cumulative errors, observations with less than 20% Atlantic water were assumed to have no Atlantic water and observations with more than 100% to have pure Atlantic water. For each occupation of the section, the width of Atlantic water was then defined as the distance (in nautical miles) from latitude 62°30′N (outer edge of shelf water) to the latitude at which the average content of Atlantic water fell below 50%.

The *Faroe Bank Channel salinity* was defined as the vertically averaged salinity of the 100–300 m depth interval for stations, located between 61°00′N and 61°30′N, 7°00′W and 9°00′W for which the bottom depth was at least 700 m and the differences between 100 and 300 m level was less than 1°C in temperature and 0.1 psu in salinity.

The *shelf water salinity* was defined as the vertically averaged salinity for stations, located between 61°30′N and 63°00′N, 5°00′W and 9°00′W excluding the fjord region between 62°01′N and 62°20′N, 6°40′W and 7°10′W, for which the bottom depth was between 50 and 100 m and the difference between uppermost and deepest level was less than 0.1°C in temperature and 0.03 psu in salinity.

Results

Variations in winds

Figure 3 shows the time history of the four wind indices defined above. It appears that since the early 1980s the frequency of winds in spring above certain speeds has increased as has the wind energy input to the sea. The windstress component towards the north shows a somewhat similar, although less dramatic, tendency, while the windstress towards the east showed exceptionally high values in 1989 to 1991.

Variations in Atlantic water dominance north of the Faroes

The time series of the width of Atlantic water north of the Faroes is shown in Figure 4. Figure 4a indicates a decrease in the width since the late 1980s. In Figures 4b and 4c the seasonal variation of the width is shown separately for the period before 1 January 1988 and after that time. The irregular timing of the older surveys makes the analysis difficult, but for the later part of the

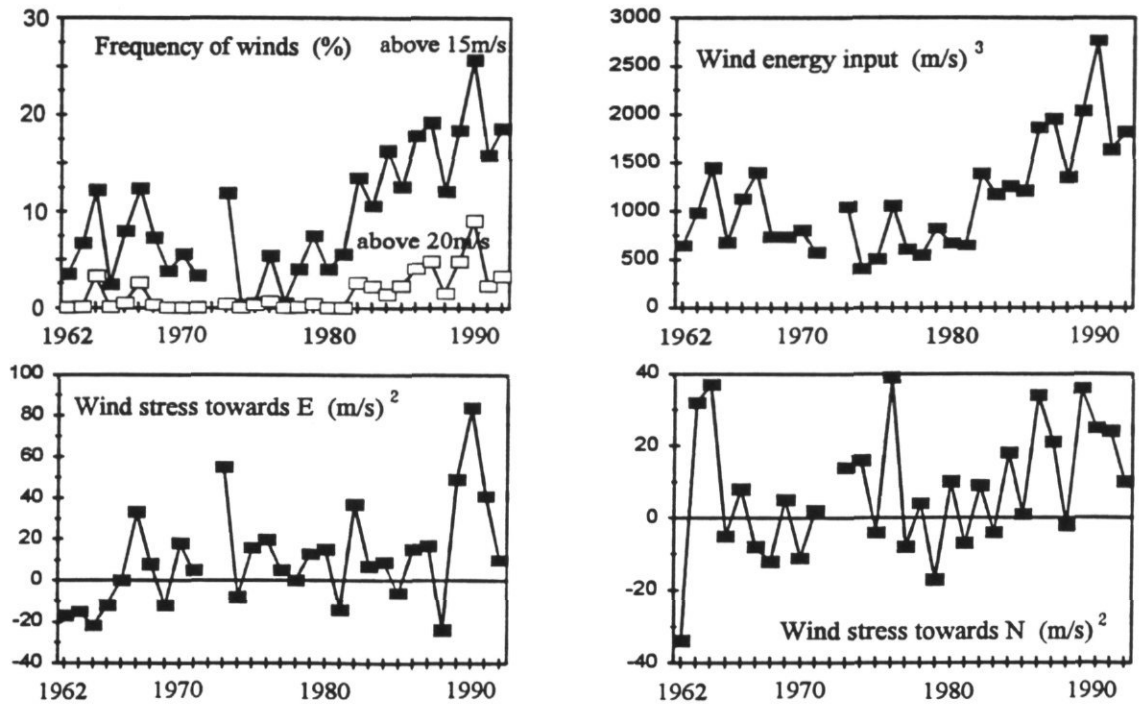


Figure 3. Time series showing four wind indices (defined in text) for the March–May period, based on synoptic meteorological observations from Akrabyrgi.

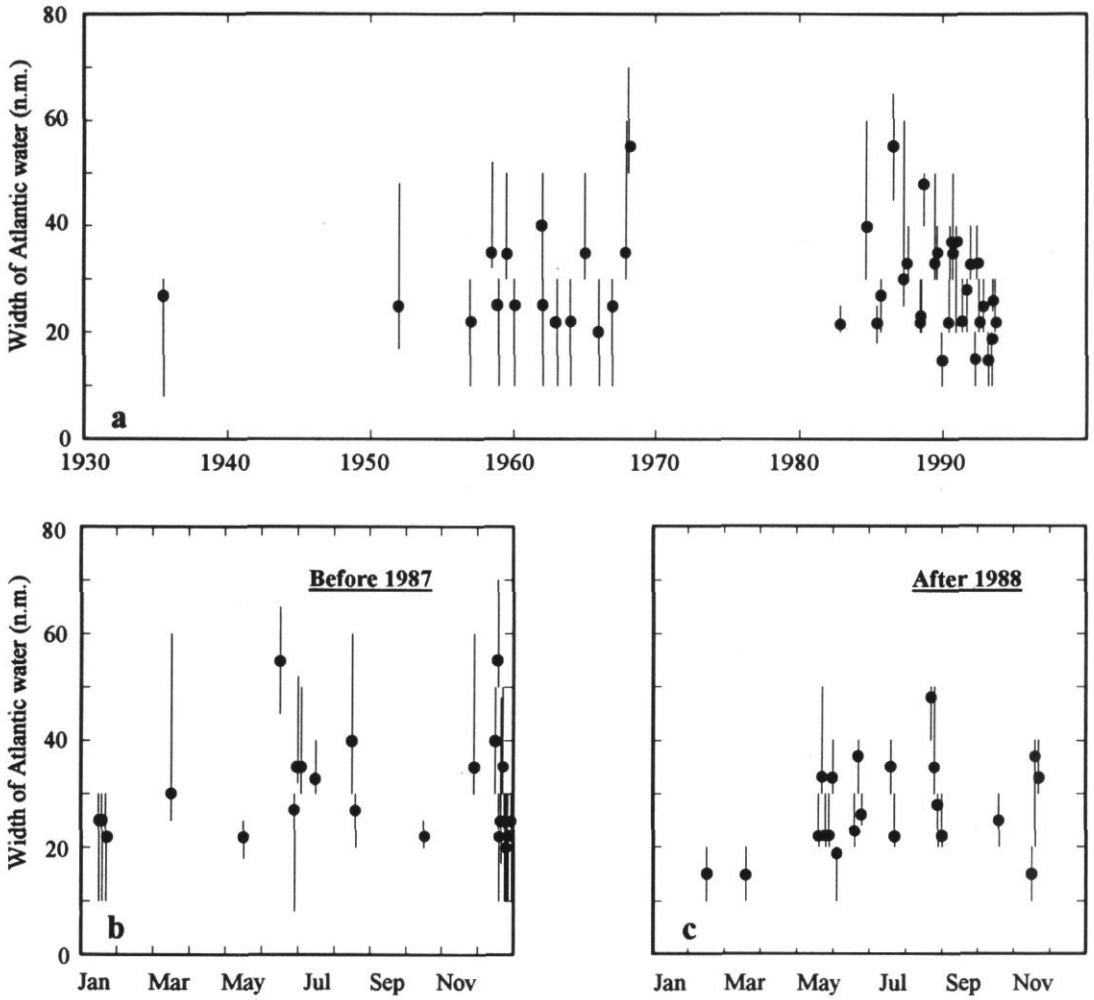


Figure 4. Width of Atlantic Water north of the Faroes (defined in text) plotted against time of observation (a) and against month of observation separately for the period before (and including) 1987 (b) and after (and including) 1988. The range indicated by the vertical lines shows distance to the stations between which the 50% Atlantic Water limit was found. The most probable distance indicated by filled circles was estimated by interpolation between these stations.

period there is at least an indication of seasonal variation in the influences of Atlantic water north of the Faroes, with a minimum in spring and maximum in late summer or autumn. A comparison of Figures 4b and 4c supports the indication in Figure 4a, namely, that the Atlantic water influence has been weaker since 1988 compared to previous years, especially for the spring period.

The influences of Atlantic water on the shelf

Figure 5 shows the salinity variation on the shelf and in the Faroe Bank Channel. It can be seen that the Shelfwater has decreased in salinity since the mid-1980s. To some extent this decrease reflects only the salinity decrease of the incoming Atlantic water, represented by the upper waters of the Faroe Bank Channel. The

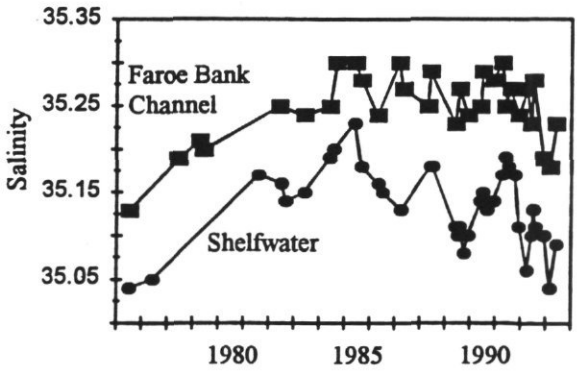


Figure 5. Average salinity of the 100–300 m layer in the Faroe Bank Channel and average salinity of the Shelfwater plotted against the time of observation.

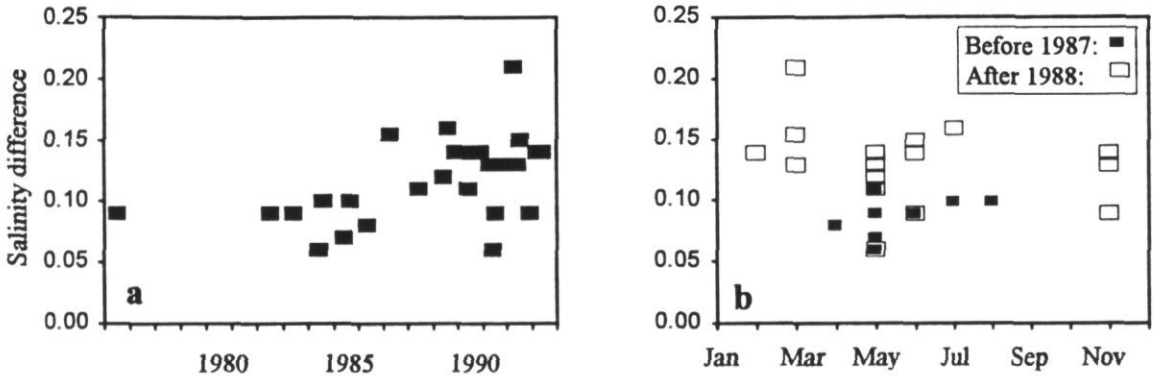


Figure 6. Salinity difference between the upper water in the Faroe Bank Channel and the Shelfwater plotted against time of observation (a) and against month of observation (b). In (b), observations before (and including) 1987 have been distinguished from observations after (and including) 1988.

difference between Faroe Bank Channel salinity and the shelfwater salinity, however, should be an indicator of Atlantic water influence on the shelf and Figure 6 shows the variation of this parameter plotted against time and against the month of observation. Here only CTD observations were used and only if they had been obtained from the Faroe Bank Channel and the shelf simultaneously (within one month).

The number of observations before 1987 is too small to warrant statistical analyses, but the figure indicates a change sometime in the late 1980s. Before that time, the Shelfwater consistently seems to have had a salinity 0.05 to 0.1 below the salinity in the Faroe Bank Channel. After 1987 the difference was much more variable and typically larger. Figure 6b indicates that the change is not due to changed sampling strategy coupled to a possible seasonal variation.

Discussion

Environmental conditions of spawning

Cod seem to spawn throughout the Faroe Plateau, but the two main spawning grounds are located to the north and west of the islands (Fig. 7). In most years the spawning occurs close to the 100 m depth contour. This bottom depth seems to coincide fairly well with the boundary between the Atlantic waters off the shelf and the well-mixed *Shelfwater* over the shallow parts of the Plateau. Thus Faroe Plateau cod in parallel with other Northeast Atlantic cod stocks (e.g. Icelandic and Arcto Norwegian) spawns in the boundary region between an Atlantic and a fresher water mass.

After fertilization, the cod eggs ascend towards the upper layers, where development up to hatching occurs after about 16–20 days. During this time the spawning products are advected by the flow. Over the deeper parts of the Plateau this is dominated by the North Atlantic Current (Fig. 1a), which in most regions circles the Plateau anticyclonically. In the shallower parts the Shelfwater has an even more persistent anticyclonic circulation around the islands (Fig. 7).

The horizontal distribution of larvae in late June–early July is available from the Faroese 0-group surveys and these show clearly (Jákupsstovu and Reinert, 1994) that the main habitat of the juveniles is the shallow part of the Faroe Shelf (shallower than 100 m). The transport

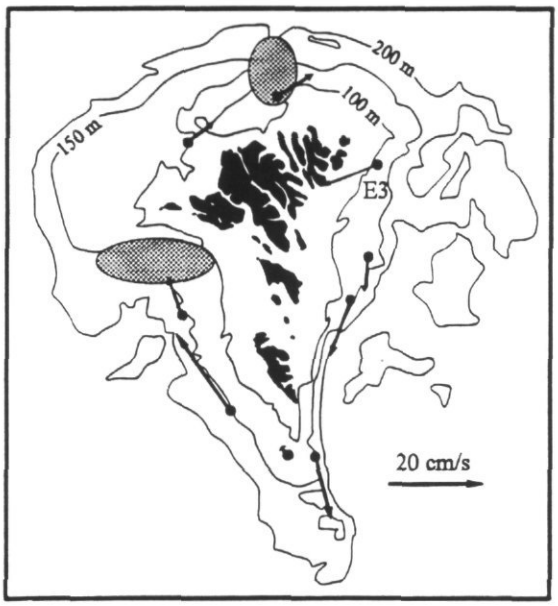


Figure 7. Bottom topography of the Faroe Shelf and residual flow vectors based on measurements from long-term current meter moorings at the sites shown (Hansen, 1992). Hatched areas indicate the main spawning grounds.

of spawning products from the spawning grounds into the shallow areas must be a critical process.

In most regions on the outer parts of the Faroe Shelf (Fig. 7) the residual current follows the bottom topography, and transport onto the shelf must occur mainly by mixing; but just south of the northeastern corner of the plateau (site E3 in Figure 7) the current meter observations indicate a flow on to the shelf (Hansen, 1992). Using current meter observations from the area (Hansen, 1992), a drift from the northern main spawning ground to the E3 site can be estimated to require in the order of 2–4 weeks.

The food items of cod larvae

It is generally assumed that a key factor for the survival of cod larvae is the availability of zooplankton of suitable sizes for the various larval stages and in the Northeast Atlantic *Calanus finmarchicus* seems to be the dominant prey item. No investigations have been made on the food of cod larvae in Faroese water, but the dominance of *C. finmarchicus* among zooplankton in Faroese waters during spring (Gaard, in prep.) indicates that this species may play a similar role for the Faroe Plateau cod as for other cod stocks.

This copepod species has been found in extensive areas in the Northeast Atlantic including the Norwegian Sea. It is known to overwinter as copepodit stages IV and V in deep water. During winter, *C. finmarchicus* is almost absent from the Faroe Plateau (Gaard, in prep.), which is consistent with this life cycle. There therefore has to be an import of these animals to the plateau during spring, and observations on the Plateau in the spring of 1992 and again in 1993 indicate that the import occurs close to the cod spawning area (Fig. 8).

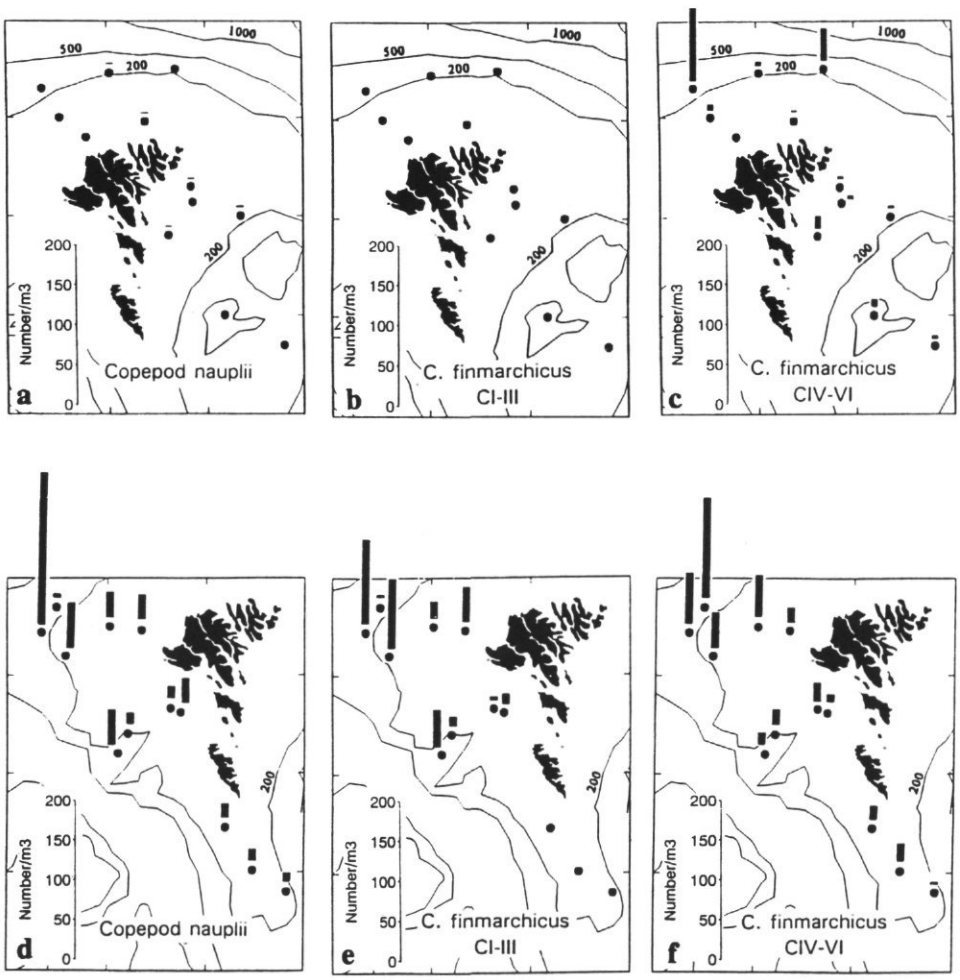


Figure 8. Concentrations of various stages of *C. finmarchicus* around the Faroes, 26 Feb–3 Mar 1993 (a–c) and 12–20 Mar 1993 (d–f). From Gaard (in prep.).

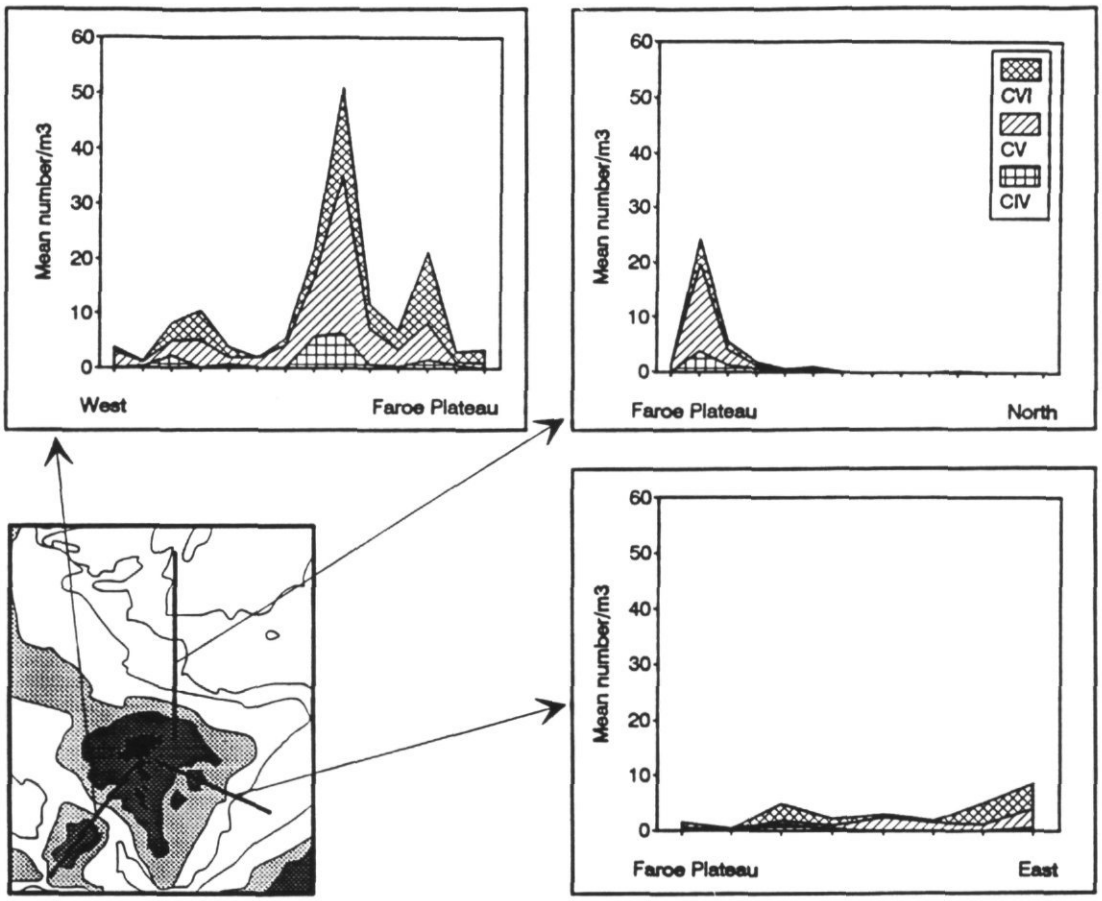


Figure 9. Concentration of *C. finmarchicus* on the standard sections, 5–8 Feb 1993. Stages are indicated by hatching as shown on one of the graphs. From Gaard (in prep.).

The most likely source region is indicated by Figure 9, showing concentrations of *C. finmarchicus* in the uppermost 50 m in offshore waters some weeks before spawning in 1993. The concentration of *C. finmarchicus* in the Faroe Bank Channel and over the shelf edge north of the Faroe Islands was about 10 times higher than in the other areas around the islands. The increase was mainly due to higher concentrations of copepodit stage V in these areas. These observations, together with the dominant flow patterns of the upper layers, point to the Faroe Bank Channel as a main supplier of *C. finmarchicus* to the Faroe Plateau. The animals may be transported to the channel either from the open North Atlantic through advection by the North Atlantic Current (Fig. 1a) or from the deep Norwegian Sea by the deep currents ending in the outflow through the channel (Fig. 1b). Recent investigations have shown high concentrations of *C. finmarchicus* in the deep water in February, confirming this as a major pathway for *C. finmarchicus* to the Faroe Plateau (Gaard, in prep.).

Effect of wind changes on recruitment

To some extent it is a matter of interpretation when the period of bad recruitment started. Since 1984 the recruitment values have been low but the most abnormal development has been from 1989. For 1988 the 0-group index was fairly high, while the other two recruitment estimators indicated a small year class. Thus it is not clear whether 1988 should be included in the period of collapse.

It was shown above (in "Variations in winds") that this period of recruitment collapse broadly coincided with increased winds from the southwest. In Figure 10 the 0-group index is plotted against the wind energy input and the windstress component towards the northeast. We would expect windstress in this direction to affect the transport of cod-spawning products and of copepods from the spawning grounds to the shelf negatively. Wind energy input to the sea also might affect the depth of the mixed layer and hence the primary production in waters

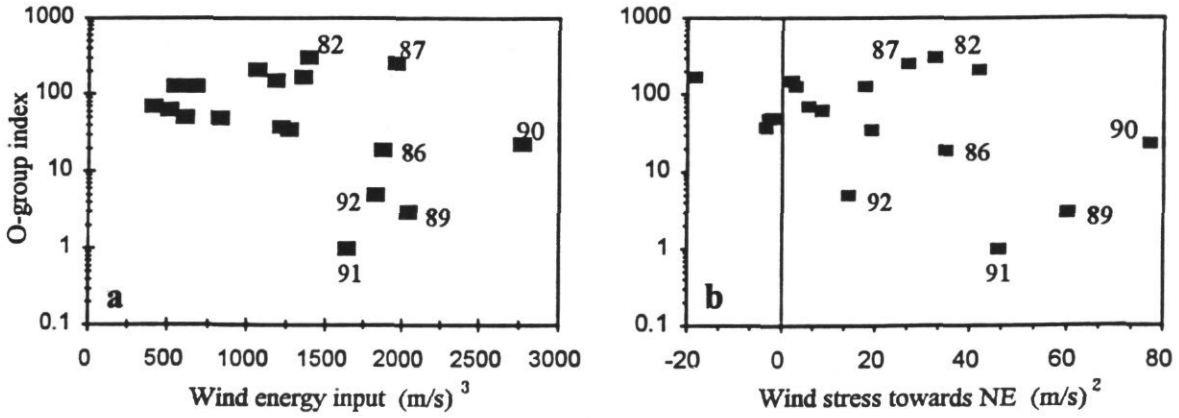


Figure 10. 0-group index plotted against wind energy input to the sea (a) and windstress towards the northeast (b) for the March–May period each year. Exceptional year classes are marked by the year of spawning.

off the shelf. As the zooplankton drift for most of the time in these waters, a high primary production is probably necessary for sufficient production of nauplii.

The correlation coefficients between the logarithm of the 0-group index and these two wind indices are just below significance at a 95% level in both cases. Also the 1991 cod year class, which was the smallest one on record according to the 0-group index, experienced much smaller wind forcings than the 1990 year class which, although small, seems to have been much better than the 1991 year class. Therefore, wind by itself does not explain all variations in year-class strength of Faroe Plateau cod; but as a whole there are indications that some of the recruitment collapse may be linked to abnormal winds. Thus the five lowest 0-group indices on record occurred in years (1986, 1989, 1990, 1991, and 1992) when the wind energy input was high, and all of these but the 92-year class had large windstresses towards the northeast.

Hansen *et al.* (1990) discussed the relative stability of cod compared to haddock recruitment on the Faroe Plateau, indicated from the data available at that time. They suggested a larger sensitivity of the planktonic stages of haddock to high wind speeds compared to cod owing to different horizontal distributions. This might seem incompatible with the results quoted here, but it must be noted that haddock recruitment on the Faroe Plateau has also collapsed in recent years. Unfortunately, less reliable 0-group indices for haddock make it difficult to compare the cod and haddock collapse quantitatively.

Effects of a weakened flow of Atlantic water

Winds were apparently not the only physical parameter behaving abnormally in this period. Although the available data set does not allow firm conclusions, we have presented time series of two independently estimated parameters (Figs. 4 and 6); both indicate a weakened influence of Atlantic water on the plateau.

The reduced dominance of Atlantic water north of the Faroes (Fig. 4) may well have resulted in a smaller import of copepods from the Faroe Bank Channel to the shallow parts of the shelf. It should also lead to a less stable transport path from the spawning grounds to the Shelfwater. Such a weakening would make the transport more vulnerable to external forcing, especially from windstress towards the northeast.

With changing conditions north of the Faroes, a change in the coupling between the Faroe Bank Channel and the shelf can also be expected, and Figure 6 indicates that this may have occurred. The change in Figure 6 may be interpreted differently; but a weakened coupling between the Faroe Bank Channel and the shelf is at least one of the possible explanations. If this explanation is supported by further investigations, this is one more indicator of a weakening in the processes transporting spawning products and copepods to the shallow parts of the shelf. The hypothesis of a weakening Atlantic water influence is not as well documented as the abnormal wind situation, but all the available data support this hypothesis.

Conclusion

If the spawning stock of Faroe Plateau cod had been in a good condition, we might well have concluded that the abnormally low recruitment that has persisted since the end of the 1980s was an effect of the changes in winds and Atlantic water influence documented in this paper. When the actual state of the spawning stock is taken into

account (Jákupsstovu and Reinert, 1994), purely biological effects cannot be excluded. On the other hand, it is not obvious either that purely biological effects suffice as an explanation for the drastic decline in recruitment observed, and we suggest that a combination of increased winds and reduced Atlantic flow be considered a main hypothesis in the further efforts to explain the recruitment collapse of the Faroe Plateau cod stock.

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Distribution, abundance, and length of pelagic juvenile cod in Icelandic waters in relation to environmental conditions

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The article summarizes available information on pelagic juvenile cod in Icelandic and nearby waters based on late summer surveys conducted since 1970. The data are analysed and discussed in relation to hydrographic conditions and available information on zooplankton biomass. The waters north of Iceland in particular are dealt with because it is there that the most important nursery grounds are located and also where the most marked hydrographic changes have occurred. 0-group cod from the Denmark Strait–East Greenland area and in the waters west of Iceland were significantly larger than those caught north and east of Iceland. Interannual changes in the relative distribution of 0-group cod north and east of Iceland appeared not to be related to varying hydrographic conditions. Similarly, the abundance indices of 0-group cod north of Iceland were found not to be significantly different during years classified as warm or cold in respect of hydrographic conditions. Densities of the 0-group cod north of Iceland were found to be 3–4-fold higher at bottom depths <50 m compared with stations where the bottom depth was 51–200 m. The length of 0-group cod over the shelf north of Iceland, however, showed only slight differences with bottom depth. A significant linear relationship was found between the zooplankton biomass southwest and west of Iceland and 0-group cod abundance, but not between zooplankton volumes and the length of 0-group cod. Finally, a significant linear relationship between 0-group indices of cod from survey data and ln of recruits as estimated by VPA of the commercial catch at the age of 3 years is presented.

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Introduction

Surveys of the distribution and abundance of 0-group fish have been carried out during August–September in Icelandic and adjacent waters since 1970. The main purpose of these investigations has been to obtain an initial index of the year-class strength of the main Icelandic commercial fish stocks at an early stage in their life history. Results have been presented annually at ICES Statutory Meetings (1972a, b, 1973, 1974, 1975, 1976, 1977, 1978, 1979a, b, 1980; Vilhjálmsson *et al.*, 1980; Vilhjálmsson and Magnússon, 1981, 1982, 1983, 1984, 1985, 1986; Magnússon *et al.*, 1987, 1988, 1989; Magnússon and Sveinbjörnsson, 1990, 1991, 1992). Vilhjálmsson and Friðgeirsson (1976) summarized the first six years of the investigations and concluded that they were of value in providing the initial year-class estimates as intended. More recently, Helgason and Sveinbjörnsson (1987) revised the indices calculations for cod and correlated 0-group cod abundance, length, and salinity to VPA estimates at age 3. With the exception of the last two papers mentioned little attempt has hitherto been made to analyse the biological information this 0-group data series contains and to discuss it in an environmental context. The present paper attempts this for the material on cod.

Material and methods

0-group sampling

During the first years of the investigations (1970–1972) only 30–40 trawling stations were covered during the surveys. In 1973 the number of stations was increased to approximately 85, while in 1975 they were further increased to about 130. Initially, the surveys did not follow a fixed survey route, but since 1980 the grid for the Icelandic area has been fixed although the route in the Irminger Sea has undergone some alterations (Fig.

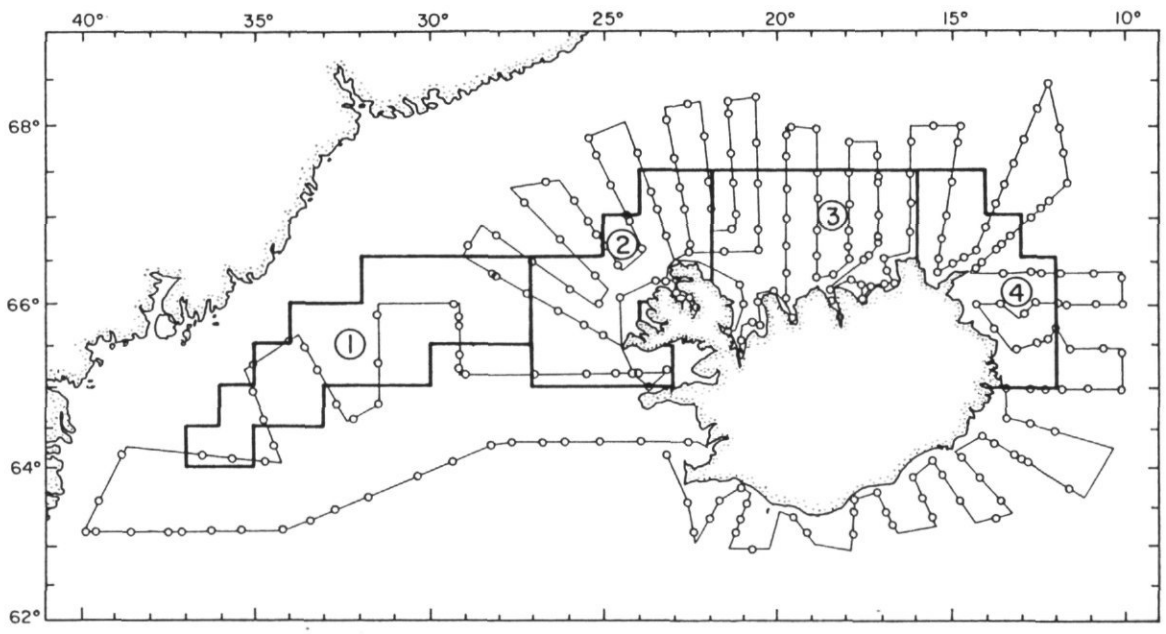


Figure 1. Typical survey grid in the Icelandic 0-group surveys of recent years (year 1986, redrawn from Vilhjálmsson and Magnússon, 1986). Also shown is the division of the investigation area into four subareas (1 Denmark Strait–East Greenland, 2 West Iceland, 3 North Iceland, 4 East Iceland) in the data analysis.

1). For the present paper we did not have access to the basic data sampled in 1972 and therefore this particular year had to be omitted from our analysis.

Although the positions of the trawling stations have not been fixed, the survey methods have remained basically unchanged from the beginning of the investigations. Acoustic records have been used to monitor changes in fish abundance and distribution and used as guidelines for trawl hauls which were usually made at a depth of 20–50 m. The working rule has been such that whenever changes in acoustic records are observed, or if no changes are observed for about 20 nautical miles, a trawl haul is undertaken (Helgason and Sveinbjörnsson, 1987).

The 0-group fish were sampled with a Harstad pelagic trawl which had an approximately 18 × 18 m opening and a 0.5 × 0.5 cm mesh in the codend. Information on trawling depth was obtained with a headline transducer and/or a Scanmar acoustic depth recorder. On deck, all 0-group fish were analysed to species, counted and their length measured. When the catch contained several hundred individuals only a subsample of approximately one hundred cod was counted and measured.

Calculation of abundance indices

The basis data for the computation of the abundance index is the catch in number per nautical mile towed (NPNM). The distribution of the catches was usually highly skewed, however, with most of the catch coming from a few stations. Therefore the catches were normalized using a logarithmic transformation before the index calculations (Pennington and Grosslein, 1978). For the present analysis the study area was divided into four subareas (Fig. 1) based on the general picture of distribution obtained through the investigation period, while it also takes into consideration some main hydrographic features. For each of the subareas the following was calculated:

$$\text{Logarithmic mean (NPNM)};\ \bar{X} = 1/N \sum_{i=1}^{N} \ln (X_i) \quad (1)$$

$$\text{Proportion of non-zero hauls};\ P = N/N_t \quad (2)$$

$$\text{Subarea index};\ I_s = \bar{X} P A_s / A_t \quad (3)$$

X_i = catch in number at station i where catch is >0; N = number of stations where catch is >0; N_t = total number of stations; A_s = area of a subarea; A_t = total area.

In the computation of $\bar{X}$, only the non-zero values are used and hence this number is reduced by using the proportion of non-zero tows when computing the subarea index. The subarea indices calculated in this manner were finally summed to arrive at the total

abundance index for a particular year. These calculations of the subarea indices follow Randa (1983), except for the multiplication by the area ratio. Estimation of the total index, however, differs from Randa as he did not use the subarea indices directly to estimate the total index.

Hydrographic and zooplankton data

The hydrographic data presented were collected in late May–early June at 50 m depth in a water of 470 m depth over the shelf north of Iceland (station Siglunes 3, 66°32′N 18°50′W). This particular station has been considered to reflect fairly well the hydrographic features of most of the shelf area north of Iceland (Malmberg, 1986).

The data presented on zooplankton biomass were sampled in late May–early June during 1971–1992 with a Hensen net (200 μm mesh size, from 50 to 0 m) at 22 standard stations on three sections southwest and west of Iceland (Astthorsson *et al.*, 1983). This sampling took place at about the same time as first-feeding larvae are most abundant off the southwest coast of Iceland (Gislason *et al.*, 1994), and is therefore likely to reflect their food availability at that time.

Results

General features of environmental conditions and cod spawning

The general features of the current system and water-mass distribution around Iceland have been described by Stefánsson (1962, 1981). The warm and saline Atlantic water (Irminger Current) flows along the south and west coasts of Iceland and off the Vestfirdir peninsula it splits into two branches (Fig. 2). The branch turning west and southwards meets the cold East Greenland Current and forms a cyclonic eddy in the Irminger Sea, while the other one flows eastward onto the northern shelf as the North Icelandic Irminger Current. On the north Icelandic shelf the Atlantic influx is evident as a tongue of relatively warm and saline water. The cold and low salinity East Icelandic Current, which is a mixture of water derived from both the North Icelandic Irminger Current and the East Greenland Current, flows southeast along the northeast Icelandic continental slope. Close to shore the freshwater-induced Coastal Current flows clockwise around Iceland (Fig. 2).

Long-term hydrographic investigations have demonstrated that during recent decades large fluctuations have taken place in the inflow of Atlantic water onto the shelf area north of Iceland (e.g. Malmberg, 1980; Malmberg and Kristmannsson, 1992; Stefánsson and Jakobsson, 1989). On the basis of the temperature and salinity conditions north of Iceland in spring, Malmberg and Kristmannsson (1992) and Malmberg and Blindheim (1994) have grouped years into those dominated by Atlantic, Polar, or Arctic conditions. In the present paper we have considered years dominated by Atlantic water as warm, while years dominated by either Polar or Arctic water have been classified as cold (Fig. 3). During three of the years (1978, 1981, 1989) the classification into warm and cold years does not conform to the salinity and/or temperature deviations. However, in this context it should be noted that the eventual evaluation of hydrographic conditions is not only based on the spring observations shown in Figure 3, but also on investigations in February, August, and November (Malmberg, pers. comm.) and from a more extensive area. This grouping of years into warm and cold is used below as a basis for the analysis and discussion of the possible effects of climate on 0-group cod in Icelandic waters.

Atlantic water predominates at the spawning grounds of the cod to the south of Iceland. Contrary to the conditions north of Iceland, year-to-year variations in the main hydrographic features off the south coast are limited and only slight changes in temperature and salinity have been observed (Malmberg, 1978, 1984; Dickson *et al.*, 1988). However, close to shore, hydrographic conditions may vary considerably from year to year, mainly due to variable timing and magnitude of freshwater runoff and variable wind force and direction (Thórdardóttir, 1986; Ólafsson, 1985).

The Icelandic cod spawns mainly in late April to early May in the Atlantic waters off the south and southwest coasts of Iceland (Jónsson, 1982; Friðgeirsson, 1979, 1982). The main spawning activity takes place relatively close to the coast in waters of temperatures between 5 and 7°C and at a salinity of 32–35 (Friðgeirsson *et al.*, 1979; Ólafsson, 1985). The eggs and larvae drift from the spawning grounds with clockwise currents to the nursery and feeding grounds in the arcto-boreal waters off the northwest, north, and the northeast coasts of Iceland. During some years a considerable fraction of the larvae may also drift to Greenland waters, where they then spend their juvenile years, before returning to Icelandic waters as mature individuals to spawn (Schopka, 1994).

Distribution and length of 0-group cod in different areas

The 22 years data series has demonstrated large fluctuations in both abundance and distribution of the 0-group cod. For example, Figure 4 shows two extreme years, 1984, when one of the highest abundance indices was recorded and a considerable fraction of the larvae drifted across the Denmark Strait and to east Greenland waters (Fig. 4A), and 1988, a year of one of the lowest

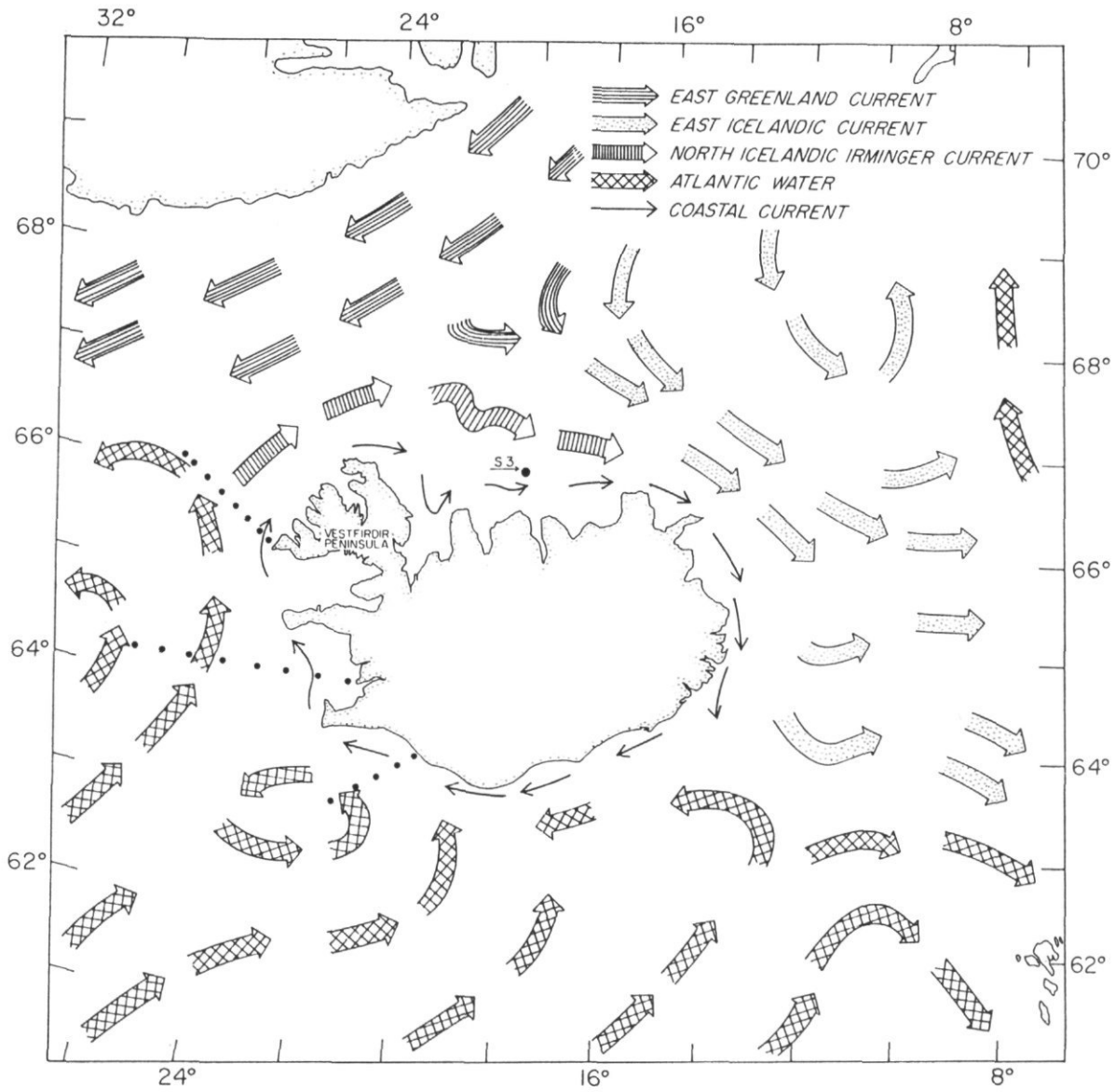


Figure 2. Ocean currents around Iceland (adapted from Stefánsson and Ólafsson, 1991). Also shown is the station Siglunes 3 (S 3) from where the hydrographic data are presented, and the stations southwest of Iceland from where data on zooplankton biomass was sampled.

abundance indices and when the distribution was confined to the shallow waters off the northwest and north coasts (Fig. 4B).

The 0-group cod abundance indices in the four subareas (Denmark Strait–East Greenland, west, north, and east of Iceland) and the total index for each year during 1970–1992 are given in Table 1. The relative contributions of the subarea indices to the total indices have been used to establish the distribution of 0-group cod in the different subareas (Fig. 5). The largest proportion of 0-group cod is generally found in the waters north of Iceland (the mean for 1970–1992 being 45% of the total index). The stock components found on the average off the west and east coasts of Iceland (28 and 19%, respectively) are roughly comparable, while by far the smallest proportion is in the Denmark Strait–East Greenland waters (8% on the average).

It is interesting to note that during most years a component of the 0-group is found in the Denmark Strait–East Greenland waters. The maxima during the

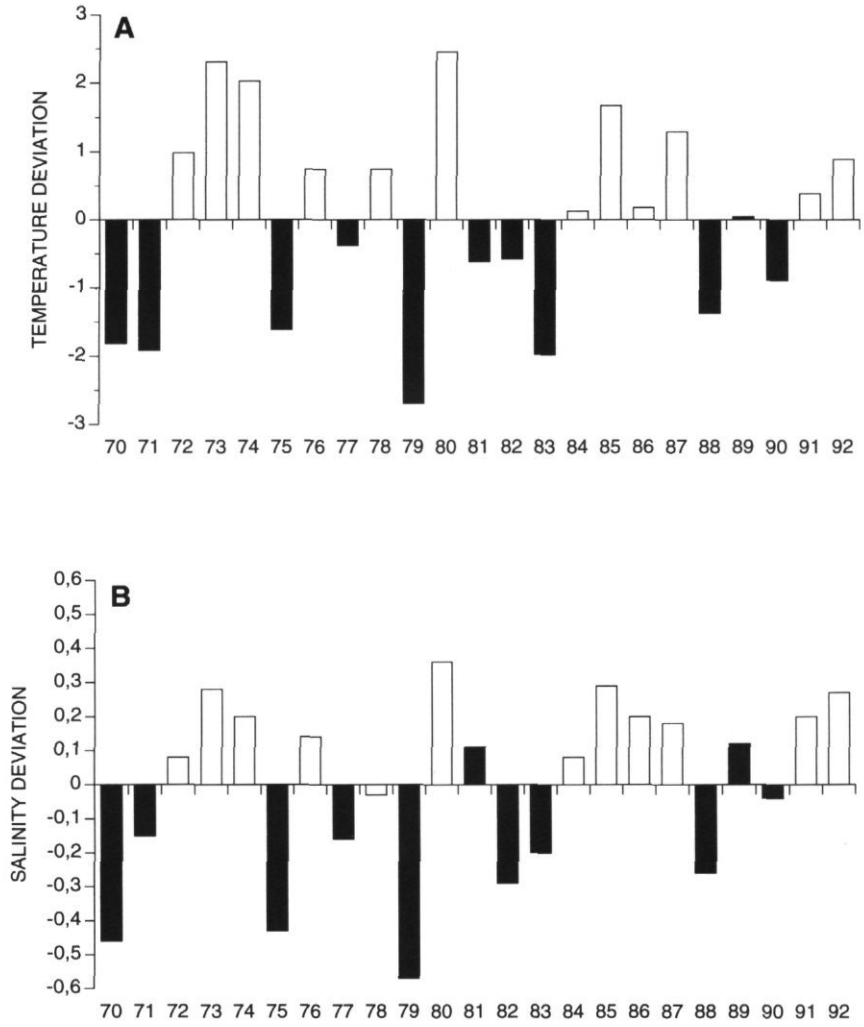


Figure 3. Temperature (A), and salinity (B) deviations (at 50 m depth) in May–June 1970–1992 at station Siglunes 3 north of Iceland. The deviations are calculated from the 1970–1992 mean and open and black columns denote warm and cold hydrographic conditions, respectively. Based on data from Malmberg (1980) and Malmberg and Kristmannsson (1992).

investigation period being 24 and 26% in 1981 and 1984, respectively. A somewhat smaller fraction (ca. 20%) has also been observed in the Denmark Strait–East Greenland area in 1973, 1985, and 1987 (Fig. 5).

If the transport of 0-group cod from spawning grounds south of Iceland and to the feeding grounds on the northern and eastern shelves is mainly determined by the flow of Atlantic water, one might expect to find a larger fraction of the cod in those areas during years of pronounced inflow than during years when this inflow is only weak or absent. When individual years are considered in relation to the grouping into warm and cold years no such pattern was evident for the northern area, the average subarea indices being 45% of the total index for both categories. Similarly, the percentage of the 0-group found in the north and east areas combined appears not to be related to the inflow of Atlantic water, being 63% for both warm and cold years.

The mean length of 0-group cod in the different areas around Iceland during 1970–1992 is shown in Figure 6. Apparently, the 0-group cod were generally larger in the Denmark Strait–East Greenland area and west of the country than off the north and east coasts. An ANOVA demonstrated no significant difference in the length of the 0-group caught in the Denmark Strait–East Greenland area and the waters west of Iceland ($p>0.05$), and similarly there was no difference between those caught north and east of Iceland ($p>0.05$). There was, however, a significant difference ($p<0.05$) between the 0-group cod from the Denmark Strait–East Greenland

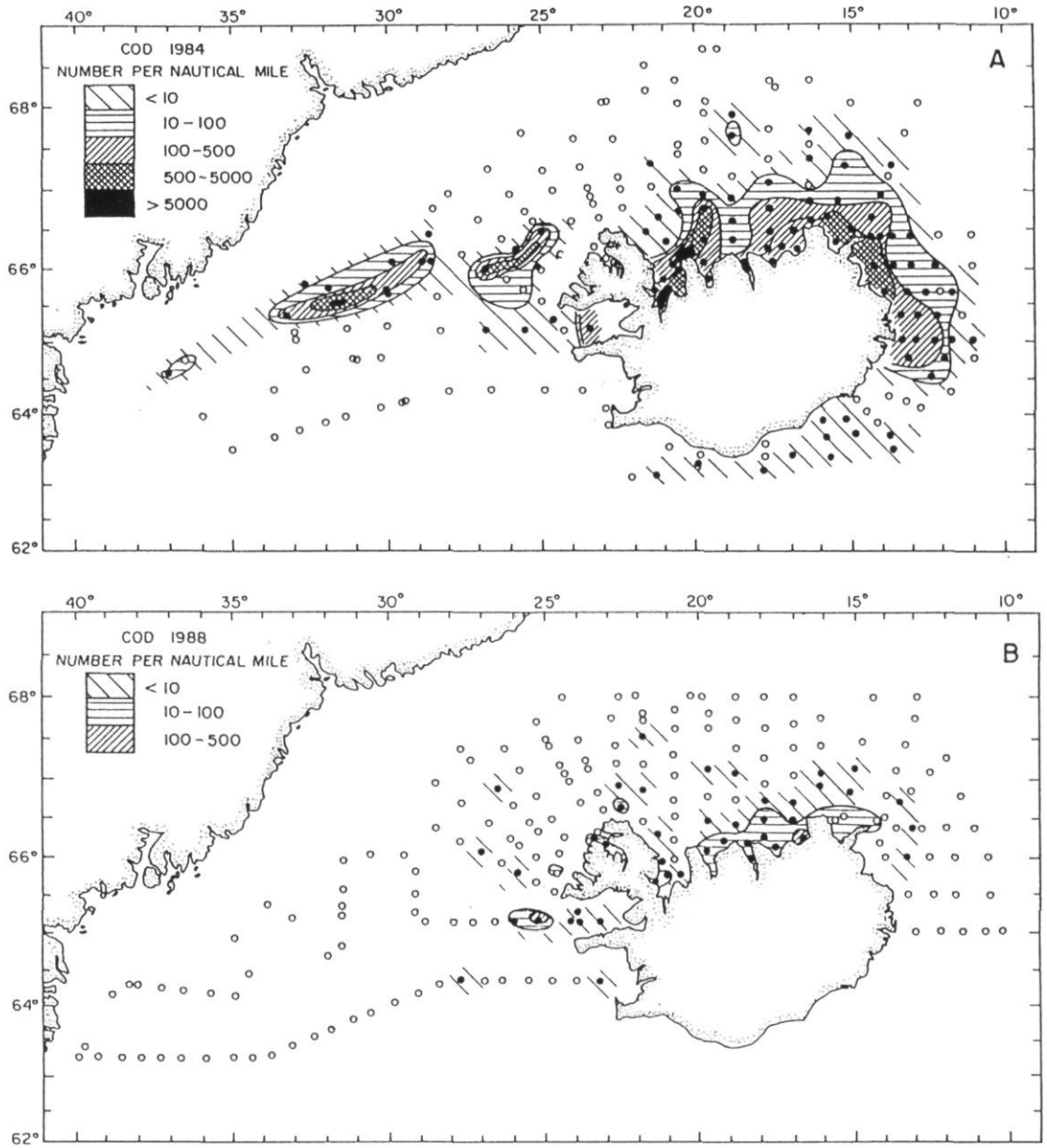


Figure 4. Distribution of 0-group cod in Icelandic waters in 1984 (A), and 1988 (B). Redrawn from Vilhjálmsson and Magnússon (1984) and Magnússon *et al.* (1988).

area and off the west coast on one hand (mean length 53.7 mm), and north and east of Iceland on the other (mean length 45.5 mm).

0-group cod in the waters north of Iceland

As demonstrated above, the largest part of the Icelandic 0-group cod is usually found in the shelf area north of the country in the late summer (Fig. 5). It is also in this area the most marked hydrographic changes have taken place during recent decades and, therefore, it was of interest to consider the available 0-group data from those waters in more detail.

The abundance indices of the 0-group cod in the waters north of Iceland are shown in Figure 7A. The bars of individual years have been shaded in order to demonstrate warm and cold hydrographic conditions (cf. Fig. 3). From 1970 to 1980 the indices were relatively

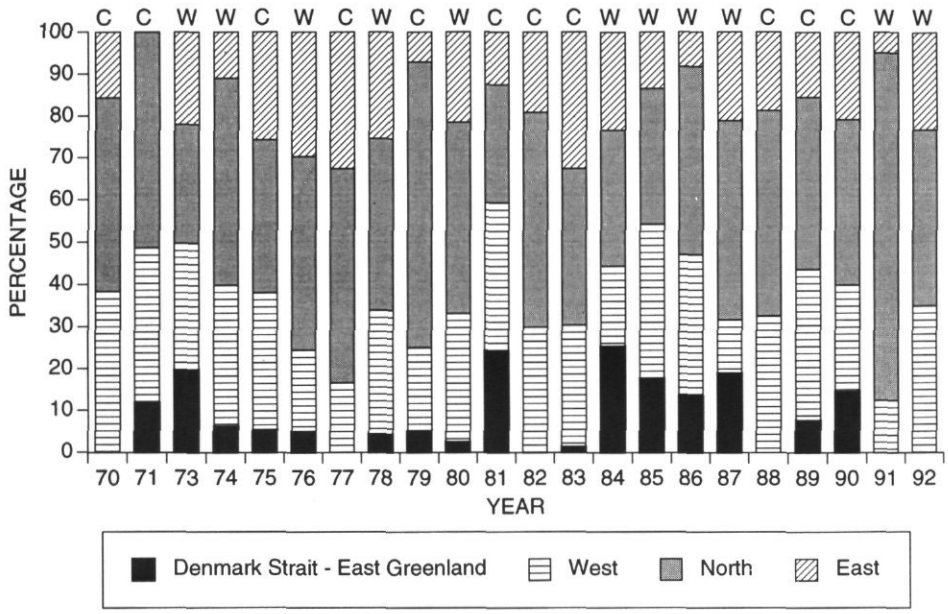


Figure 5. Relative abundance indices of 0-group cod in four subareas around Iceland (Denmark Strait–East Greenland, west, north, and east of Iceland) during 1970–1992. The capital letters, W and C above the figure denote warm and cold hydrographic conditions, respectively, in the water north of Iceland.

high irrespective of whether hydrographic conditions were warm or cold. There then followed three consecutive cold years, 1981–1983, during which the abundance indices were low. During the warm year of 1984 the abundance index increased again, and since then has been gradually decreasing, again irrespective of whether hydrographic conditions have been warm or cold. A *t*-test further demonstrated that there was no difference ($p < 0.05$) between indices of warm and cold years (means of 0.83 and 0.72, respectively).

Table 1. Abundance indices of 0-group cod in different areas around Iceland 1970–1992. DS–EG, Denmark Strait–East Greenland; W, West Iceland; N, North Iceland; E, East Iceland.

Year	DS–EG	W	N	E	Total
1970	0.00	1.08	1.29	0.44	2.81
1971	0.27	0.81	1.13	0.00	2.21
1973	0.55	0.83	0.78	0.61	2.77
1974	0.08	0.40	0.59	0.13	1.20
1975	0.13	0.80	0.89	0.63	2.45
1976	0.19	0.71	1.68	1.09	3.67
1977	0.00	0.41	1.23	0.79	2.43
1978	0.11	0.75	1.04	0.65	2.55
1979	0.09	0.32	1.11	0.12	1.64
1980	0.06	0.76	1.12	0.53	2.47
1981	0.29	0.42	0.33	0.15	1.19
1982	0.00	0.08	0.14	0.05	0.27
1983	0.02	0.35	0.45	0.39	1.21
1984	0.96	0.71	1.21	0.88	3.76
1985	0.49	1.01	0.89	0.38	2.77
1986	0.16	0.39	0.53	0.10	1.18
1987	0.28	0.18	0.69	0.31	1.46
1988	0.00	0.22	0.33	0.13	0.68
1989	0.10	0.46	0.53	0.20	1.29
1990	0.17	0.29	0.45	0.24	1.15
1991	0.00	0.03	0.21	0.01	0.25
1992	0.00	0.35	0.42	0.23	1.00

The mean length of the 0-group cod caught north of Iceland during the period 1970–1992 is shown in Figure 7B. Apparently there is a considerable variation in the length of the juvenile cod between individual years and

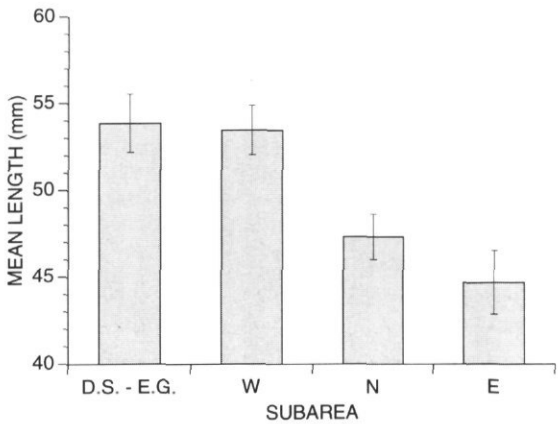


Figure 6. Mean length of 0-group cod in four subareas around Iceland during 1970–1992 (Denmark Strait–East Greenland, west, north, and east of Iceland). Vertical lines show standard error of the mean.

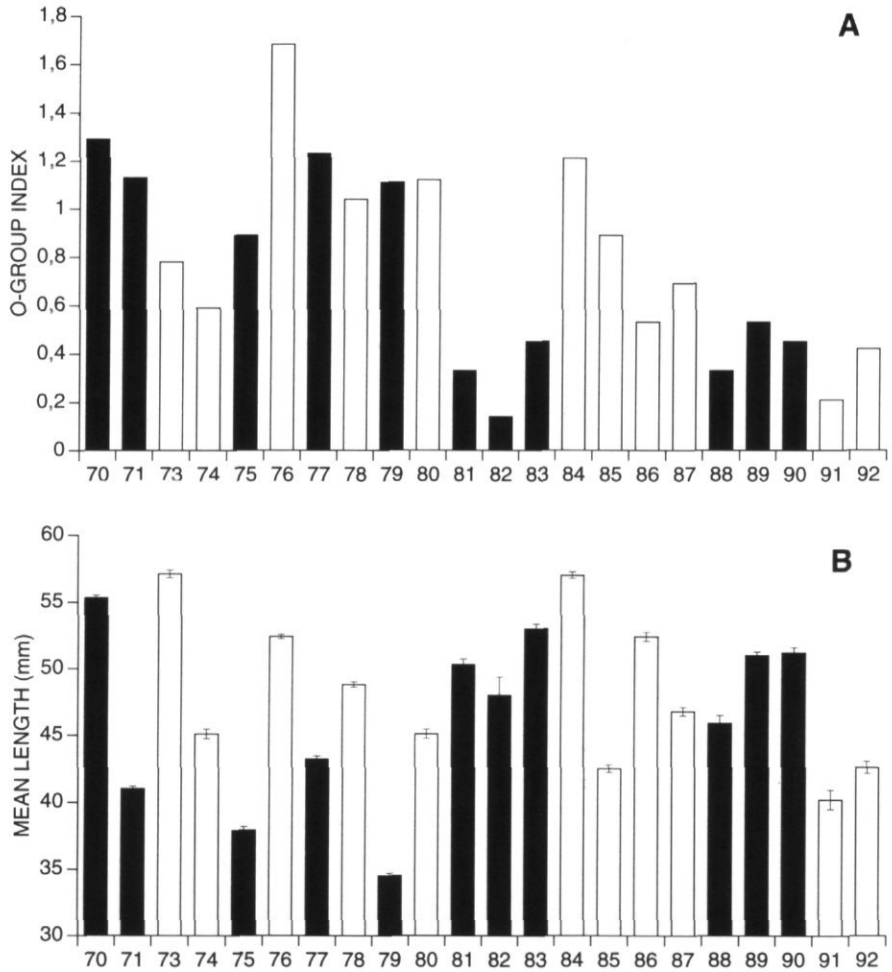


Figure 7. Abundance indices of 0-group cod (A), and mean length of 0-group cod (B) north of Iceland during 1970–1992. Open and black columns denote warm and cold hydrographic conditions, respectively. Vertical lines show standard error of the mean.

also within both hydrographic regimes. The largest mean length has been observed during the warm years of 1973 and 1984 (57.1 mm), while the smallest 0-group cod were observed in the cold years of 1979 and 1975 (34.5 and 38.0 mm, respectively). A *t*-test, however, demonstrated no significant difference ($p > 0.05$) in the mean lengths (respectively, 48.2 and 46.5 mm for warm and cold years) during the two hydrographic regimes.

The density of 0-group cod (positive catches only) north of Iceland in relation to bottom depth for 50 m depth zones is shown in Figure 8A. By far the highest catches (mean ca. 2600 cod per nautical mile) have been taken in the shallowest waters (0–50 m), while in that zone the catch is also most variable. At bottom depths from 51 to 200 m the catch has been relatively high (ca. 500–800 cod per nautical mile), whereas at station depths >200 m the density gradually decreased to very low catches at depths greater than 500 m, except for relatively high densities in the depth interval 351–400 m.

The mean length of the 0-group cod in the waters north of Iceland in relation to bottom depth is shown in Figure 8B. At station depths <500 m the 0-group cod showed only a limited variation in mean length (minimum 44.2 mm at 251–300 m and maximum 49.6 mm at 451–500 m). At station depths between 501 and 900 m there appeared to be a gradual decrease in the lengths of the cod. However, because of the very limited number of fish caught over these greater depths the findings must be interpreted with reservation.

0-group cod and zooplankton

The zooplankton biomass on the spawning grounds and the drift route of cod larvae southwest and west of Iceland in May are likely to affect both the survival and condition of the 0-group fish found in late summer.

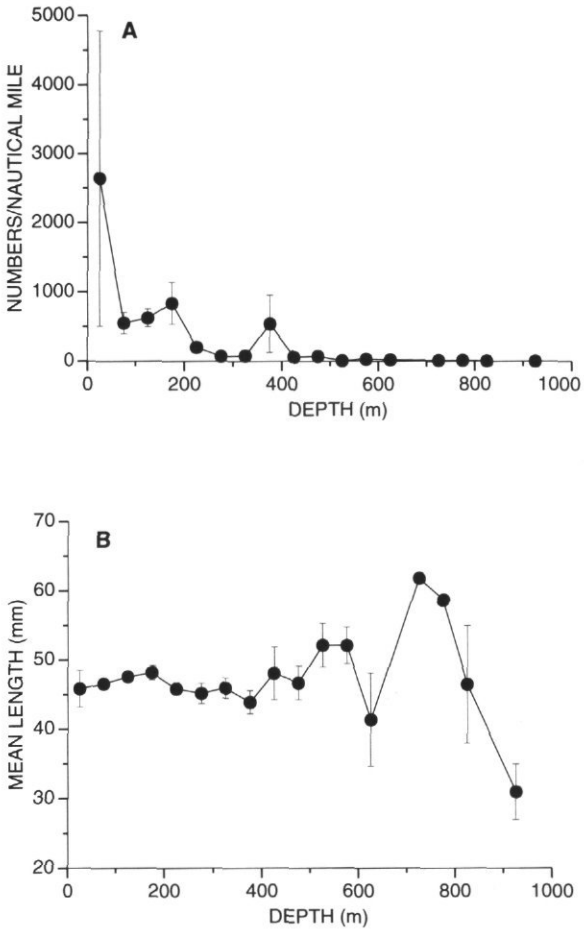


Figure 8. Relationship between 0-group cod abundances (mean number caught per nautical mile) and bottom depth in the waters north of Iceland (A), and between mean length of 0-group cod and bottom depth (B) during 1970–1992. Vertical lines show standard error of the mean.

Because of this we considered it of interest to examine whether high abundances and mean lengths of 0-group fish occurred together with high biomass values of zooplankton. As nearly all of the cod larvae and 0-group cod drift clockwise along the same mean route through the waters in which the zooplankton was sampled this exercise was undertaken using the total abundance indices and similarly the length data from all of the subareas combined.

Figure 9A demonstrates that there was a significant and positive linear relationship between zooplankton biomass southwest of Iceland and 0-group cod abundance indices ($r^2 = 0.37$, $p < 0.05$). On the other hand, the relationship between zooplankton biomass southwest of Iceland and the length of 0-group cod was not significant ($r^2 = 0.12$, $p > 0.05$, Fig. 9B). Because the zooplankton biomass data tend not to be normally distributed these relationships were also tested after a log transformation of the data, but that had no effect on the results.

0-group cod abundance and recruitment

As mentioned above, the main purpose of the 0-group surveys in Icelandic waters has been to get initial information on the year-class strength of the most important commercial fish stocks, particularly the cod stock because of its economic and ecological importance. The relationship between the total 0-group abundance index of cod as estimated in August and the VPA estimate of the same year class at the age of 3 years is shown in Figure 10. This relationship is significant ($r^2 = 0.46$, $p < 0.05$) and demonstrates that the 0-group indices of cod in Icelandic waters have a predicting value for providing a first estimate of the later recruitment to the fishable stock.

Discussion

In most years only a small fraction of the 0-group cod was found in the Denmark Strait–East Greenland area, but in five years (1973, 1981, 1984, 1985, 1987) the fraction increased to 18–26% (Fig. 5). This suggests, in accordance with tagging results (ICES, 1971), that 0-group cod are transported to Greenland more often than they appear as returning mature adults to Iceland. Thus, only two year classes of mature cod (those of 1973 and 1984) returning from Greenland were detectable in the Icelandic spawning stock during this period (Schopka, 1994). However, in this context it is worth noting that when estimated in Icelandic waters the cod which grew up in Greenland waters has been subjected to both natural and fishing mortality of unknown magnitudes for several years. Further, as pointed out by Schopka (1994), compared with the stock size at Iceland an immigration from Greenland of several million fish is difficult to detect.

The relative abundance indices of 0-group cod in waters north and east of Iceland appeared not to be related to the inflow of Atlantic water onto the northern shelf (Fig. 5). This may indicate that the Atlantic inflow, which is usually at its strongest near the shelf edge, does not control the drift of 0-group cod to the northern shelf. Possibly, the flow of the Coastal Current is more important in this respect, but at present this will remain mere speculation. Much more detailed ecological studies are needed to elucidate the factors governing distribution of the 0-group cod in the waters around Iceland.

The 0-group cod were generally larger off the west coast of Iceland and in the Denmark Strait–East Greenland area than in the waters north and east of Iceland

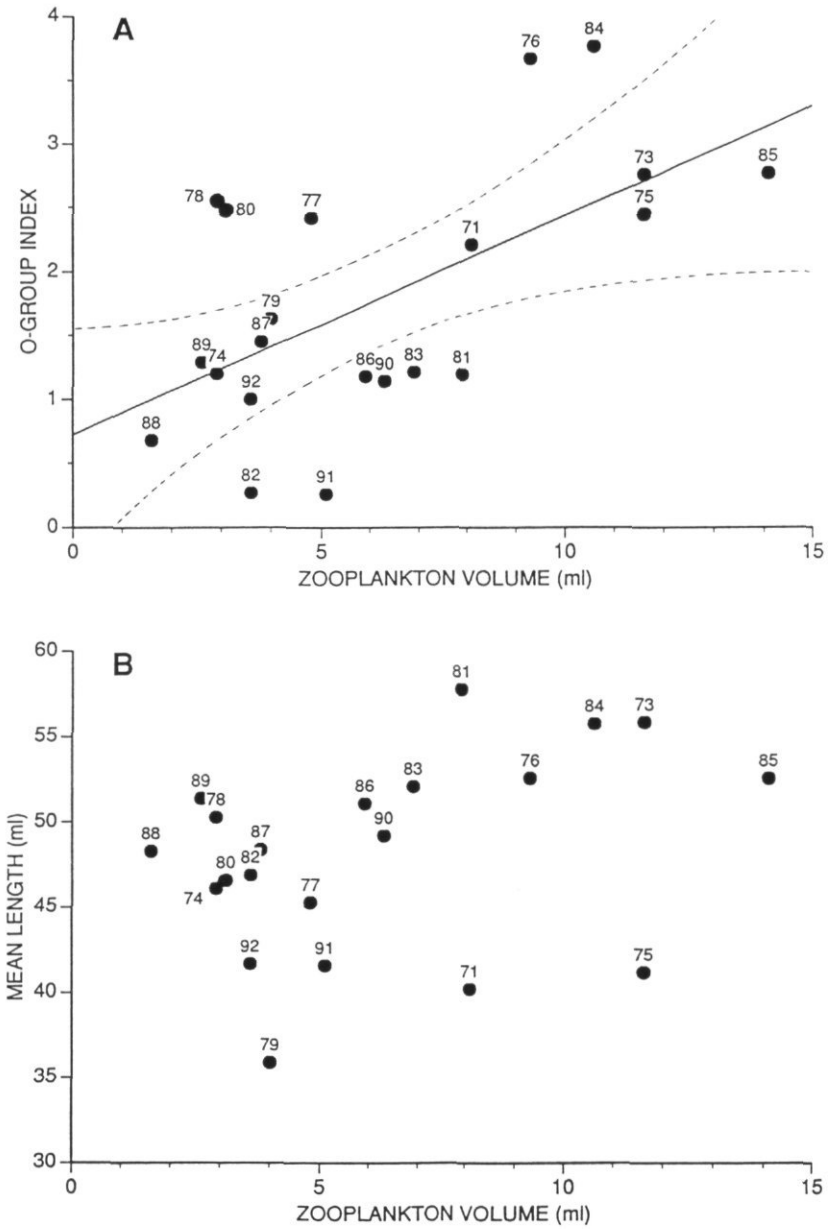


Figure 9. Relationship between zooplankton volume in May–June southwest and west of Iceland and abundance indices of 0-group cod in Icelandic waters in August (A), and zooplankton volume southwest and west of Iceland and mean length of 0-group cod (B) during 1971–1992. Broken lines in A show 95% confidence limits for the regression line.

(Fig. 6). Possibly mesoscale eddies off the northwest coast prevented some of the larvae and 0-group from drifting to the nursery grounds on the northern and eastern shelfs, and cod caught there might thus possibly be of the same age or even older than those caught at the same time off the north and east coasts. If this is the case, the 0-group cod caught in the Denmark Strait–East Greenland area and off the west coast of Iceland have also, for most of the summer, been living at temperatures 1–3°C higher than those inhabiting the waters of the north and east coasts. Faster growth rates at higher temperatures could then possibly explain their larger size in late summer (Fig. 6). Loeng and Gjøsæter (1990) similarly attributed high mean length of 0-group in August in the Barents Sea to high temperatures in the water masses where they have spent most of their life.

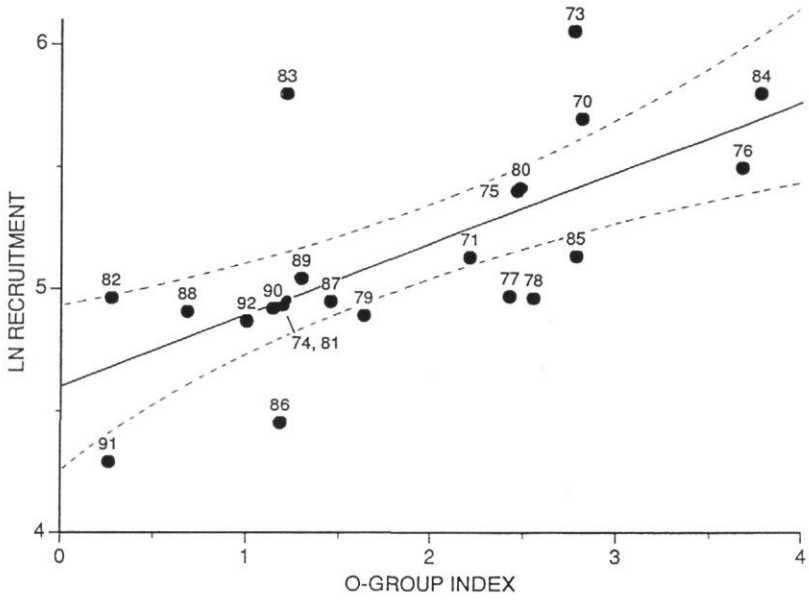


Figure 10. Relationship between 0-group abundance indices and ln of recruitment at the age of three years for the Icelandic cod stock during 1970–1991. Broken lines show 95% confidence limits for the regression line.

Also, spawning of cod off the north and east coasts of Iceland, even though believed to be limited (Friðgeirsson, 1982; Jónsson, 1982), may complicate the picture and possibly lead to lower average lengths being observed in those waters. In combination, several factors may thus contribute to the observed differences in length between the 0-group cod west of Iceland and in the Denmark Strait–East Greenland area on the one hand and north and east of Iceland on the other.

Neither the abundance indices nor the length of the 0-group cod in the waters north of Iceland (Fig. 7A, B) were found to be significantly different between warm and cold years. However, in addition to temperature, both abundance and growth are likely to be influenced by factors such as food availability and predators. Therefore, the influences of temperature on both 0-group cod abundance and length are likely to be much more complicated than implied by our simple grouping into warm and cold hydrographic conditions. Ottersen *et al.* (1994), however, found in fact that the inflow of Atlantic water influenced the abundance of 0-group cod in the Barents Sea; they also pointed out this was not the only cause of the fluctuations in abundance. Possibly this suggests that inflow of Atlantic water has a greater effect on 0-group abundance in the Barents Sea than in the waters north of Iceland. In this context it is worth noting that Jakobsson (1992) has pointed out that the Barents Sea ecosystem is a shallow marginal sea, highly dependent on the inflow of Atlantic water.

An examination of the distribution of the 0-group cod in the waters north of Iceland in relation to bottom depth demonstrated that by far the highest numbers were caught at depths <50 m (Fig. 8A). These observations are supported by Pálsson's (1976) findings that in September the largest numbers of newly settled cod in Isafjord-deep on the northwest coast of Iceland were caught at depths <50 m. From Browns Bank, southwestern Nova Scotia, Suthers and Frank (1989) reported that in some years the density of larval and pelagic cod juveniles might be up to threefold greater in nearshore areas (<50 m depth) than in offshore areas. Similarly, Godø *et al.* (1989) found that off mid-Norway, settling 0-group cod were mainly found in sheltered areas in the littoral zone and at a depth of 20–50 m in more exposed locations. The high abundance of 0-group cod in the nearshore areas north of Iceland by the end of their pelagic phase and when they are just settling may be an indication of the importance of the nearshore waters as nursery areas during the first winter.

The length of the 0-group cod was virtually the same at all depths in the waters north of Iceland (Fig. 8B). This may indicate that the growth conditions are similar throughout most of the shelf area. However, the high abundance of the larvae sometimes observed in the shallow waters compared to the deeper waters may suggest that intrinsic growth conditions are better nearshore, because they can support high densities without a fall in growth rate.

The significant positive regression between zooplankton biomass southwest of Iceland and 0-group

abundance indices (Fig. 9A) suggests that through better feeding conditions the zooplankton was having a beneficial effect on the survival of the 0-group cod. The finding that the length of the 0-group cod was not related to the zooplankton biomass (Fig. 9B) seems to some extent to contradict this. However, survival may have been determined by the food availability in the very early stages, without affecting length-at-age survival several months later.

Figure 10 demonstrated that for the Icelandic cod stock there is a significant relationship between 0-group abundance and recruitment at the age of three years. The variability in the data, however, was considerable and only about 46% is explained by the abundance indices. Notable outliers are the year classes of 1973 and 1983 and as the VPA estimates are considered more accurate than the 0-group ones (Schopka, pers. comm.) they seem to have been grossly underestimated by the 0-group survey. The mean lengths of the 1973 and 1983 year classes were, however, above the average (Fig. 8), which could possibly explain their greater survival until estimation as 3-year recruits. Also, if the settling of the 0-group depends on size, then the large individuals of the 1973 and 1983 year classes might to some extent have begun to settle at the time of investigation. If, on the contrary, the 0-group abundance indices are accepted as valid estimates of the number of cod in the sea at the time of surveying, then Figure 3 probably demonstrates that in some years the recruitment, as it appears at the age of 3 years, is not fully determined until some time after the pelagic stage.

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Changes in distribution of Atlantic cod and thermal variations in Newfoundland waters, 1980–1992

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Rose, G. A., Atkinson, B. A., Baird, J., Bishop, C. A., and Kulka, D. W. 1994. Changes in distribution of Atlantic cod and thermal variations in Newfoundland waters, 1980–1992. – ICES mar. Sci. Symp., 198: 542–552.

We examined cod distribution patterns relative to thermal conditions in Newfoundland waters (NAFO 2J 3KL), especially from 1980 to 1992. Sea temperature declines evident since the 1960s continued in this period. Very cold ocean conditions characterized 1984–1985 and 1990–1992. Sea temperatures at which cod were located were region- and age-dependent. Cod off Labrador (NAFO 2J) of age 3 were widely distributed from −1.0 to 3.5°C (the maximum recorded) in fall surveys. From ages 4 to 6 an increasing proportion occupied warmer waters; at age 6, most Labrador cod (>75%) occupied waters with temperatures >1.5°C. Cod on the NE Newfoundland Shelf (NAFO 3K and northern 3L) were concentrated at temperatures between 2 and 3.5°C at all ages >3 years in early spring and fall. Most cod on the northern Grand Banks (>3 years old) inhabited cooler waters with temperatures from −1 to 0.5°C. Temperatures at which cod were concentrated from year to year did not correlate with annual thermal conditions. Cod were located during fall surveys and winter fisheries at more northerly locations during warm periods and to the south in cold periods. A regression of mean latitude of cod distribution on temperature (latitude = 51.4 + 1.83 temperature, $p < 0.05$, $r^2 = 0.8$) was used to hindcast cod distributions to 1960. Hindcast latitudes were similar to those derived from commercial fishing statistics. Cod may be responding to thermal changes or to other correlated abiotic or biotic changes in their environment. Southerly redistributions since 1989 may have increased vulnerability to overfishing and compounded recent abundance declines.

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Introduction

Changes in the availability of cod (*Gadus morhua* L.) to the fisheries of Atlantic Canada in response to interannual and longer scale sea temperature fluctuations have been reported since the early 1700s and the advent of accounts of these fisheries. Innis (1940), based on earlier Colonial Office reports of the Newfoundland fisheries, wrote that "a series of bad fishing years had begun with the severe and prolonged winter of 1713–1714. It had chilled the water along the coast, and it had been followed by the worst season for many years. Up to 1720 the average yearly catch was only 90 000 quintals". Catches in the years preceding and following this period were many times this level (Innis, 1940). During this period of poor fishing a new "offshore" fishery on the Banks was initiated. There are implicit assumptions in this account that cod migrate relative to warmer waters and that such waters holding cod were known to be present offshore but only seasonally nearshore (although no records of temperature profiles are known to exist from that era). There are several other recorded periods of cold conditions that led to apparent changes in cod distributions and poor fisheries. Innis (1940) also wrote that: "From 1789 to 1792 harbors northward from Ferryland, as had happened thirty years before, suffered from a migration of fish because of an unusually large quantity of ice, which chilled the water." During this period an unprofitable fishery was reported to the north and east of Ferryland (Innis, 1940).

The Northwest Atlantic region has been enduring a cooling trend since the 1960s (Chapman and Walsh, 1993). This thermal trend has been strengthened by severely cold ocean conditions in the past decade, particularly in 1984–1985 and since 1989. Of note, the sea ice coverage in 1991 was the most extensive ever recorded (Colbourne *et al.*, 1994). Beginning in 1990 the fishery has failed completely in the northern portions of

the northeast coast, particularly off Labrador. These conditions appear somewhat similar to those described from 1713–1720. Cod abundance levels in Newfoundland waters have declined coincident with this cooling trend (Bishop *et al.*, 1993). Moreover, distribution patterns from the Hamilton Bank to the northern Grand Banks (NAFO 2J 3KL) have shifted strikingly southward and seaward since 1989 (deYoung and Rose, 1993; Taggart *et al.*, 1994).

deYoung and Rose (1993) proposed a recruitment–distribution model, and argued that northern distributions of this stock are essential to strong recruitment; hence southward shifts in distributions may lead to poor recruitment. A key assumption of this paradigm is that cod at times shift their distributions northward and southward along the shelf in association with environmental events and that as a consequence spawning sites may not be invariable. Small-scale movements of cod in inshore waters around Newfoundland in response to water mass movements and prey distributions are well documented (Jeffers, 1931; Templeman, 1966; Rose and Leggett, 1988, 1989). However, large-scale open ocean distribution shifts, especially as they might influence spawning locations, have not been demonstrated. Distributional shifts have been observed for Barents Sea cod (e.g., Lee, 1952; Beverton and Lee, 1965), although not for spawning regions. Greenland cod stocks prosper only during warm ocean periods (Hansen, 1949).

In the Northwest Atlantic cod occur over a wide range of thermal conditions from Subarctic (Greenland, northern Labrador) to temperate (Georges Bank). Cod are generally considered to be eurythermal fish (Harden Jones and Scholes, 1974). However, a comparison of temperatures at which cod are typically found suggests a tendency to occupy stable thermal ranges that vary among regions and populations (Hansen, 1949; Beverton and Lee, 1965; Woodhead and Woodhead, 1965; Scott, 1982; Bergstad *et al.*, 1987; Rose and Leggett, 1989). Regional differences may arise in part from environmental and acclimation differences, but recent evidence indicates that genetically based physiological adaptations could exist at the population level (Tang *et al.*, 1993). Age differences in thermal adaptations are certain. Young cod in Newfoundland waters produce blood antifreeze proteins more readily than do mature fish and hence have superior abilities to survive cold conditions (Fletcher *et al.*, 1987).

Cod inhabiting the Labrador to Grand Banks zone (NAFO 2J + 3KL) may comprise several populations associated with the Hamilton Bank, NE Newfoundland Shelf, and northern Grand Banks regions (deYoung and Rose, 1993) (Fig. 1). The basis for these populations (biogeographic, genetic) is unknown. However, cod found in these areas have been reported to occur at very different sea temperatures (e.g., Thompson, 1943).

In this paper, we examine the occurrences of cod from the Labrador Shelf to the northern Grand Banks relative to sea temperatures during the past decade. We test a key assumption of the recruitment–distribution model (deYoung and Rose, 1993), namely that large-scale changes in north–south cod distribution patterns are correlated with year-to-year thermal changes. We also test the hypothesis that thermal conditions are correlated with cod distributions relative to depth. We use temperature as an indicator of environmental change in full recognition that temperature may be a proxy for other correlated environmental influences, both abiotic and biotic. Finally, we discuss distribution patterns "hindcast" from our analyses in relation to historically known distribution patterns of cod in Newfoundland waters.

Methods

The data utilized in these analyses originate from two regular programs of the Canadian Department of Fisheries and Oceans (DFO) and a research program conducted jointly by the DFO's Northern Cod Science Program and the Ocean Production Enhancement Network (OPEN). Additional information on these programs is available through cited sources.

The DFO has conducted a bottom trawl survey of NAFO 2J 3KL utilizing a stratified random design each fall (Oct.–Dec.) since 1978 (Bishop *et al.*, 1993). A temperature profile using an expendable bathythermograph or a net mounted CTD has been recorded with most sets. A stratified sample of fish from the catch was aged using otolith methods according to standard practices. Survey data from 1981 to 1992 are used in these analyses.

The DFO has also conducted an observer program on Canadian fishing vessels throughout the period of this study (Kulka and Firth, 1992). Prior to 1986, approximately 20% of vessel days were monitored; since then, 100% coverage has been in place. A total of 121 889 otter trawl sets taken during the winter fisheries (Jan. to Apr., 1981–1991) north of 46°N were used in these analyses. Each set was monitored as to location, duration, gear type, depth, and catch by species. Catch data were standardized by vessel and gear type and duration prior to analyses.

For spatial analyses, the survey and fishery data were divided into three latitudinally based strata: (1) Labrador (north of 52°N); (2) NE Newfoundland Shelf (48–52°N); and (3) northern Grand Banks (46–48°N). The stratification was based on historically derived distribution patterns (Bishop *et al.*, 1993; deYoung and Rose, 1993), and corresponds approximately (but not exactly) with NAFO Divisions 2J, 3K, and 3L.

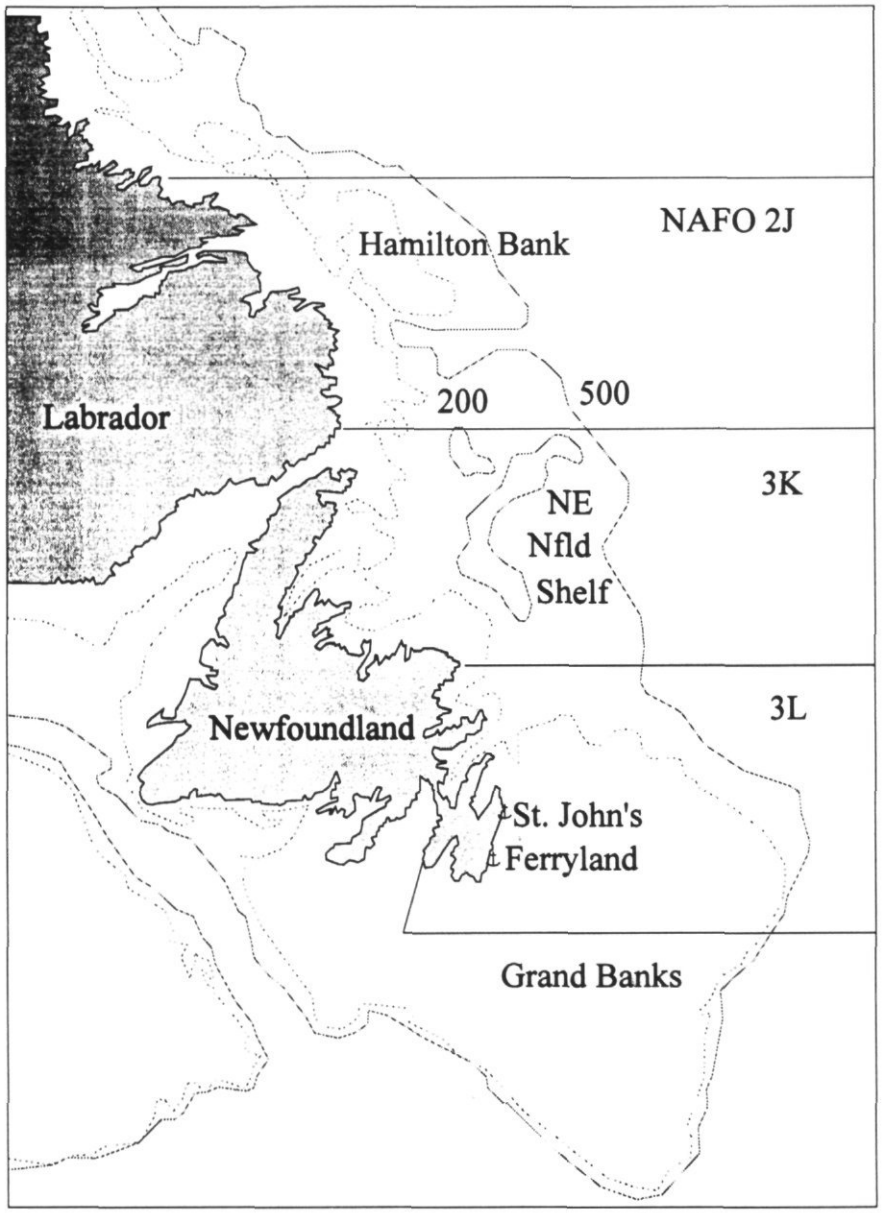


Figure 1. Map of study region from Labrador to northern Grand Banks (NAFO Divisions 2J + 3KL).

Acoustic surveys of migrating cod have been conducted by the DFO and OPEN from 1990 to 1993. These surveys utilized 38 and 49 kHz echosounders to map distributions of cod during their spring post-spawning migrations (Rose, 1993). All acoustic data interpretations were supported by bottom and mid-water trawling. Thermal maps of the ocean were constructed using XBT and CTD data during these surveys.

Depth-averaged temperatures (seasonal signals removed) from station 27 near St John's (190 m) were used as the index of annual thermal conditions on the Labrador and NE Newfoundland Shelves (Fig. 1). Thermal conditions at Station 27 have been shown to be a reasonable indicator for this area (Petrie *et al.*, 1992).

Results

Thermal conditions 1981–1992

The period 1981–1992 has been one of general cooling of the Labrador Current and the coastal waters around Newfoundland (Fig. 2). During this period there have

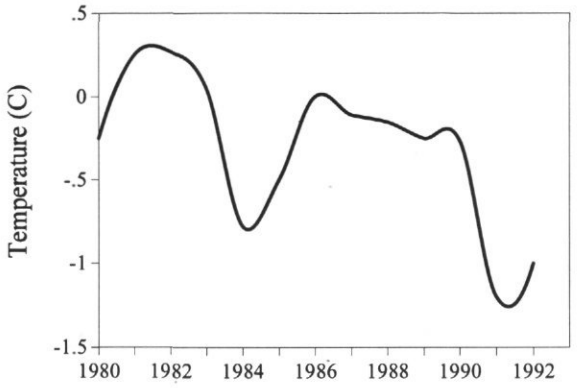


Figure 2. Depth-integrated annual temperature signal at Station 27 off St John's, Newfoundland.

been two periods of intense cooling: 1984–1985 and 1990–1992. The years 1981 and 1982 were the warmest of the decade. Following the cold period 1984–1985, ocean temperatures rebounded in 1986 to warm conditions then declined slowly until 1990 and the onset of severe cooling.

Cod location and immediate temperatures

Cod distributions relative to near-bottom sea temperatures were examined by age and region from the fall research surveys (Fig. 3). Distributions of cod relative to temperature showed evidence of age dependence only off Labrador. Labrador cod of age 3 years were distributed widely across the surveyed range of temperatures from −1.0 to 3.5°C. From ages 4 to 6 an increasing proportion occupied warmer waters; at ages 6 to 7 years >80% inhabited waters having temperatures >1.5°C. The small numbers of cod of ages >8 years were distributed across the range of temperatures >−0.5°C. In contrast, on the NE Newfoundland Shelf, cod older than 3 years inhabited waters having sea temperatures between 2 and 3.5°C. On the northern Grand Bank, >80% of cod of the same ages inhabited cooler waters (−1 to 0.5°C). In all cases distributions differed from those expected under a null hypothesis that distributions would not differ from random occurrences relative to temperature availability (chi-squared tests, $p < 0.01$).

Interannual patterns of distributions relative to sea temperatures also appeared to be regionally dependent (Fig. 4). From year to year, of the three regions examined, Labrador cod were concentrated over the greatest range of average temperatures (−0.5 to 3.0°C) (Fig. 4a). Immature (3–5-year-old) cod were located at colder temperatures than older fish in 9 out of 12 years on the Labrador Shelf (and at approximately equal temperatures in the other 3 years). Northeast Newfoundland Shelf cod were consistently concentrated at the warmest temperatures of any region (1.0 to 3.2°C), while northern Grand Banks cod were consistently found at colder temperatures (−0.4 to 1.7°C) (Fig. 4b,c).

Cod distributions relative to sea temperatures were not consistently related to interannual variability in thermal conditions as measured by the annual depth-averaged temperature at Station 27 (Fig. 4). Cod were not consistently located at warmer temperatures during warmer years nor at colder temperatures during cold years on the Labrador and NE Newfoundland Shelf (Fig. 4a,b). On the northern Grand Banks there is some evidence that cod were located at slightly lower temperatures during cool years ($p < 0.05$) (Fig. 4c).

The temperature ranges where cod concentrate are likely to change seasonally, in particular as cod migrate inshore to feed (Jeffers, 1931; Templeman, 1966; Rose and Leggett, 1989). However, during the early springtime portion of the inshore migration on the outer portions of the NE Newfoundland Shelf, cod were observed to migrate within waters having temperatures similar to those where cod concentrate during the fall (2–3°C) (Fig. 5).

Cod distributions and large-scale temperatures

In general, both the fall survey and winter fishery data indicated that cod exhibited more northerly distributions during warm years and more southerly distributions in cold years (Fig. 6). For example, the periods 1981–1983 and 1986–1988 were characterized by markedly northerly cod distributions. These were the warmest periods of the decade (Fig. 2). Two periods of more southerly distributions were evident: 1984–1985 and 1990–1992. These southerly distributions corresponded with cool periods. For example, in the winter of 1983, following the warm years of 1981 and 1982, cod were distributed well to the north, but distributions appear to be shifting southward by the fall of 1983 (Fig. 6). Throughout 1984 and 1985 the proportion of fish occurring to the north is well below levels of previous years. By the winter of 1986 a more northerly distribution was just beginning to be evident and this northerly trend continues through the warm years of 1986 and 1987 (there is independent evidence from spring acoustic surveys that by the spring of 1986 cod were redistributing northwards (deYoung and Rose, 1993)). Similar patterns but much more severe distribution shifts have been evident since 1989.

Distribution centroids as calculated from the fall research surveys and winter fisheries were similar in every year but 1986 (Fig. 7). Hence, to compare overall cod distribution patterns with annual temperatures the sur-

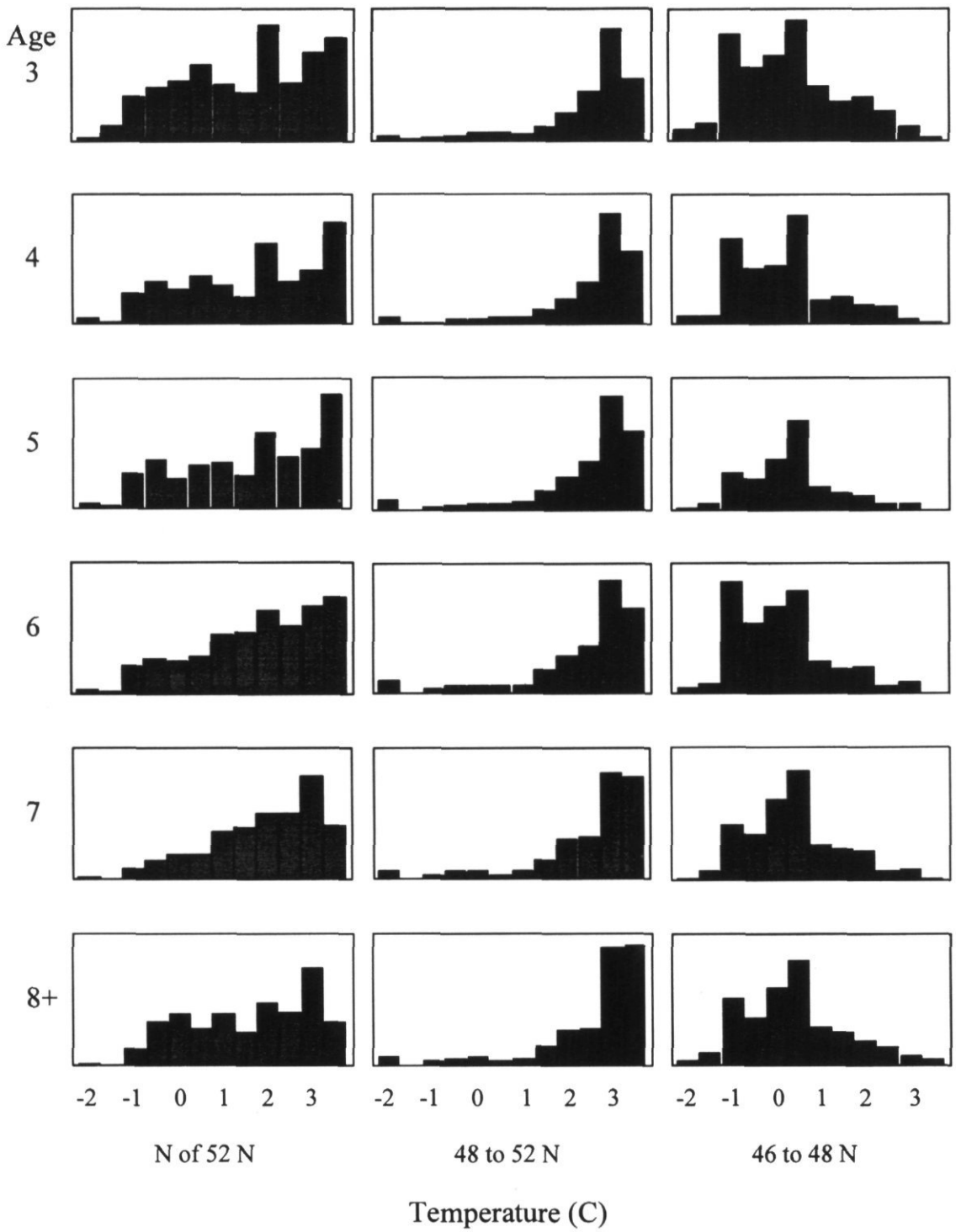


Figure 3. Relative numbers of cod of ages 3–8+ inhabiting regions defined by bottom temperature. Values are totals located at each temperature. Data from fall stratified random trawl surveys divided into three latitudinally defined zones.

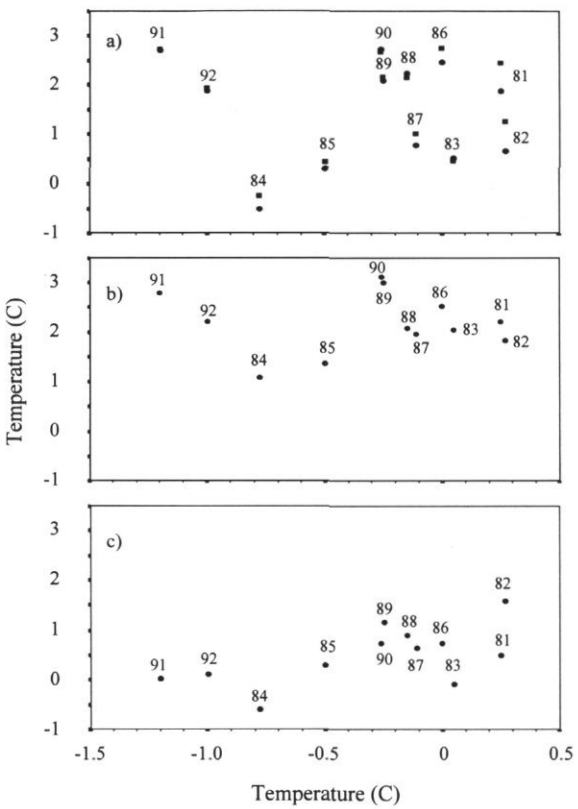


Figure 4. Mean temperature at which cod were located against annual depth-averaged temperature signal from Station 27, near St John's, Newfoundland, for 1981–1992: (a) north of 52°N (circles are 3–5-year-olds, squares age 6+); (b) 48–52°N; (c) 46–48°N. Data are weighted by total biomass of cod caught.

vey and fishery data were pooled (averaged). The mean latitude at which cod were located was positively correlated with the annual sea temperature signal as assessed at Station 27 (latitude = 51.4 + 1.83 temperature (°C), $r^2 = 0.8$, $p < 0.05$) (Fig. 8).

Distribution and depth

Cod have been located at more seaward locations at greater depths during the fall research surveys since 1989 (Fig. 9a). Mean catches increased in deeper waters (>400 m; the shelf break) (Fig. 9b). A similar trend toward deeper catches in recent years is evident in the winter otter trawl fishery (Fig. 9c). C.p.u.e. also increased in deeper waters (Fig. 9d). However, the location of cod relative to depth was not correlated with immediate or large-scale thermal conditions ($p > 0.05$). In particular, during the cold years of 1984–1985 cod were caught at shallower and more variable depths rather than at deeper offshore locations during surveys and by the commercial fleet.

Discussion

Our data indicate that cod from the Labrador and NE Newfoundland shelves to the northern Grand Banks are consistently distributed more to the north in warm ocean periods and more to the south in cold periods, as hypothesized by deYoung and Rose (1993). The magnitudes of the shifts appear to be substantial (at least several degrees of latitude). The southerly shift since 1989 has been particularly severe and longlasting. It is noteworthy that in the spring of 1990, a very large aggregation of age 4+ cod (ca. 20 by 30 nmi) was observed and tracked as it migrated southward and inshore from southern 3K to northern 3L on the NE Shelf (estimated numbers $5.8E^8$, biomass >500 000 t) (Rose, 1993). A comparison of SPA estimates of total stock abundance (age 4+ from Bishop *et al.*, 1993) and these acoustic estimates suggests that this aggregation contained >80% of the full 2J 3KL stock. There exists corroborating evidence that the stock moved southward and became concentrated in the southerly reaches of its range in the spring of 1990: (1) the 1990 inshore fisheries of 3L were the best of the decade, while those of 3K and 2J failed badly (Bishop *et al.*, 1993); and (2) fish tagged from the migrating aggregation were recaptured throughout the range of the good fisheries (Rose, 1993). These patterns in the fisheries and with tag returns continued through 1991 and 1992. It is also evident that these fish, if still present in any numbers (e.g., have not been caught by the southern fisheries), have by 1993 not returned north.

North–south alongshelf movement may lead to variations in spawning locations (deYoung and Rose, 1993). Major spawning events were observed in the southerly portions of the range (northern 3L) in the springs of 1991 and 1992 (Rose, 1993) in areas not historically considered to be major spawning grounds (Hutchings *et al.*, 1993). These recent reports are consistent with the hypothesis that spawning locations may not be invariable in this stock.

Our data also show that young cod are more sedentary and do not shift their distributions as much as older fish do (at least on the Labrador Shelf). It has long been known that young cod are less migratory than older fish (Thompson, 1943).

The correlation of cod distributions and annual environmental signals appears to be somewhat enigmatic. The annual thermal signal at Station 27 (190 m) measures the thermal conditions of the southerly flowing Labrador Current that dominates circulation in this region (Petrie *et al.*, 1992). But cod do not typically inhabit the Labrador Current (Lear *et al.*, 1986), which is characterized by very low temperatures (<−1°C), although they do inhabit waters greatly influenced by the Current, especially off Labrador and on the Grand

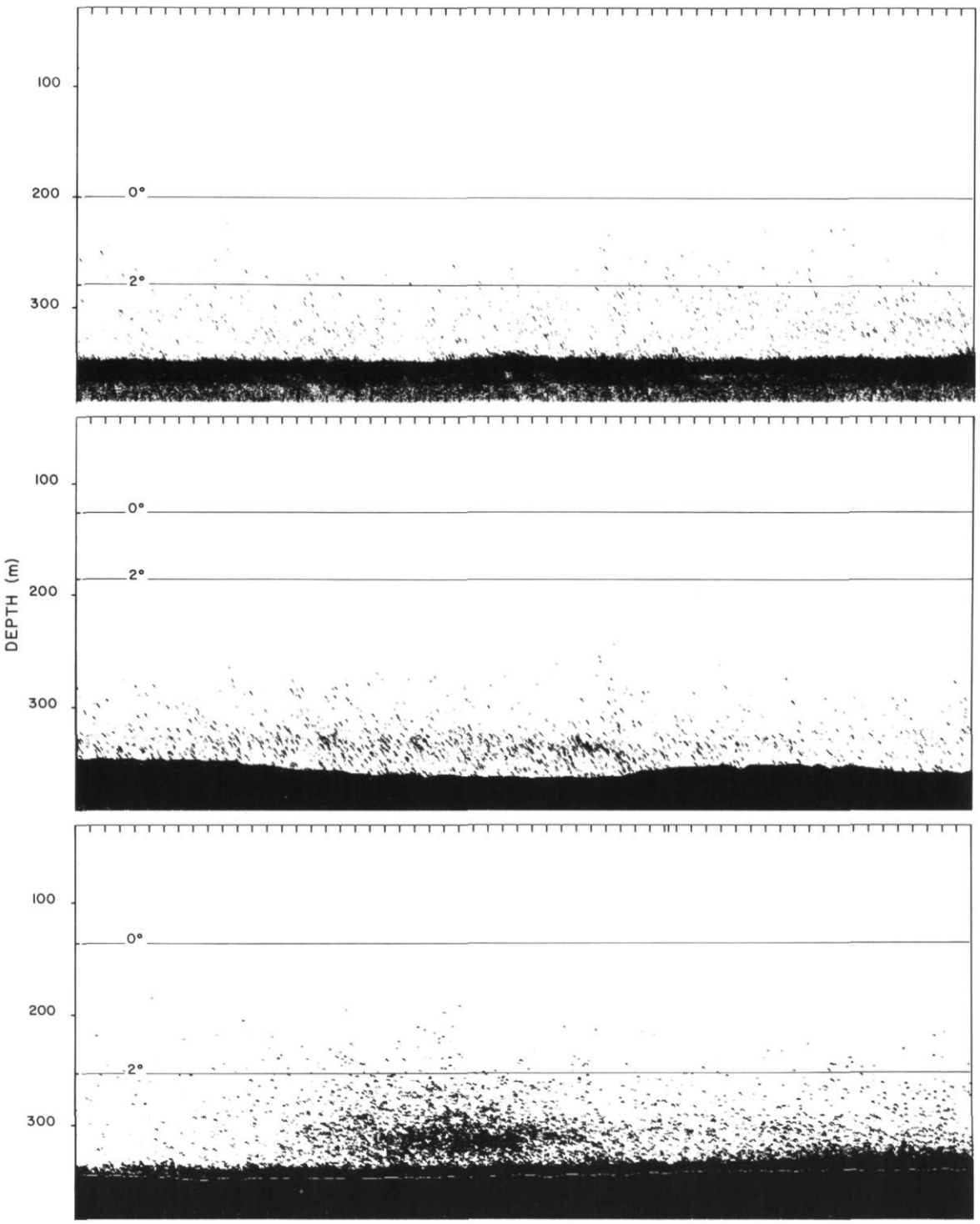


Figure 5. Echograms of migrating cod from June, 1990, 1991, and July 1992. Isotherms in °C. Each panel represents approximately 5 nm.

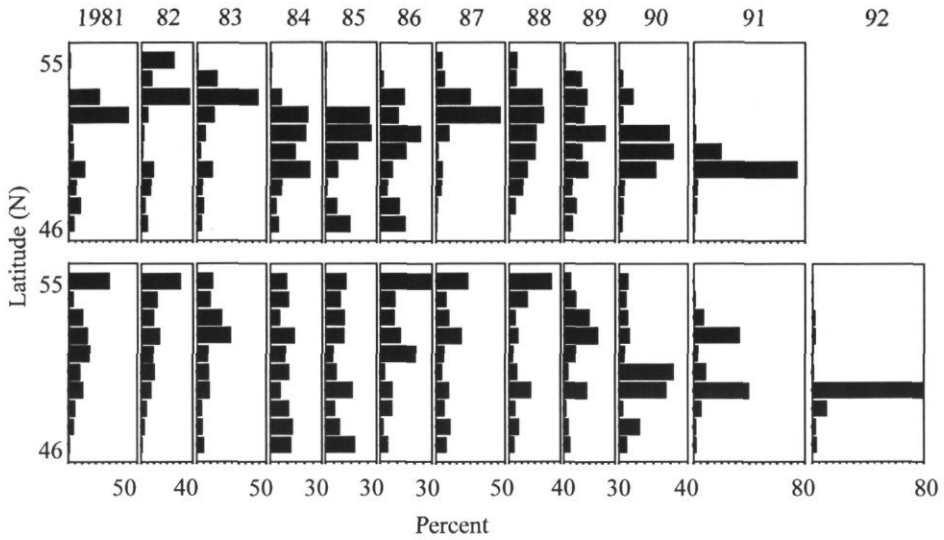


Figure 6. Percentage of cod catch by latitudinal position from winter otter trawl fishery (Jan–Apr 1981–1991; (top panels) north of 46°N latitude on the Grand Banks and NE Newfoundland and Labrador shelves, and from the DFO fall research trawl surveys over the same zone (bottom panels). Fishery data are weighted by a standardized index of c.p.u.e. Survey data weighted by biomass. Survey coverage approximately equal in all years.

Banks. There are several possible explanations. Cod may be responding directly to temperature variations. It is possible that during the twice yearly migrations across the Labrador Current that the signal is "measured" as they "dart in through the cold Arctic Current" (Thompson, 1943). Under this hypothesis, the encountering of very cold conditions during the spring and fall would lead to more southerly offshore migration and wintering areas. But other explanations are possible. It is noteworthy that southward shifts appear to begin in 1989, a year before major declines in sea temperatures at Station 27. It is not clear whether this phase shift results from the particular indices used here (Station 27 is well south of Labrador), or is an indication that other factors are involved. For example, thermal conditions may be a correlate of a more immediate signal coming from other abiotic or biotic factors. A prime candidate is food availability (Lilly, 1994). Capelin are the chief food of cod in this region (Lilly, 1994). Capelin distributions shifted southward after 1989 and have not yet returned to the northerly patterns of the early and mid-1980s (Lilly, 1994). Shifts in distribution of cod in response to thermal conditions and prey distributions have been described at both large (Beverton and Lee, 1965) and

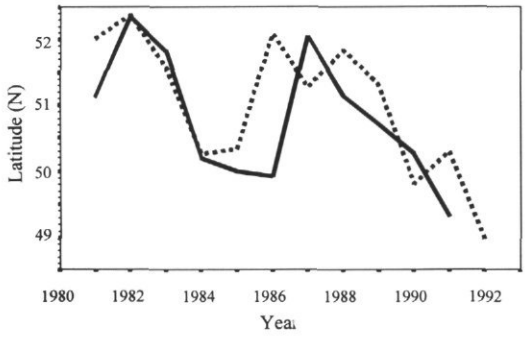


Figure 7. Mean latitudes of cod concentration from the fall research surveys and the winter trawl fishery for the years 1981–1992 (no winter fishery in 1992). Fishery data are weighted by a standardized index of c.p.u.e. Survey data weighted by biomass.

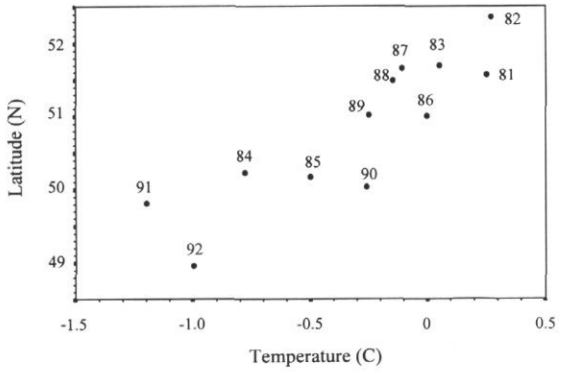


Figure 8. Mean latitudes of cod concentration from fall research surveys and winter trawl fishery against annual depth-averaged temperature from Station 27 near St John's, Newfoundland (latitude = 51.4 + 1.83 temperature, $r^2 = 0.8$, $p < 0.05$).

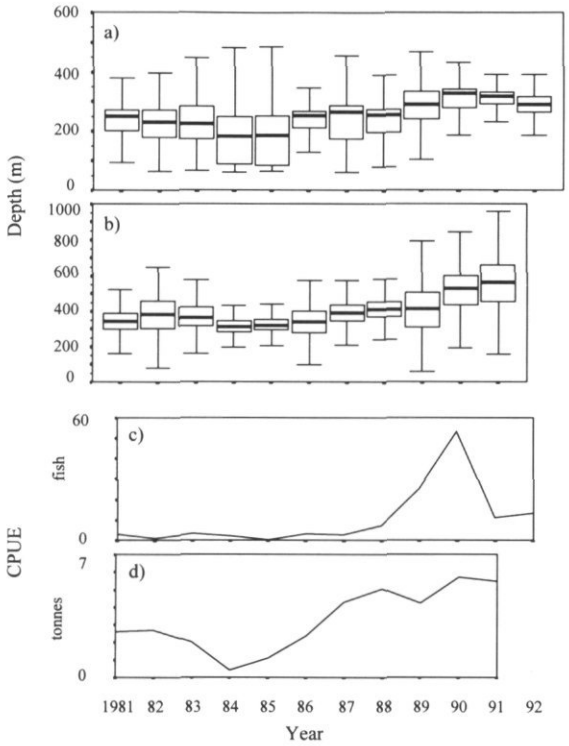


Figure 9. Boxplots of depth of catches of cod in the fall research vessel trawl surveys (a) the winter trawl fishery (b) north of 46°N (NAFO 2J + 3KL) from 1981–1992. Data weighted by total numbers of cod caught (survey) and c.p.u.e. (fishery). Mean catch (c) and mean c.p.u.e. (d) at depths >400 m.

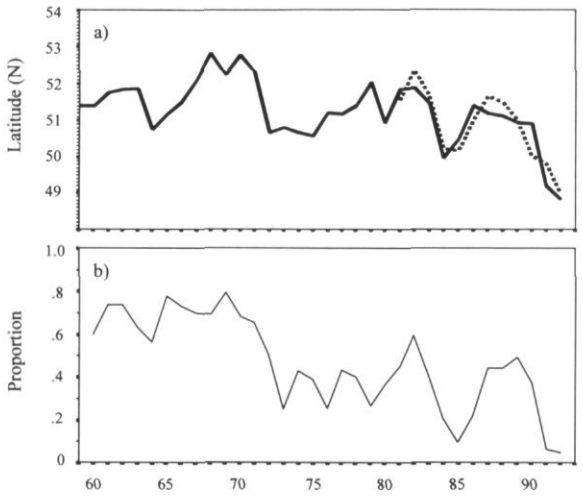


Figure 10. (a) Observed mean latitudes for cod concentration on the NE Newfoundland and Labrador shelves and those predicted by latitude = 54.1 + 1.82 temperature. Predicted values hindcast to 1960. (b) Total fish caught in NAFO 2J (see Fig. 1) as proportion of total catch on Labrador and NE Newfoundland shelves (NAFO 2J + 3K).

small spatial scales (Rose and Leggett, 1989, 1990). Moreover, it is almost certain that fish distribution patterns are not controlled by single factors. Both free-ranging and experimental studies have shown fish distributions to be influenced by a variety of biotic and abiotic factors, especially temperature and food availability (e.g. Rose and Leggett, 1989; Wildhaber and Crowder, 1990). In keeping with these ideas, multi-factorial studies are underway under the Ocean Production Enhancement Network and the Northern Cod Science Program to test the simultaneous influences of physical factors and prey on cod distribution.

To further examine the relationship between sea temperatures and cod distribution patterns, we hindcast the mean distribution centroids back to 1960, when total catch records became available (Fig. 10). The hindcast series suggests that cod were concentrated in the northern areas in the 1960s, with a notable southern movement in 1964. After 1971, the hindcasts suggest cod were concentrated in the mid-latitudes (ca. 51°N) until 1979. There is no direct way these hindcast distributions can be evaluated. However, until 1977 no meaningful catch quotas were in place and the fishery was by and large unregulated. Hence the proportion of the total catch in NAFO 2J (corresponds approximately with our Labrador strata) relative to the full catch north of the Grand Banks (NAFO 3K) gives a general idea of the northward shift of cod on the NE Newfoundland and Labrador shelves (notwithstanding the well-known difficulties of interpreting this type of fishery data). We found that there is general agreement between the hindcast mean latitudes and the proportions of cod caught in the northern zone. Both suggest that cod were distributed well to the north in the 1960s and southward in the 1970s. The hindcast southward distribution shift of 1964 is evident in the fishery data.

Our data confirm a long held contention that the thermal environments that cod inhabit in Newfoundland waters vary among regions (e.g., Thompson, 1943). Young cod in the northern regions appear to have adapted to the cold environments of these regions and show little preference for warmer waters. However, older and presumably mature Labrador cod inhabit warmer waters (1–3.5°C), as do all cod of ages >3 years on the NE Newfoundland Shelf. Cod on the Grand Banks inhabit much cooler waters (to −1°C) at all ages than do cod on the NE Newfoundland Shelf. In all areas the coldest waters (<−1°C) hold very few fish. Younger Barents Sea cod have been reported to inhabit colder waters than older fish (Nakken and Raknes, 1987). It is not known whether these spatial differences are related to physiological differences among fish inhabiting these

regions or are simply the result of acclimation differences. The age differences shown for Labrador cod are consistent with the physiological evidence that younger fish produce greater levels of blood anti-freeze than older fish do (Fletcher *et al.*, 1987; Goddard *et al.*, 1992).

Our analyses of movement patterns assume that fish migrations into and out of the large-scale region employed in this study have been minimal. At scales smaller than those of the full study region, it becomes problematic to judge redistribution patterns (e.g., Lilly, 1994). On the one hand, fish could be redistributing over the full north–south range from the Grand Banks to Labrador. On the other hand, movements could be occurring at smaller scales, to some extent in unison. deYoung and Rose (1993) recently summarized evidence that this cod stock (NAFO 2J 3KL) comprises several populations.

This interpretation would suggest that populations move northward and southward at scales smaller than the full range of our distribution data (even within NAFO zones). At present we cannot judge the correct scale at which to assess substock movements. As a consequence, measures of density dynamics at scales less than the full range may not be diagnostic of movement. For example, unless the small-scale range measured coincides with the very edge of the distribution, then fish that have moved south may be replaced by migrants from the north. One interpretation of such small-scale data could be that no movement had taken place (or even that northward movement had occurred), even though at larger scales the overall southward shift would be apparent. We believe that the definition of the substock spatial structure of cod in NAFO 2J 3KL and documentation of their migratory patterns should be a priority for research.

Our data suggest that Labrador cod moved into the northern areas of the NE Newfoundland Shelf in 1984 and 1985 and then ventured back north in the spring of 1986 (Fig. 6). Moreover, deYoung and Rose (1993) point out that since 1989 a much greater proportion of mature Labrador cod may have moved southward to the NE Newfoundland Shelf than in 1984 (perhaps beyond their former range). Given the tendency of cod to hold temperatures (or water masses), southward voyaging cod from the northern regions would be expected to concentrate in the similarly warm waters of the southern reaches of the NE Newfoundland Shelf and to the north and northeast of the Grand Banks (where temperatures are similar to their typical range, 1.5–3.5°C), and to avoid the colder waters on the Grand Banks. The distribution patterns of cod since 1989 and the apparent retreat of adult cod from the northern ranges mirror this expectation.

The severity of the distribution changes evident since 1989 merits additional comment. Although the initial mean distribution of cod did not differ between the cold years of 1984–1985 and 1990–1991, it is evident that the follow-up to these events has differed greatly. The spring of 1986 brought very warm conditions and cod redistribution northward. The spring of 1992 brought continued cold and retrenchment of southerly positions. We note that capelin distributions also shifted southward in the early 1990s in a manner not seen in the mid-1980s. Sea temperatures remained below normal through much of 1993 but a warming trend was evident by the last half of 1993. Hence it appears that the events of the two periods share some initial characteristics but then differ substantially. If the warming trend evident in late 1993 continues, then the distribution of the extant population in the spring of 1994 should be more northerly than observed in 1993 (reported in deYoung and Rose, 1993).

We conclude that cod distribution patterns in Newfoundland waters are substantially influenced by ocean climate changes. North to south along-shelf movements appear typical in association with warming and cooling oceans. Although the mechanistic links between climate and distribution remain uncertain, there is scant evidence that the observed distribution changes could be caused by spatially differential "pulses" of mortality. Cases of acute environmental stress causing mortality in cod have been reported (e.g., freezing to death; see Thompson (1943) and Woodhead and Woodhead (1965) for examples), but there is no evidence that such mortality has occurred at scales sufficiently large to influence population levels. Cod are very mobile and migratory by nature (Rose, 1993). In the face of a deteriorating environment, cod (at least the more migratory adults) would almost certainly move to seek better conditions.

Could fishing have caused the redistributions, in particular, the most severe shift since 1989? There are several lines of evidence that suggest that fishing mortality is unlikely to have been the primary cause of the observed distribution changes. First, as pointed out by deYoung and Rose (1993), fishing levels were higher in the south than in the north throughout the last decade. Second, unregulated fishing by foreign vessels occurred only in the south. Third, the similar patterns of fishery and the research surveys in regard to latitude (Fig. 10) suggests that distribution controls the fishery and not vice versa. Finally, and perhaps most convincingly, further southward distribution changes have occurred since 1992 in the absence of any fishing pressure to the north (see deYoung and Rose, 1993). Still, we believe that fishing precipitated the declines in abundance in the north, and that fishing mortality contributed substantially to the overall decreases in abundance which have paralleled changes in distribution (Bishop *et al.*, 1993). Thus, natural fluctuations in distribution and declines in abundance have likely been compounded by overfishing to the extent that rebounds in distribution and abun-

dance may have been seriously jeopardized. It is noteworthy that the commercial fisheries in early 1991, both domestic and foreign, capitalized on the southward distributions of cod (see Bishop *et al.*, 1993). Indeed, abrupt increases in fishing mortality in the southern parts of the range after 1989 (Shelton and Morgan, 1993) may have occurred as a direct consequence of the changed distribution patterns.

Acknowledgments

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A review of the trophic interactions of cod stocks in the North Atlantic

Ólafur K. Pálsson

Pálsson, O. K. 1994. A review of the trophic interactions of cod stocks in the North Atlantic. – ICES mar. Sci. Symp., 198: 553–575.

Trophic interactions of the cod stocks in the waters of Newfoundland, Iceland, the Barents Sea, and the North Sea are described on the basis of the available literature and some unpublished material. This includes the feeding habits of the cod stocks and their role as prey of a variety of predators through development stages of the cod, i.e.: (1) the food composition of the cod stocks with respect to major prey groups (fish, crustaceans, other food), as well as stomach content weight; (2) predation by invertebrates (medusae, cephalopods, crustaceans, and chaetognaths) on eggs, larvae, and juveniles of cod; (3) predation by fish, including cod, on cod; (4) predation by seals; (5) predations by whales; and (6) predation by seabirds. In general, predation on cod has been recorded for a number of predators in the taxonomic groups of invertebrates, fish, birds, and marine mammals. In most cases the predatory impact appears to be fairly limited. However, marked predation has been recorded by some predators in most of the taxonomic groups covered. Among these are species like the scyphomedusa *Aurelia aurita*, herring, cod, thorny skate, kittiwake, grey seal, and minke whale.

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Introduction

Studies on the food and feeding of cod and other marine fishes have been part of fisheries research during all of this century and even longer. However, quantitative studies specifically aimed at multispecies analysis have been carried out only during one or two decades. The predation by cod with respect to some major prey groups is briefly summarized in the first section of the paper. The main part reviews available information on the predatory impact on cod by other species of the marine fauna in the Arctic-boreal regions of Newfoundland, Iceland, and the Barents Sea as well as in the North Sea. The purpose of this review is to describe the trophic interactions of the cod stocks, and to identify trophic interactions of particular importance in an ecological context or in terms of management implications. This review will also focus on the shortcomings in the present state of knowledge and, it is hoped, give an impetus to further research.

Materials and methods

For the evaluation of predation by cod with respect to major prey groups, existing databases have been used. For Newfoundland, the data were collected during autumn 1981–1983 and 1985–1989 in NAFO areas 2J 3KL (Lilly, pers. comm.). The Icelandic data were collected in 1979–1992, mainly during March and September–November, on the Icelandic continental shelf. The Barents Sea data cover the period 1984–1992 and the waters of the Barents Sea and Spitsbergen (Mehl, pers. comm.). The North Sea data used are described by Daan (1983).

The existing literature has been scanned for information on predation on cod by marine invertebrates, fish, mammals, and birds. In most cases predation is quantified as frequency of occurrence of the prey in either the total number of stomachs analysed or only in those stomachs containing food. When available, the former measure has been selected, since this can be

regarded as an index of the proportion of the predator stock preying on cod. When available, the percentage weight of cod in the stomach content is preferred above frequency of occurrence. As a rule the percentage weight is given on a length group basis. An average across predator length group is evaluated as an index of predation based on percentage weight of cod in stomach content. In a few cases the proportion of the number of cod as prey against total number of prey (% by number) has been evaluated. Although this procedure of averaging may blur some important detail, it draws attention to the main features in the predator–prey interaction.

Predation by cod

Food composition

Average values of food composition of cod in the four areas have been calculated by predator length groups for three groups of prey, i.e. fish, crustaceans, and other food (Fig. 1). The contribution of fish as food is distinctly lower for North Sea cod compared with the other stocks and somewhat higher for Icelandic cod. The proportion of fish shows a general increase with predator length for all stocks. The increase follows basically a straight line for North Sea cod. For Barents Sea and, especially, Newfoundland cod there is a sharp increase in the proportion of fish in the lower predator length range (<40 cm), but a much slower increase for the larger predators. For Iceland cod the proportion of fish is relatively high in the smallest predators (<20 cm).

The contribution of crustaceans in the stomach content weight is highest for North Sea cod and lowest for Iceland cod, but intermediate and similar for Newfoundland and Barents Sea cod. The overall trend with respect to predator length is the opposite to the proportion of fish for all stocks.

The highest level of other food is observed for North Sea cod, lowest for Barents Sea cod, and intermediate for the other two stocks. The trend generally decreases with predator length. However, the proportion of this group in Barents Sea cod is fairly constant except for the largest and the smallest length groups.

Overall, fish clearly dominates the food constituting more than 50% of the stomach content weight already in the predator length range of 20–39 cm for the Arcto-boreal stocks. For North Sea cod, however, this level is not reached until length group 50–69 cm. The overall contribution of crustaceans is higher than 50% for the Newfoundland, Barents Sea, and North Sea stocks in the predator length range below 20 cm. For Icelandic cod the proportion of crustaceans below 20 cm predator length is reduced in correspondence with high values of fish prey. Clearly, other food is the least important prey group for all stocks, with maximum proportions around 15%.

Stomach content weight

Double logarithmic plots of average weight of total stomach content versus the median of predator length groups generally follow straight lines for all stocks, indicating power relationships (Fig. 2). The power is 3.32, 2.79, 2.86, and 3.09 for Newfoundland, Icelandic, Barents Sea, and North Sea cod, respectively. The value for Newfoundland cod is the only one significantly different from 3 ($p < 0.01$). Thus, in general the weight of the stomach content appears to be linearly related to the weight of the predator.

Predation on cod

Invertebrates

Medusae and ctenophores

Melle (1985) studied the predation induced by the ctenophore *Bolinopsis infundibulum* and the scyphomedusa *Aurelia aurita* in Lofoten. Both species were identified as predators of cod eggs and larvae, in particular *A. aurita* (Table 1). Furthermore, one example of the scyphomedusa *Tiaropsis multicirrata* was observed containing one cod larva.

Laboratory and field studies of the predation by medusae and ctenophores on eggs and larvae of marine fishes have identified at least 34 species of piscivorous medusae and 5 species of ctenophores according to a review by Hunter (1984). Attempts have been made to roughly estimate the consumption by these predators. Fraser (1969) estimates a probable consumption of 50–250 larval fish per hydromedusa during its lifetime, about 450–500 by *Aurelia*, and in the order of 15 000 by *Cyanea*.

Möller (1980) studied the predation by *A. aurita* on herring larvae in Kiel Bight and identified this scyphomedusa both as a competitor for food and as a predator of the larvae. The estimated predation was 2–5% of the total stock of yolk-sac larvae per day. The author concludes that his findings support Fraser's (1969) estimates of predation by medusae.

Based on enclosure experiments, Øiestad (1983) suggested predation by hydromedusae as the most likely cause of the rapid decline in abundance of cod larvae. In addition, he identified medusae as important competitors with larvae for food.

Cephalopods

The abundance of cephalopods in the waters of Newfoundland, Iceland, and Norway is subject to large fluctuations from year to year. In the Northwest Atlantic the short-finned squid (*Illex illecebrosus*) and the long-finned squid (*Loligo pealei*) are most abundant and of

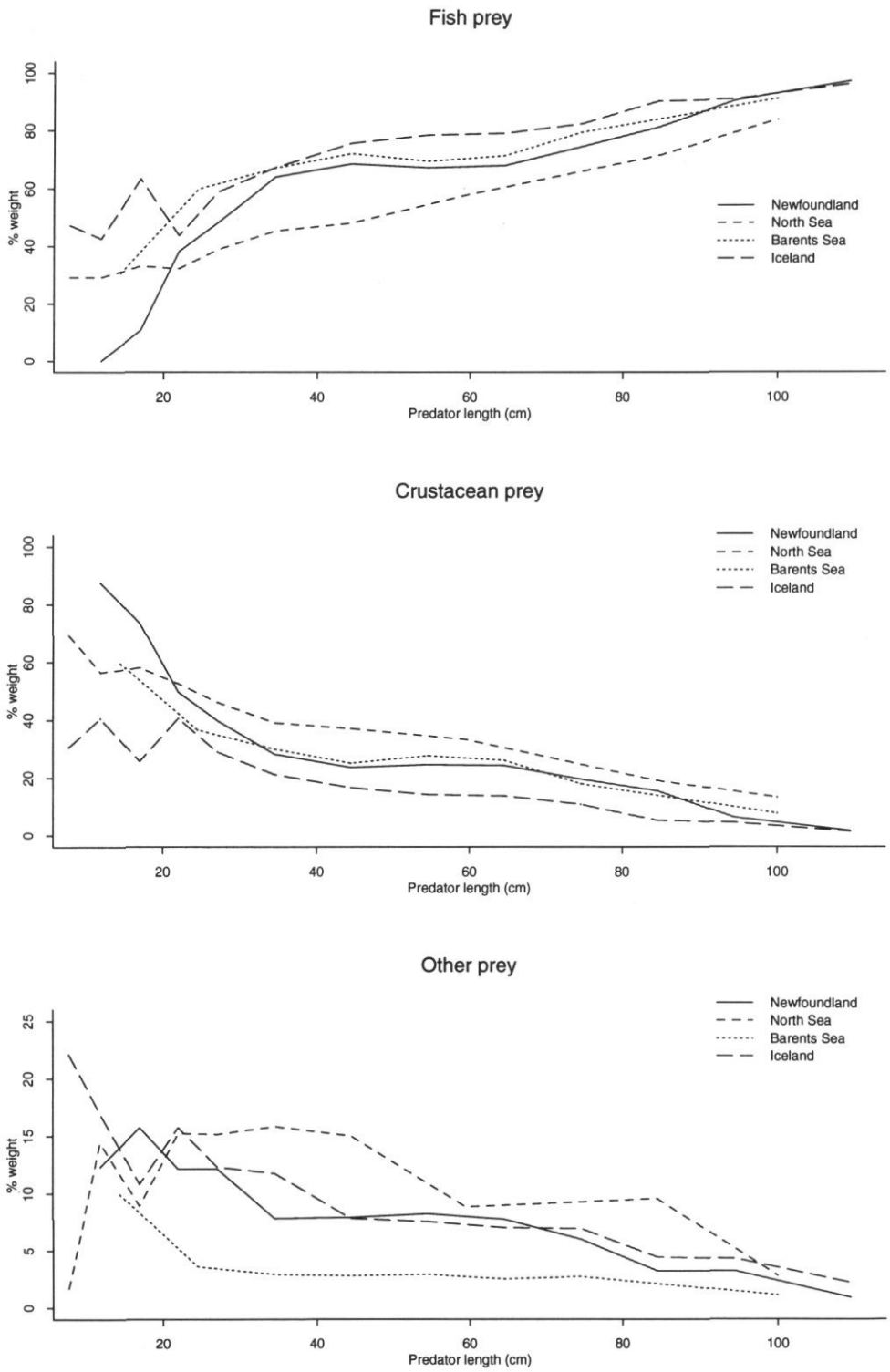


Figure 1. Average composition of the food (% weight of stomach content) of cod: (a) fish prey, (b) crustacean prey, (c) other prey, in four areas.

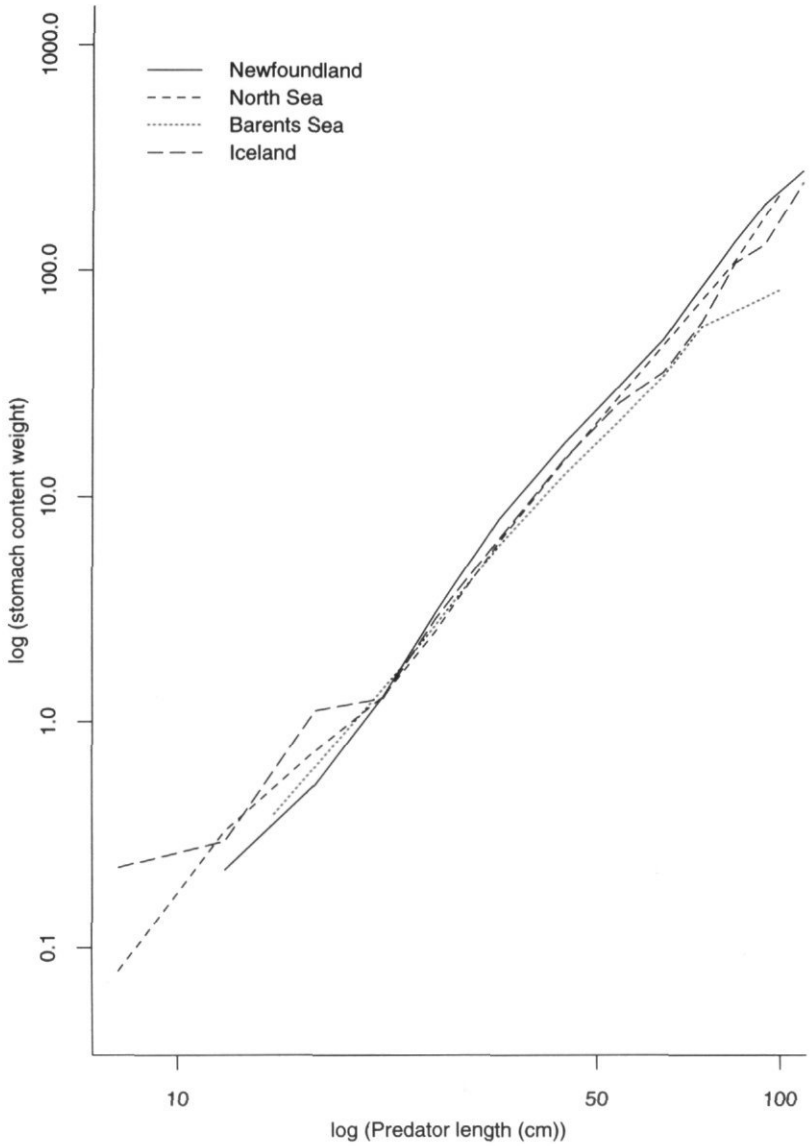


Figure 2. Average stomach-content weight of cod by areas with respect to predator length (log-log scale).

Table 1. Predation by invertebrates on cod eggs and larvae in the Lofoten area indicated as average number of eggs and larvae per 100 predators (n.a. = not available).

Predator	Eggs /100 pred.	Larvae /100 pred.	*n*	Year of sampling	Reference
B. infundibulum	0.7	0.3	4666	1983–1984	Melle (1985)
A. aurita	2.4	3.9	461	1983–1984	Melle (1985)
T. multicirrata	—	1[a]	n.a.	1983–1984	Melle (1985)

[a] One stomach containing 1 larva recorded.

commercial importance, with annual catches of 2000–87 000 t for *Illex* and 11 000–25 000 t for *Loligo* during the last decade (NAFO Stat. Bull.). Short-finned squid migrate northwards to Newfoundland in summer, whereas long-finned squid migrate to shallow waters from Cape Cod to Chesapeake Bay in spring and summer (Maurer and Bowman, 1985).

In Icelandic waters the main species is flying squid (*Todarodes sagittatus*), which migrates occasionally to the southwestern grounds during summer and autumn. It has rarely been recorded since 1966. However, during 1958–1966 the flying squid was more frequently recorded although annual nominal catches were less than 1000 t (Jónsson, 1980).

Flying squid is also the most abundant species in the Barents Sea and the Norwegian Sea, with annual catches of up to 18 000 t during the last decade (Bulletin Statistique and ICES Fisheries Statistics). In the North Sea, cephalopods appear to be less abundant, judging by annual catches, which were mostly less than 1000 t for squid and less than 500 t for cuttlefish during the last decade (Bulletin Statistique and ICES Statistics). In groundfish surveys in the North Sea (IYFS and EGFS), catches of cephalopods have also been very small (ICES, 1987).

Dawe (1992) analysed 11 562 stomachs of short-finned squid at eight coastal Newfoundland localities in 1980–1990, finding that most otoliths occurring in the squid stomachs were from 0-group cod. The average frequency of occurrence of cod was 8.0%. This author also measured almost 4000 cod as prey of short-finned squid at Newfoundland. The size range was 6–175 mm (total length), but only a few specimens were larger than 85 mm. It was recognized by Dawe that the squid may reject the head of 0-group cod larger than 80 mm.

Maurer and Bowman (1985) calculated the consumption by squid (*Illex* and *Loligo*) off the Northeastern United States in 1979 and 1980, concluding that predation by squid on fish of several species, including Atlantic cod, may be a significant source of pre-recruit mortality. Jónsson (1980) analysed the stomach content of flying squid in Icelandic waters in 1979. Fish were the most abundant prey (42% by volume of stomach content), whereas herring was the only fish species quantified (12% by volume). Of other fish species, 0-group cod and haddock were the most frequently recorded as prey. Breiby and Jobling (1985) analysed the food of flying squid in North Norwegian waters in 1982–1983 and identified 11 fish species. Pelagic species were more frequently recorded than gadoid species. The approximate size range of cod as prey was 7–13 cm.

In view of the limited observations available on predation on cod by cephalopods, a quantitative analysis of their predatory impact is not feasible. However, the studies carried out in the different areas clearly show that pre-recruit cod (0-group) are preyed upon by cephalopods in all areas. In view of the regularity and apparent intensity of cephalopod migrations, the cod stocks of the Northwest Atlantic and northern Norway are probably most affected by these predators, whereas their effect on cod in the North Sea and, particularly, in Icelandic waters should be regarded as negligible.

Crustaceans

No direct information is available on predation by crustaceans on eggs or larvae of cod in the field or in experiments. However, consumption of other marine fish larvae by a variety of crustacean groups, e.g. copepods, euphausiids, and hyperiids, has been observed in field as well as laboratory studies (Hunter, 1984). Few crustaceans have been identified as predators of pelagic fish eggs, but very few species have been studied so far (Hunter, 1984). Among the predators of fish larvae, the euphausiid shrimp *Euphausia pacifica* (Theilacker and Lasker, 1974), the hyperiid amphipod *Hyperoche medusarum* (Westernhagen and Rosenthal, 1976; Westernhagen, 1976), the hyperiid amphipod, *Parathemisto gaudichaudi* (Shaeder and Evans, 1975), and marine copepods (Lillelund and Lasker, 1971) have been identified as important invertebrate predators of fish larvae.

Thus, field studies indicate that fish larvae are vulnerable to predation by marine crustaceans such as copepods and hyperiid amphipods. This is supported by observations in freshwater lakes (Hunter, 1984). In view of these findings the predatory impact by crustaceans on cod should be classified as a potentially important source of mortality requiring further research.

Chaetognaths

No information is available on chaetognath predation on cod. An experiment on the feeding behaviour of *Sagitta setosa* and *S. elegans* (Kuhlmann, 1977) indicated no predation on fish eggs. Predation on fish larvae was found to be limited, since copepods are the preferred prey and fish larvae were only preyed on in significant numbers after a starvation period of more than 24 h. These findings suggest that chaetognaths of the genus *Sagitta* are not important predators of fish larvae in general.

Fish

Some pelagic fish species have been identified as predators of cod eggs and larvae (Table 2). Jespersen (1932) analysed stomach contents of 4900 herring (*Clupea harengus*) around Iceland during 1926–1931 and identified approximately 50 postlarval cod, 1.5–3.0 cm in length, in one sample of herring stomachs.

Table 2. Predation by fish on cod eggs and larvae by areas indicated as average number of eggs and larvae per 100 predators and percent of eggs eaten per day of the total egg production (% predation).

Area	Predator	Eggs /100 pred.	Larvae /100 pred.	% predation	*n*	Year of sampling	Reference
Lofoten	Herring	185 000	0	1.4	81	1983	Melle (1985)
Lofoten	Norway pout	0 [a]	0	n.a.	20	1983	Melle (1985)
Lofoten	Cod	0	0	0	13	1983	Melle (1985)
Southern Bight	Herring	360		n.a.	311	1976	Daan 1976
North Sea	Herring	30		0.04–0.19	5 408	1980–1983	Daan *et al.* (1985)
Southern Bight	Sprat	200		n.a.	254	1976	Daan *et al.* (1985)
German Bight	Three spined stickleback	20		n.a.	15	1976	Daan *et al.* (1985)
North Sea	Anchovy		70		363	1976	Garrod and Harding (1981)
North Sea	Sprat		0.1		1 377	1976	Garrod and Harding (1981)
North Sea	Herring		3		81	1976	Garrod and Harding (1981)
North Sea	Whiting		0.2		592	1976	Garrod and Harding (1981)
North Sea	Sandeels		2		394	1976	Garrod and Harding (1981)
North Sea	Grey gurnard		0		283	1976	Garrod and Harding (1981)
North Sea	Dab		0		362	1976	Garrod and Harding (1981)

[a] One stomach contained 37 fish eggs.

Melle (1985) studied the predation by fish on cod eggs and larvae in the Lofoten area during 4 days in April 1983. He identified the herring as a heavy predator of cod eggs. The predatory impact by a herring population of 47 million fish on cod eggs was estimated at 1.4% per day of the total egg production in that area and period (66×10^9 eggs).

More fish species have been investigated in this respect in the North Sea. Cod eggs have mainly been recorded in stomachs of herring and sprat (Fig. 3). Garrod and Harding (1981) examined the frequency at which eggs and larvae of plaice and other fishes occurred in the diets of 3721 fish belonging to 27 species spawning in the west central North Sea in 1976. Fish eggs, other than of the plaice, were found in the stomachs of eight predator species, but not identified to species level. Thus, it can be concluded that at least 19 of the 27 species did not prey on cod eggs. However, for most of the 19 species the number of stomachs analysed was very low (<10 stomachs). Of the seven predator species analysed

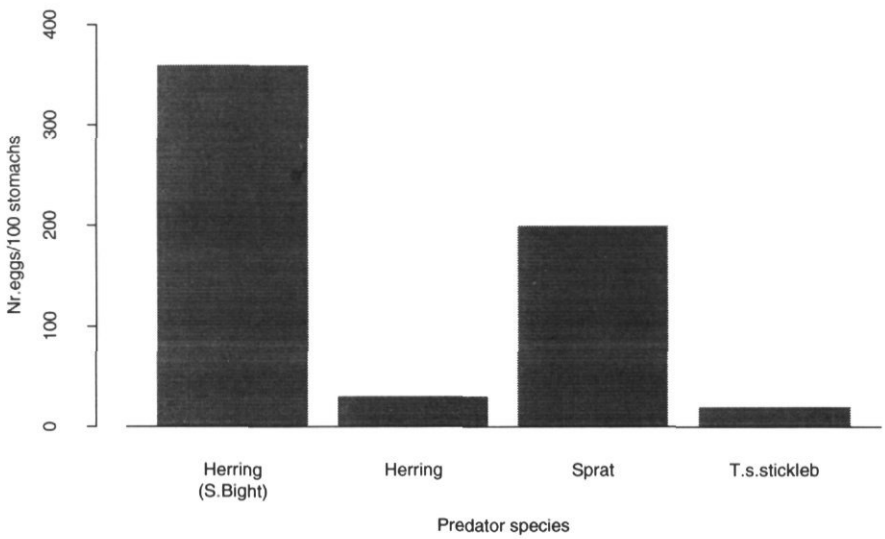


Figure 3. Predation by fish on eggs of North Sea cod.

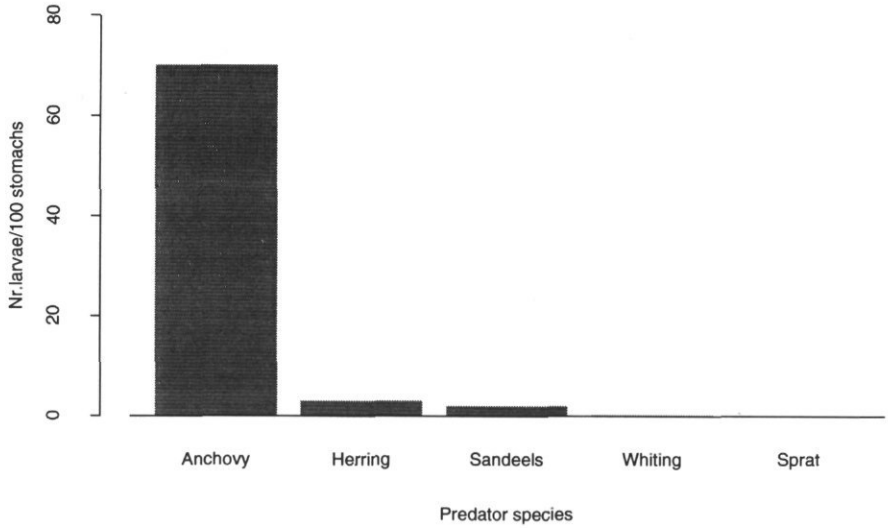


Figure 4. Predation by fish on larvae of North Sea cod.

in the highest numbers (anchovy *Engraulis encrasicolus*, sprat, *Spratus sprattus*, herring, whiting *Merlangius merlangus*, sandeels Ammodytidae, grey gurnard *Eutrigla gurnardus*, and dab *Limanda limanda*), five contained cod larvae (Fig. 4); the largest number (24 larvae) was found in the anchovy.

Stomach content studies of demersal fish are relatively frequent in the four areas covered in this review (Table 3, Fig. 5). Of nine species examined in Newfoundland waters, five were found to prey on cod. Of these, thorny skate (*Raja radiata*), Greenland halibut (*Reinhardtius hippoglossoides*), and cod were identified as relatively outstanding predators of cod, but redfish (*Sebastes* spp.) and spotted wolffish (*Anarhichas minor*) as of very limited importance. Of 12 demersal species examined in Iceland waters, 7 were found to be eating cod. Among these, cod and long rough dab (*Hippoglossoides platessoides*) were more pronounced as cod predators than saithe (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*), Greenland halibut, catfish, and redfish. Of

Table 3. Predation by fish on cod by area waters measured as average (over years and length groups) percent weight of stomach content (% weight) and percent occurrence of cod in stomachs by samples (% occurr.). (+ indicates a very low or an uncertain value of occurrence or weight. n = number of stomachs examined; n.a. = not available.

Area	Predator	% weight	% occurr.	n	Year of sampling	Reference
Newfoundland	Cod	1.1	0.3	1 898	1979	Lilly and Rice (1983)
Newfoundland	Cod	n.a.	0.6	n.a.	1980–1991	Lilly pers. comm.
Newfoundland	Haddock	0	0	452	1963–1975	Podrazhanskaya and Shestov (1981)
Newfoundland	Redfish	+	+	2 669	n.a.	Lambert (1960)
Newfoundland	Atlantic wolffish	0	0	149	n.a.	Templeman (1985)
Newfoundland	Atlantic wolffish	0	0	n.a.	1981	Albikovskaya (1983)
Newfoundland	Spotted wolffish	+	+	n.a.	1981	Albikovskaya (1983)
Newfoundland	Northern wolffish	0	0	n.a.	1981	Albikovskaya (1983)
Newfoundland	Halibut	0	0	5	1950	McIntyre (1953)
Newfoundland	Greenland halibut	5.7	0.5	10 309	1981–1984	Bowering and Lilly (1992)
Newfoundland	Greenland halibut	n.a.	0.8	26 426	1969–1981	Chumakov and Podrazhanskaya 1986
Newfoundland	Thorny skate	4.1	1.5	446	1947–1967	Templeman (1982)
Iceland	Cod	6.0	2.5	43 143	1979–1992	Pálsson (1983)
Iceland	Haddock	0.7	0.8	3 048	1979–1981	Pálsson (1983)
Iceland	Saithe	3.0	0.8	1 755	1979–1981	Pálsson (1983)

Continued overleaf.

Table 3 continued

Area	Predator	% weight	% occurr.	*n*	Year of sampling	Reference
Iceland	Redfish	0.03	0.3	1 614	1979–1981	Pálsson (1983)
Iceland	Catfish	0.1	0.5	2 182	1979–1981	Pálsson (1983)
Iceland	Long rough dab	1.6	1.7	438	1979–1981	Pálsson (1983)
Iceland	Megrim	0	0	205	1976–1977	Steinarsson (1979)
Iceland	Witch	0	0	153	1976–1977	Steinarsson (1979)
Iceland	Lemon sole	0	0	119	1976–1977	Steinarsson (1979)
Iceland	Halibut	0	0	630	1948–1950	McIntyre (1953)
Iceland	Megrim	0	0	428	1938–1960	Rae (1963)
Iceland	Witch	0	0	105	1949–1952	Rae (1969)
Iceland	Greenland halibut	0.4	0.2	1 478	1991–1992	Sólmundsson 1993
Iceland	Black grenadier	0	0	132	1967	Podrazhanskaya 1968
Barents Sea	Cod	3.9	1.4	57 126	1949–1992	Bogstad *et al.* (1993)
Barents Sea	Haddock	0	0	1984	1984–1986	Burgos and Mehl (1987)
Barents Sea	Greenland halibut	0	0	87	1982	Haug and Gulliksen (1982)
Barents Sea	Greenland halibut	n.a.	1.3	43 304	1980–1989	Shvagzhdis (1990)
Barents Sea	Witch	0	0	355	1975–1976	Mattson (1981)
Barents Sea	Fourbeard rockling	0	0	329	1975–1976	Mattson (1981)
Barents Sea	Norway pout	0	0	268	1975–1976	Mattson (1981)
Barents Sea	Silvery pout	0	0	468	1975–1976	Mattson (1981)
Barents Sea	*Galeus melastomus*	0	0	59	1975–1976	Mattson (1981)
Barents Sea	Thorny skate	8.8	8.2	1 352	1983–1987	Berestovsky (1989)
Barents Sea	Round skate	0	0	108	1983–1987	Berestovsky (1989)
North Sea	L.-sp. dogfish		0	613	1921–1963	Rae and Shelton (1982)
North Sea	Bl.-m. dogfish		0	200	1928–1961	Rae and Shelton (1982)
North Sea	Cuckoo ray		0	430	1924–1961	Rae and Shelton (1982)
North Sea	Shagreen ray		0	130	1928–1960	Rae and Shelton (1982)
North Sea	Blonde ray		0	56	1928–1959	Rae and Shelton (1982)
North Sea	Skate		0	255	1928–1959	Rae and Shelton (1982)
North Sea	Starry ray		0	253	1928–1959	Rae and Shelton (1982)
North Sea	Thornback ray		0	334	1928–1959	Rae and Shelton (1982)
North Sea	Spotted ray		0	172	1928–1959	Rae and Shelton (1982)
North Sea	Angler fish		0.4	1 630	1921–1958	Rae and Shelton (1982)
North Sea	Catfish		0	437	1921–1959	Rae and Shelton (1982)
North Sea	Hake		0	416	1923–1959	Rae and Shelton (1982)
North Sea	Brill		0	178	1948–1959	Rae and Shelton (1982)
North Sea	Ling		2[a]	45 [b]	1951–1959	Rae and Shelton (1982)
North Sea	Lythe		0	56 [b]	1951–1959	Rae and Shelton (1982)
North Sea	Tusk		0	20 [b]	1951–1959	Rae and Shelton (1982)
North Sea	Conger eel		0	16 [b]	1951–1959	Rae and Shelton (1982)
North Sea	Halibut		0	13	1949–1951	McIntyre (1953)
North Sea	Megrim		0.1	2 503	1938–1960	Rae (1963)
North Sea	Witch		0	1 751	1938–1953	Rae (1969)
North Sea	Lemon sole		0	4 987	1935–1955	Rae (1956)
North Sea	Norway pout		0	1 129	1960–1962	Raitt and Adams (1965)
North Sea	Cod	4		11 418	1981	Daan (1989)
North Sea	Cod	1.6		9 723	1991	Kikkert (1993)
North Sea	Haddock	0		17 396	1981	Daan (1989)
North Sea	Whiting	0.3		9 217	1981	Daan (1989)
North Sea	Saithe	0.1		2 190	1981	Daan (1989)
North Sea	Mackerel	0.1		4 945	1981	Daan (1989)
North Sea	Horse mackerel	4		395	1986	Dahl and Kirkegård (1987)
North Sea	Starry ray	0		1 838	1983–1986	Vinther (1989)
North Sea	Starry ray	0.6		3 201	1991	Daan *et al.* (1993)
North Sea	*Raja naevus*	0		192	1991	Daan *et al.* (1993)
North Sea	*R. montagui*	0		133	1991	Daan *et al.* (1993)
North Sea	*R. clavata*	0		206	1991	Daan *et al.* (1993)
North Sea	Grey gurnard	1.8		11 700	1991	Gee and Kikkert (1993)

[a] Of stomachs containing food.

[b] Stomachs containing food.

L.-sp. dogfish = Lesser-spotted dogfish, Bl.-m. dogfish = Black-mouthed dogfish.

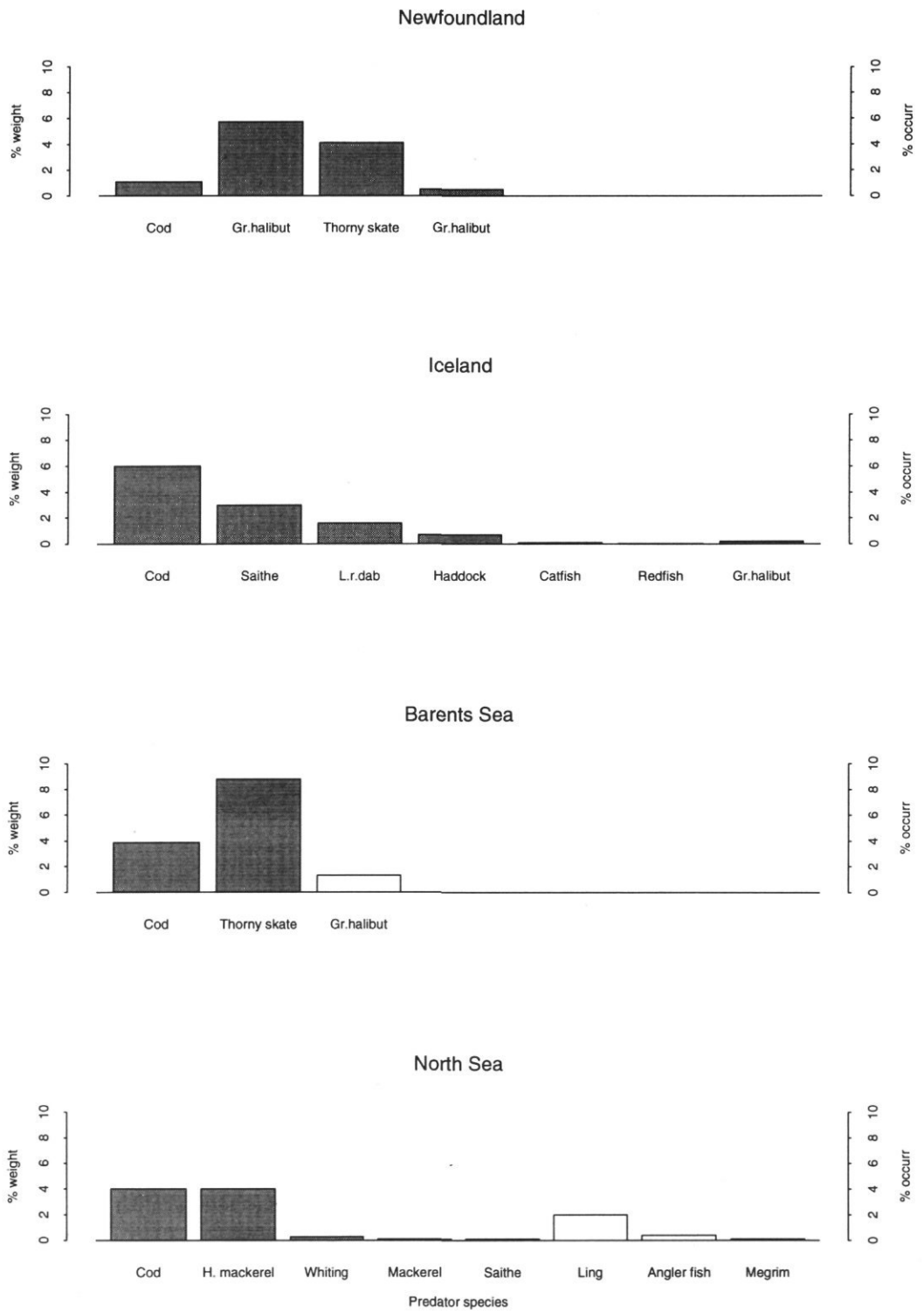


Figure 5. Predation by fish on cod by areas, indicated as % weight (black columns) or % occurrence (white columns).

10 species examined in Norwegian waters only three were found to prey on cod, i.e. thorny skate, cod, and Greenland halibut. Of 33 species in the North Sea, 10 were identified as predators of cod. Most pronounced as predators were cod, horse mackerel (*Trachurus trachurus*), and grey gurnard, where starry ray, whiting, saithe, and mackerel (*Scomber scombrus*) were of relatively minor importance in this respect.

Cannibalism in cod appears to be a relatively important source of predation compared with predation by other demersal fish in most of the areas considered (Table 3, Fig. 5). In Icelandic waters cannibalism occurred in 2.5% of the samples examined and comprised 6% of the average stomach content. Using the correction procedure described in Bogstad *et al.* (1994) it can be calculated that, on an individual fish basis, 0.6% of the cod had consumed cod. Cannibalism in cod in the Barents Sea is analysed by Bogstad *et al.* The incidence of cannibalism in this analysis was 3.9% by weight and 1.4% by occurrence. In the North Sea, cannibalism was more pronounced in 1981 than in 1991 in terms of average weight of stomach content or 4% and 1.6%, respectively. The incidence of cannibalism in cod in the waters of Newfoundland has been found to be low, or 0.6% by frequency of occurrence in divisions 2J 3KL in 1980–1991, (Lilly, pers. comm.), and 1.1% by weight in the northern Grand Bank in 1979 (Lilly and Rice, 1983).

Seals

The most important stocks of seals in the context of fish predation are probably the harbour seal (*Phoca vitulina*), the grey seal (*Halichoerus grypus*), and the harp seal (*Phoca groenlandica*). These stocks differ greatly in population sizes with respect to the various areas. In areas where all three stocks are found (Northwest Atlantic and Barents Sea/Norwegian coast) the harp seal stocks are the largest. In Icelandic waters and in the Baltic, the harbour seal population is larger than the grey seal population, whereas grey seals outnumber harbour seals in the North Sea. Estimates of seal stock sizes in the different areas are summarized in Table 4.

Results of feeding studies on the three seal species in different areas are summarized in Table 5 and shown in Figure 6. In recent years, the method of recalculated weight of the stomach content has mainly been applied, although the less quantitative method of frequency of occurrence is still in use. In the former method, undigested parts, such as otoliths, are used to recalculate the size of the prey.

In general, the predation on cod is most intense in the case of the grey seal (% by weight 19–42%; % by occurrence 11–41%), intermediate for the harbour seal (% by weight <24%; % by occurrence <9%), and relatively limited for the harp seal (% by weight <14%).

There is a marked difference in predation by areas. The harbour seals prey more intensively on cod off Iceland and in the Skagerrak–Kattegat than in the North Sea, Norway, and eastern Canada. The grey seals, on the other hand, seem to prey more heavily on cod in the Gulf of St Lawrence than in the North Sea or off Iceland. For harp seals, increased predation on cod was observed in 1986–1988 during migrations from the Barents Sea to the Norwegian coast. In their Arctic habitats (Canadian arctic, West Greenland, Barents Sea) the predation by harp seals on cod is negligible.

Length measurements and age analyses of cod as the prey of seals indicate that the bulk of the cod belong within the youngest age groups (0–II) and the length range 10–50 cm, although older and larger fish are also recorded. For North Sea grey seals, predation has been recorded on age groups 0–IV, but mainly on the age groups 0–III (Sea Mammal Research Unit, 1988). Cod as prey of grey seals at Anticosti Island, Gulf of St Lawrence, were mainly (≥90%) in this length range (Benoit and Bowen, 1990b). Age analyses of cod as the prey of harbour seals and grey seals in Icelandic waters have shown that approximately 90% or more of the cod belong within age groups 0–II. Age groups III- and IV were also recorded (Hauksson, 1984) and even cod up to 6 years old on occasion (Hauksson, pers. comm.). Cod eaten by harbour seals in the Moray Firth, Northeast Scotland were virtually all 0-group fish (Thompson *et al.*, 1991). Length distribution of cod recorded in harp seal

Table 4. Approximate ranges of seal population sizes for various areas as indicated by available information (total population in thousands).

Area	Harbour seal	Grey seal	Harp seal	Reference
Eastern Canada	10–20	50–100	1000–2500	Templeman (1990)
Iceland	40–50	10–20		Hauksson (1989)
Barents Sea			800–1000	Benjaminsen and Christensen (1979)
Norwegian coast	4.5+	3+		Thompson *et al.* (1990)
North Sea	25+	100		Thompson *et al.* (1990)
Baltic	2	2		Almkvist *et al.* (1980)

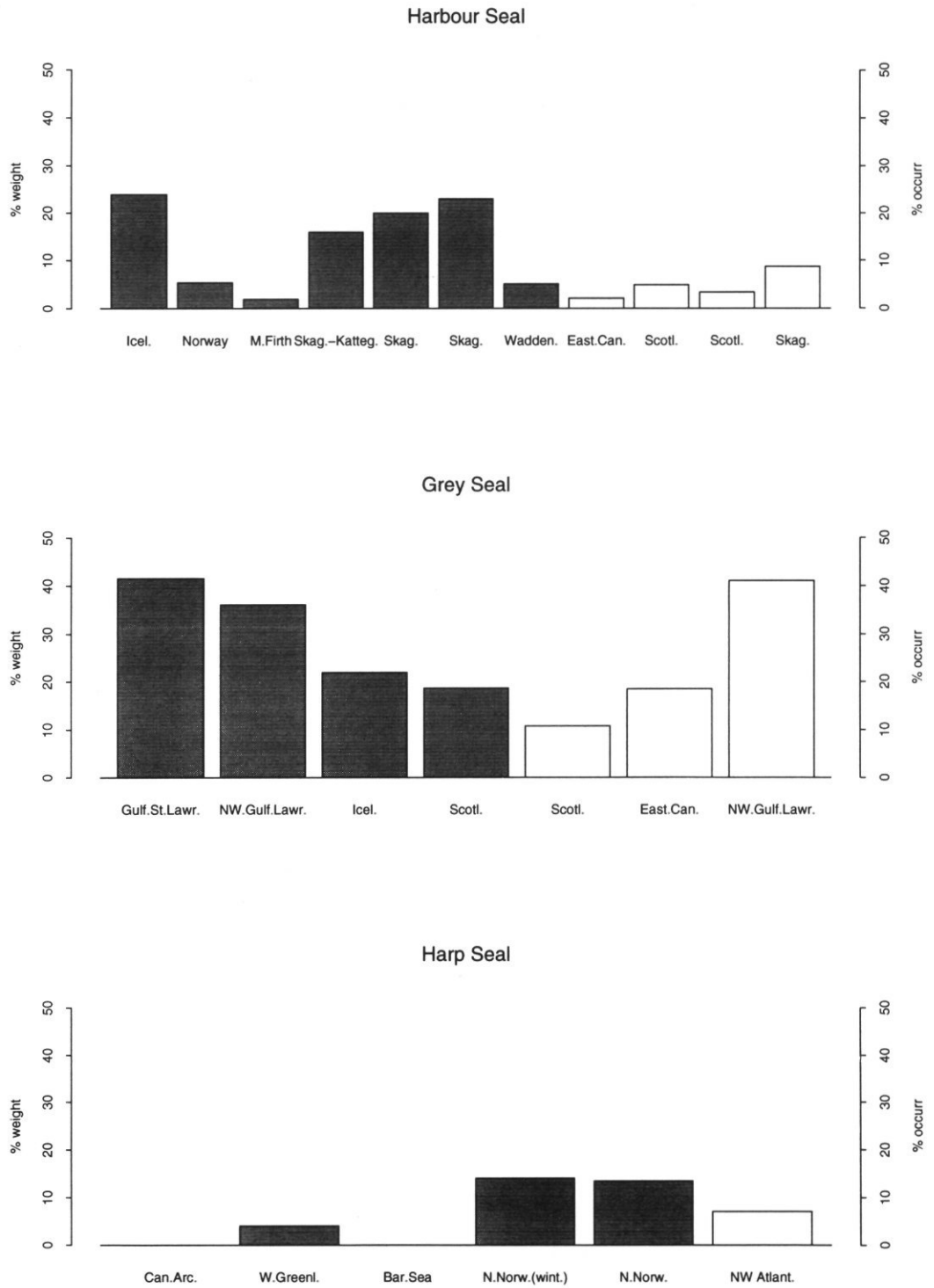


Figure 6. Predation by seals on cod by areas, indicated as % weight (black columns) or % occurrence (white columns).

Table 5. Predation by seals on cod by areas measured as percent recalculated weight or percent frequency of occurrence of cod in stomach or faecal samples.

Predator	Area	% weight	% occurr.	*n*	Year of sampling	Reference
Harbour seal	Eastern Canada	n.a.	2.1	602	1968–1973	Boulva and McLaren (1979)
Harbour seal	Iceland	23.9	n.a.	140	1979–1982	Hauksson (1984)
Harbour seal	Norway coast	5.4	3.4	238	1978–1982	Bjørge *et al.* (1993)
Harbour seal	Scotland	n.a.	4.9	78	1967–1971	Rae (1973)
Harbour seal	Scotland	n.a.	3.4	508	1986–1988	Pierce *et al.* (1990)
Harbour seal	Moray F. (NE Scotland)	1.9	n.a.	40 [a]	1988–1989	Thompson *et al.* (1991)
Harbour seal	Skagerrak-Kattegat	16.0	n.a.	103 [a]	1980	Härkönen (1988)
Harbour seal	Skagerrak	20.0	n.a.	314 [a]	1977–1979	Härkönen (1987)
Harbour seal	Skagerrak	23.0	n.a.	n.a.	1989	Härkönen *et al.* (1991)
Harbour seal	Skagerrak	n.a.	8.8	193 [a]	1990–1991	Olsen and Björge (1992)
Harbour seal	Wadden Sea (North Sea)	5.1	n.a.	138	1981–1984	Sievers (1989)
Grey seal	Eastern Canada	n.a.	18.5	1 878	1950–1987	Benoit and Bowen (1990a)
Grey seal	Gulf St Lawrence	41.5	n.a.	744	1982–1987	Benoit and Bowen (1990b)
Grey seal	NW Gulf St Lawrence	36.0	41.0	82	1983	Murie and Lavigne (1992)
Grey seal	Iceland	30.5	n.a.	215	1990–1991	Hauksson (pers. comm.)
Grey seal	Iceland	22.0	n.a.	89	1979–1982	Hauksson (1984)
Grey seal	Scotland	n.a.	10.8	241	1967–1971	Rae (1973)
Grey seal	Scotland	18.7	n.a.	1 401	1983–1988	Hammond and Prime (1990)
Grey seal	SW North Sea	17.6	n.a.	481	1985	Prime and Hammond (1990)
Harp seal	NW Atlantic	7[b]		n.a.	1949–1971	Sergeant (1973)
Harp seal	Canadian Arctic	0	n.a.	157	1978–1979	Finley *et al.* (1990)
Harp seal	W Greenland	4	n.a.	818	1986–88	Kapel and Angantyr (1989)
Harp seal	Barents Sea (summer)	0	n.a.	58	1987	Lydersen *et al.* (1991)
Harp seal	N Norway (winter)	14.0	n.a.	59	1986, 1988	Nilssen *et al.* (1992)
Harp seal	N Norway	13.5	n.a.	153	1986–1988	Haug *et al.* (1991)

[a] Faecal samples.
[b] % numbers.

stomachs off North Norway covered the length range 5–70 cm, but was mainly (>90%) in the range of 10–55 cm (Nilssen *et al.*, 1992).

Boulva and McLaren (1979) estimated that a harbour seal population of 12 700 in eastern Canada in 1973 could have consumed about 8500 t, mainly fish, and classified the overall economic impact of such a take as negligible.

Hauksson (1989) estimated the consumption of harbour seal and grey seal in Icelandic waters based on population sizes of 43 000 and 12 000 animals, respectively. The calculated total fish consumption by harbour seal and grey seal was 20 431 t and 15 844 t, respectively; the consumption by cod was 6680 and 4145 t respectively. Clearly, such an impact would have major implications for fisheries management.

The annual amount of cod consumed by grey seals in the North Sea has been estimated based on data collected in 1985 (ICES, 1988, Table 2.5.4; Sea Mammal Research Unit, 1988). The number of cod consumed at ages 1–4 was 14.3 million or 4.8% of the size of this stock component (299.2 million). The partial coefficient of natural mortality by age caused by this predation was in the range 0.0034–0.1259.

Hammond and Prime (1990) concluded that a great deal of information is required to assess the impact of seal consumption on commercial fish stocks and fisheries. In addition to consumption of fish and seal population size, data are needed on the local distribution and movements of the fish prey and on the distribution of grey seal feeding effort.

Whales

The stomach content of minke whales (*Balaenoptera acutorostrata*) in various areas of the North Atlantic has been described (Table 6 and Fig. 7). Sergeant (1963) and Mitchell (1974a) analysed the stomach contents of minke whales in the Northwest Atlantic and identified capelin as the predominant food. Cod was the second most important prey with 9% and 12% frequency of occurrence, respectively. The material (32 animals) analysed by Sergeant (1963) was sampled in June–July. However, the occurrence of cod in the food of 338 minke

Table 6. Predation by minke whale on cod by areas measured as percent frequency of occurrence of cod in stomach samples.

Area	% occurr.	*n*	Year of sampling	Reference
Barents Sea	0	13	1950	Jonsgård (1982)
Bear Island	0	53	1950	Jonsgård (1982)
Spitsbergen	4	26	1950	Jonsgård (1982)
Coast of Norway	13	107	1943–1950	Jonsgård (1982)
Coast of Norway	21	34	1988, 1990	Nordöy and Blix (1992)
Spitsbergen	0	17	1989	Nordöy and Blix (1992)
W Spitsbergen	6	16	1992	Haug *et al.* (1993)
Bear Island	5	19	1992	Haug *et al.* (1993)
Kola coast	47	19	1992	Haug *et al.* (1993)
Finnmark coast	15	20	1992	Haug *et al.* (1993)
Lofoten/Vesterålen	16	18	1992	Haug *et al.* (1993)
Iceland	2	58	1977–1978	Sigurjónsson and Galan (1990)
Newfoundland	9	32	n.a.	Sergeant (1963)
Newfoundland	1	338	1948, 1951–1961	Sergeant (1963)
Newfoundland	12	172	1966, 1969–1972	Mitchell (1974a)
Greenland	0	36	1968	Jonsgård (1982)

whales, as reported in whaling statistics from 1948 and 1951–1961, was markedly lower (approximately 1%), (Sergeant, 1963).

Of 237 minke whales from several areas, 15 animals caught in Lofoten and at Spitsbergen contained cod as prey. Some stomachs were completely full of cod and one stomach contained 40 large fresh cod (Jonsgård, 1982). In material sampled off the Norwegian coast in 1988 and 1990, 6 animals out of 29 contained cod (Nordøy and Blix, 1992). In the most recent study of the feeding habits of minke whales caught during scientific whaling operations in the Northeast Atlantic in the summer of 1992, a higher level of predation on cod was recorded in all areas (Haug *et al.*, 1993).

Limited information is available on the size of cod as the prey of whales. "Large" cod were recorded in the stomachs of minke whales sampled in coastal north Norwegian waters during summer 1992 (Haug *et al.*, 1993) and in 1990 (Nordøy and Blix, 1992). Jonsgård (1982) reported one minke whale caught off Spitsbergen with its stomach half full of small fish, probably cod. Furthermore, 14 minke whales from Lofoten contained large cod; one stomach contained 40 large, fresh cod. According to these findings, "large" cod seem to be more frequent as the prey of minke whales than "small" cod.

In one analysis of 58 minke whales from Icelandic waters, one stomach was almost full of cod and another with cod or a cod-like species (Sigurjónsson and Galan, 1990).

Thus, the minke whale has been identified as a predator of cod in some areas. This stock is one of the largest

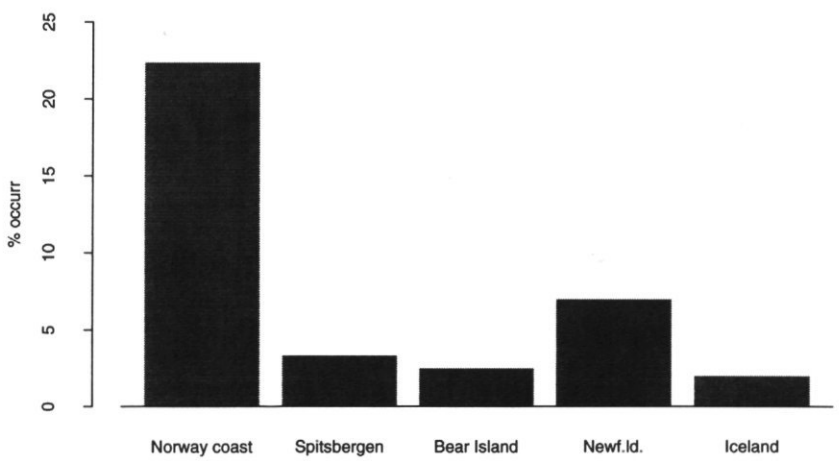


Figure 7. Predation by minke whale on cod by areas, indicated as % occurrence (average values of available results, Table 6).

whale stocks in the North Atlantic. The stock has been estimated at 27 000 animals in Icelandic and adjacent waters (Sigurjónsson and Víkingsson, 1992) and at about 80 000 animals in Norwegian waters (International Whaling Commission, 1991). The annual consumption by minke whales of fish in Icelandic waters has been estimated at about 200 000 t (Sigurjónsson and Víkingsson, 1992). The impact of minke whale predation on cod obviously depends on the reliability of the stomach data. The Icelandic material indicates markedly lower predation by minke whale on cod than observed off Norway and Newfoundland. In general, however, the predator–prey interaction of minke whale and cod must be considered as one of the major whale–cod interactions in the North Atlantic.

Jonsgård (1966) reviewed observations on the food of fin whales (*Balaenoptera physalus*) in Norwegian, Icelandic, and western North Atlantic waters as well as off the British Isles. The fish prey found in stomachs consisted almost exclusively of pelagic species such as herring, capelin, and blue whiting. Cod as prey was recorded only from southwest Greenland waters, where 600 cod were found in one fin whale and 800 in another (Brown, 1875; cited in Jonsgård, 1966). However, this information is considered doubtful (Allen, 1916; cited in Jonsgård, 1966). In an analysis of the food of 435 fin whales caught off the Norwegian coast in 1952–1953, none was found to contain cod, whereas pelagic fish species (capelin, herring, blue whiting (*Micromeristius pontasson*), and mackerel) were found in 22 stomachs (Jonsgård, 1966). This author concluded "that the North Atlantic fin whales do not seem to feed on large fish". Comparable results were reported by Mitchell (1974) for fin whales in the Northwest Atlantic (Table 7).

Mitchell (1973) reported on the stomach content of 41 humpback whales (*Megaptera novaeangliae*) caught off Newfoundland and Nova Scotia in 1969–1971. No cod were identified in the stomachs, but capelin was the prey found in most stomachs containing food. Similar results were found in the case of the sei whale (*Balaenoptera borealis*) in the Northwest Atlantic (Mitchell, 1974b) and in the Norwegian Sea (Hjort and Ruud, 1929). The same is true for blue whale (*Balaenoptera musculus*) in the Norwegian Sea (Hjort and Ruud, 1929) and in the Northwest Atlantic, where several hundred stomachs of blue whale from the region of Newfoundland were analysed (Tomilin, 1967). Thus, the highly specialized foraging of the large baleeen whales on zooplanktonic prey has been recognized for more than a century. Cod has very rarely been identified as prey. The predatory impact of these whale stocks on cod must therefore be regarded as virtually zero.

Roe (1969) examined 57 sperm whales (*Physeter macrocephalus*) caught off the west coast of Iceland in 1967. Cod was identified in the stomach of three animals (Table 7). Martin and Clarke (1986) examined 221 sperm whales captured between Iceland and Greenland in 1977–1981, finding that cod was commonly represented by otoliths but rarely, if ever, by flesh. They concluded that it would seem reasonable to classify cod, along with a number of other fish species, as of secondary importance in the fish biomass consumed by sperm whales, whereas lumpfish (*Cyclopterus lumpus*) provided at least 50% of the fish biomass. Stomach content analyses of northern bottlenose whale (*Hyperoodon ampullatus*) and pilot whale (*Globicephala melas*) indicate that these species do not prey on cod (Table 7).

More limited information is available on the food of other toothed whales, such as the killer whale (*Orcinus orca*), the white-beaked dolphin (*Lagenorhynchus albirostris*), the white-sided dolphin (*L. acutus*), and the harbour porpoise (*Hyperoodon ampullatus*). According

Table 7. Predation by baleen whales, other than minke whale and toothed whales, on cod by areas measured as percent frequency of occurrence of cod in stomach samples.

Predator	Area	% occurr.	*n*	Year of sampling	Reference
Blue whale	Norwegian Sea	0	n.a.	n.a.	Hjort and Ruud (1929)
Blue whale	NW Atlantic	0	n.a.	n.a.	Tomilin (1967)
Fin whale	Coast of Norway	0	435	1952–1953	Jonsgård (1966)
Fin whale	NW Atlantic	<1	n.a.	1967–1972	Mitchell (1974b)
Humpback whale	NW Atlantic	0	41	1969–1971	Mitchell (1973)
Sei whale	Norwegian Sea	0	n.a.	n.a.	Hjort and Ruud (1929)
Sei whale	NW Atlantic	0	n.a.	1967–1972	Mitchell (1974b)
Sperm whale	Iceland	5	57	1967	Roe (1969)
Northern bottlenose	Labrador	0	108	1971	Benjaminsen and Christensen (1979)
Northern bottlenose	Iceland	0	46	1967	
Pilot whale	Faroe Is.	0	720	1986–1987	Desportes and Mouritsen 1988

to Tomilin (1967), cod have been identified in the stomachs of three of these species, i.e., killer whale, white-beaked dolphin, and harbour porpoise. According to Lepektin (1805, cited by Tomilin 1967), a killer whale which ran aground in Norway contained "600 codfishes, numerous birds and an enormous quantity of still undigested herrings".

Sigurjónsson and Víkingsson (1992) have estimated the annual consumption of whales in Icelandic and adjacent waters. The total fish consumption by toothed whales was estimated to be 850 000 t. Thereof, the fish consumption by the four cod predator species (sperm whale, killer whale, white-beaked dolphin, and harbour porpoise) was about 300 000 t. Killer whales consumed almost 50% of this amount, or 140 000 t, and the other three species 46 000 to 68 000 t each. Further stomach content analyses of the toothed whales are needed to identify the prey species composition of the fish consumed by these predators.

Seabirds

Few studies are available of predation by seabirds on cod in the Northwest Atlantic (Table 8). Studies of the feeding habits of three species of seabirds, mainly in the high Arctic, indicate limited predation on cod. Brünnich's guillemot (thick-billed murre, *Uria lomvia*), northern fulmar (*Fulmarus glacialis*), and little auk (*Alle alle*), taken off Baffin Island and Northwest Greenland, did not prey on cod (Roby *et al.*, 1981; Bradstreet, 1982; Bradstreet and Cross, 1982). Stomachs of Brünnich's guillemot sampled in Ungava Bay, Hudson Strait, contained many otoliths of Atlantic cod (Tuck and Squires, 1955).

In Icelandic waters studies in this field are also limited (Table 8). Tåning (1930) described the food of auks in Icelandic waters in a popular article. His findings, based on an unknown number of stomachs, indicated postlarval fish as an important food, especially haddock as well as cod and also whiting, Norway pout (*Trisopterus esmerkii*) and capelin (*Mallotus villosus*).

Ingólfsson (1976), in analysing the stomach contents of great black-backed gulls (*Larus marinus*) and glaucous gulls (*L. hyperboreus*), found that the fish prey were mostly sand lance and capelin. Other fish, usually young gadoids, were recorded from 28 great black-backed gulls (13.4% occurrence) and 11 glaucous gulls (4.6% occurrence). Cod were not identified as a species.

Lilliendahl (1990) studied the feeding of two guillemot species and razorbill in three fjords (Faxaflói, Eyjafjörður, and Skjálfandi) during September–May and recorded no predation on cod. However, four gadoid fish were recorded in one Brünnich's guillemot in Eyjafjörður in April 1983.

A large number of studies on the feeding habits of seabirds have been carried out in the Barents Sea (Table 8). Erikstad (1990) studied the feeding of four seabird species in the open water of the southeastern Barents Sea, near the ice edge. 1-group cod were recorded in all species, most frequently in Brünnich's guillemot (58.3% frequency of occurrence) and kittiwake (*Rissa tridactyla*) (57.7%), followed by glaucous gull (18.2%) and northern fulmar.

Barrett *et al.* (1990) studied the diets of shags (*Phalacrocorax aristotelis*) and cormorants (*P. carbo*) along the Norwegian coast through analyses of regurgitated pellets. Cod was recorded in cormorants, and unidentified gadoids (cod or saithe), mainly 0- and 1-group, occurred frequently in both bird species.

Cod as the prey of fulmar, kittiwake, glaucous gull, and Brünnich's guillemot in the Barents Sea in March 1987, were 1-group fish in the length range 1.9–13.6 cm, but differing between species (Erikstad, 1990). Cormorants and shags in coastal Norwegian waters were found to prey on 0–II group gadoids (cod and saithe) in the length range 2–36 cm (Barrett *et al.*, 1990).

In the North Sea, numerous studies have covered the predatory aspects of seabirds (Table 8). Pearson (1968) studied the diet of nine seabird species through analysis of regurgitated food. Ammodytidae and Clupeidae were the commonest food of most species. Cod were recorded in four species, i.e., kittiwake, lesser black-backed gull (*Larus fuscus*), shag, and cormorant, but their quantity was not measured. However, the percentage by weight of Gadidae in the diet of the four species were 21%, 52%, 30%, and 19%, respectively.

Harris and Hislop (1978) and Hislop and Harris (1985) analysed fish dropped by puffins (*Fratercula arctica*) feeding youngs at colonies around the coast of Scotland. Cod were recorded in the diet on the Isle of May. Gadoids were recorded on the Isle of May and on Hermaness. Furness and Hislop (1981) studied pellets of the great skua (*Catharacta skua*) in Shetland and did not record cod as prey. Blake *et al.* (1985), in studying the feeding ecology of guillemots off North and East Scotland, recorded cod only occasionally, whereas gadoids (mainly saithe and *Trisopterus* sp.) were more abundant and sandeel the commonest prey. Blake (1984) studied the diet of auks in the North Sea. Cod were not identified but some other gadoids occurred occasionally. Galbraith (1983) examined chick regurgitations of kittiwakes on the Isle of May, Firth of Forth, Scotland, identifying mainly sand-eels but no cod as prey. Comparable results were obtained by Furness and Todd (1984) for the diet of fulmars at Foula, Shetland. Harris and Wanless (1991) analysed regurgitated food and pellets from shags on the Isle of May. Sandeels dominated in the diet but cod were recorded in 18.2% of the pellets although in low numbers. Cod were not recorded in the regurgitations.

Table 8. Predation by marine birds on cod by areas measured as percent by numbers of prey and percent frequency of occurrence.

Area	Predator	% number	% occurr.	*n*	Year sampling	Reference
NW Atlantic	Brünnich's guillemot	+	+	34[a]	1954	Tuck and Squires (1955)
NW Atlantic	Brünnich's guillemot	0	0	n.a.[b]	1954	Tuck and Squires (1955)
NW Atlantic	Brünnich's guillemot	0	0	115	1978–1979	Bradstreet and Cross (1982)
NW Atlantic	Northern fulmar	0	0	115	1978–1979	Bradstreet and Cross (1982)
NW Atlantic	Little auk	0	0	410	1976–1979	Bradstreet (1982)
NW Atlantic	Little auk	0	0	204	1978	Roby *et al.* (1981)
Iceland	Great black-backed gull	0	0	223	1964–1965	Ingólfsson (1976)
Iceland	Glaucous gull	0	0	244	1964–1965	Ingólfsson (1976)
Iceland	Brünnich's guillemot	0	0	37[c]	1982–1983	Lilliendahl (1990)
Iceland	Razorbill	0	0	101	1982–1983	Lilliendahl (1990)
Iceland	Common guillemot	0	0	123	1982–1983	Lilliendahl (1990)
Barents Sea	Kittiwake	29	58	26	1987	Erikstad (1990)
Barents Sea	Kittiwake	+	+	34	1985	Lønne and Gabrielsen (1992)
Barents Sea	Kittiwake	0	0	20	1984	Lydersen *et al.* (1989)
Barents Sea	Kittiwake	0	0	72	1983	Furness and Barnett (1985)
Barents Sea	Glaucous gull	15	18	11	1987	Erikstad (1990)
Barents Sea	Glaucous gull	0	0	18	1984	Lydersen *et al.* (1989)
Barents Sea	Great black-backed gull	0	0	12	1983	Furness and Barnett (1985)
Barents Sea	Herring gull	0	0	45	1983	Furness and Barnett (1985)
Barents Sea	Northern fulmar	8	17	30	1987	Erikstad (1990)
Barents Sea	Northern fulmar	0	0	20	1984	Lydersen *et al.* (1989)
Barents Sea	Puffin	0	0	14	1984	Lydersen *et al.* (1989)
Barents Sea	Puffin	0	0	193	1983	Furness and Barnett (1985)
Barents Sea	Black guillemot	0	0	20	1984	Lydersen *et al.* (1989)
Barents Sea	Black guillemot	0	0	13	1985	Lønne and Gabrielsen (1992)
Barents Sea	Black guillemot	0	0	20	1983	Furness and Barnett (1985)
Barents Sea	Common guillemot	0	0	1 580	1983	Furness and Barnett (1985)
Barents Sea	Brünnich's guillemot	81	58	24	1987	Erikstad (1990)
Barents Sea	Brünnich's guillemot	0	0	50	1983	Furness and Barnett (1985)
Barents Sea	Brünnich's guillemot	0	0	34	1985	Lønne and Gabrielsen (1992)
Barents Sea	Brünnich's guillemot	0	0	21	1984	Lydersen *et al.* (1989)
Barents Sea	Shag	0	0[d]	204	1985–1986	Barrett *et al.* (1990)
Barents Sea	Shag	0	0	9	1983	Furness and Barnett (1985)
Barents Sea	Cormorant	14	3[e]	100	1989	Barrett *et al.* (1990)
Barents Sea	Eider	0	0	20	1984	Lydersen *et al.* (1989)
Barents Sea	Little auk	0	0	11	1984	Lydersen *et al.* (1989)
Barents Sea	Razorbill	0	0	24	1983	Furness and Barnett (1985)
North Sea	Common guillemot	+	+	750	1982–1983	Blake *et al.* (1985)
North Sea	Common guillemot	0	0	403	1983	Blake (1984)
North Sea	Razorbill	0	0	503	1983	Blake (1984)
North Sea	Kittiwake	0	0	147[f]	1982	Galbraith (1983)
North Sea	Kittiwake	+	+	218	1961–1963	Pearson (1968)
North Sea	Lesser black-backed gull	+	+	68	1961–1963	Pearson (1968)
North Sea	Fulmar	0	0	177[f]	1978–1982	Furness and Todd (1984)
North Sea	Shag	+	+	24	1961–1963	Pearson (1968)
North Sea	Shag	0.2	18.2	1 476	1985–1990	Harris and Wanless (1991)
North Sea	Cormorant	+	+	100	1961–1963	Pearson (1968)
North Sea	Puffin	0	+	638[g]	1971–1976	Harris and Hislop (1978)
North Sea	Puffin	0.9	n.a.	1 062[h]	1973–1982	Hislop and Harris (1985)
North Sea	Great skua	0	0	n.a.	1975–1976	Furness and Hislop (1981)

[a]Stomachs of adults. [b]Food to young. [c]Gadoid fish in one stomach. [d]Unid. gadoids 20–71% occurrence. [e]Unid. gadoids 9–17% occurrence. [f]Chick regurgitations. [g]Sampling on Isle of May, Fair Isle and Hermaness. [h]Number of loads to young, Isle of May.

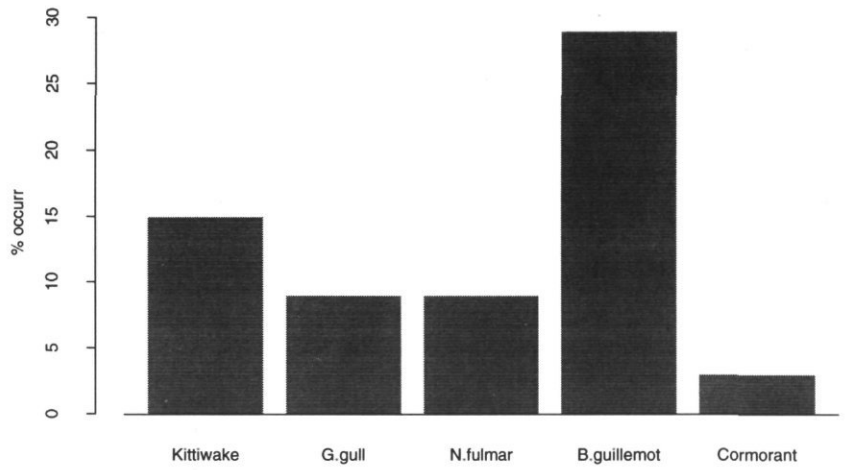


Figure 8. Predation by marine birds on cod in the Barents Sea, indicated as % occurrence.

Conclusions and discussion

The main findings regarding life-stage, size, and age of cod falling prey to other marine animals, based on the studies mentioned earlier, are summarized in Figure 9. Cod eggs were identified in relatively few predators, and were mainly preyed on by invertebrates and pelagic fish, especially herring. Cod larvae were also primarily identified as the prey of invertebrates and pelagic fish.

0-group cod appear to be the life-stage most vulnerable to predation and were identified as the prey of most predators, the exceptions being invertebrates and small pelagic fish. 1-group cod were identified as the prey of predators other than invertebrates and pelagic fish. Older cod were only found as the prey of cod, seals, and minke whale as well as cormorants (2-group). The length range of the prey varies accordingly, the largest prey, up to 70 cm, being found in cod, seals, and minke whale, whereas for other predators the prey length was usually less than 20 cm.

The food composition of cod on a prey group basis indicates a similar trophic level for the four cod stocks, in particular of the three Arcto-boreal stocks. Fish prey is clearly the main level of food. However, it is well known that prey species are different between North Sea cod and the other stocks, capelin being the main fish prey for the northern cod stocks and various demersal and pelagic species for the North Sea cod. The crustacean group is most important for the smallest cod (<30 cm), but contributes also markedly to the diet of small and medium-sized cod (30–70 cm). Other food contributes the least to the diet of cod in all areas.

The trophic interactions of the cod stocks are summarized in Table 9. Clearly, this information is subject to considerable uncertainty in view of the differences in methods, data treatment, time of studies, predator species studied in the different areas, and other aspects. The findings should, therefore, be regarded as a first indication of relevant trophic interactions of the cod stocks in question. The absolute predatory impact is obviously very much dependent upon the size of the respective predator stock, which is only occasionally dealt with in this review.

Two species of marine invertebrates have been identified as relatively important, i.e. *A. aurita* as a predator of eggs and larvae in the Barents Sea and short-finned squid as a predator of 0-group cod in Newfoundland waters. The scarcity of invertebrate predators can hardly be interpreted as an indication of the limited predatory impact of this predator group on cod. Studies of the predation of marine invertebrates on fish as prey as well as laboratory experiments suggest interesting and relevant trophic interactions between marine invertebrates and eggs and larvae of fish. Intensive studies are obviously required in this field.

Predation by fish on cod has been recorded for various groups, e.g., pelagic and demersal fish, flatfish, and elasmobranch fish. The predation covers all life-stages of cod as prey, from eggs and larvae to medium-sized fish, although the main predatory impact seems to be on the pre-recruit phase. However, predation by pelagic fish has only been recorded on eggs, larvae, and 0-group cod. Most noticeable is the predation by herring on eggs in the Lofoten area, by anchovy in the North Sea on cod larvae, and by horse mackerel in the North Sea on 0-group cod. Among demersal fish, cod is apparently the most important predator of juvenile cod, especially age groups 0–II, in three of the four areas, followed by thorny skate and Greenland halibut.

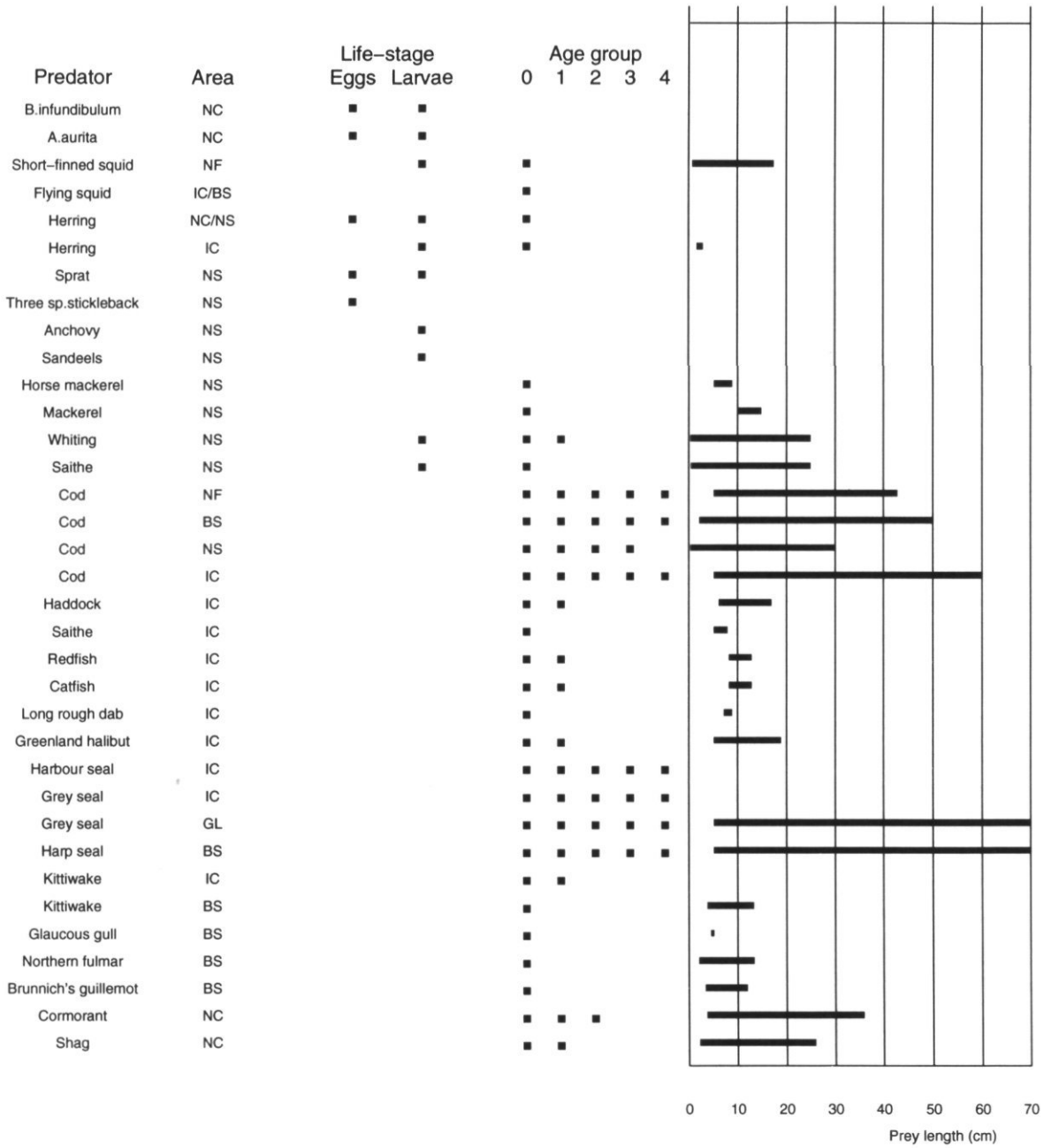


Figure 9. Predation on cod with respect to life-stage, age, or length range of cod as prey. BS = Barents Sea, IC = Iceland, NF = Newfoundland, NS = North Sea, NC = Norway coast, GL = Gulf of St Lawrence.

The grey seal is probably the main predator seal in most of the areas affecting the juvenile cod stock component, in particular age groups 0–II. In general, the prey selection of seals and cod on cod as prey appears to be similar in terms of size and age of the prey.

Minke whales are apparently the only baleen whales which are of some relevance as predators of cod. Their predatory impact seems to be most pronounced in the Barents Sea and Newfoundland waters, and more limited in Icelandic waters. They are indicated as predators of a broad size spectrum of cod.

Predation by seabirds on cod has been recorded

Table 9. Trophic interactions of cod stocks in the four areas indicated as average percent weight (w) or percent occurrence (o) of cod as prey. (+ indicates a low or uncertain value).

	Area			
Predator	Newfoundland	Iceland	Barents Sea	North Sea
B. infundibulum			+	
A. aurita			5 (o)	
T. multicirrata			+	
Short-finned squid	8 (o)			
Flying squid		+	+	
Herring		+	+	+
Sprat				+
Sandeels				+
Anchovy				+
Three sp. stickleback				+
Horse mackerel				4 (w)
Saithe		3 (w)		0.1 (w)
Cod	1 (w)	6 (w)	4 (w)	3 (w)
Haddock		1 (w)		
Whiting				0.3 (w)
Ling				2 (o)
Redfish	+	+		
Catfish		0.1 (w)		
Spotted wolffish	+			
Megrim				0.1 (o)
Greenland halibut	6 (w)	0.4 (w)	1 (o)	
Long rough dab		2 (w)		
Starry ray	4 (o)		9 (o)	0.3 (w)
Angler fish				0.4 (o)
Grey gurnard				2 (w)
Harbour seal	2 (o)	24 (w)	5 (w)	4 (o)
Grey seal	19 (o)	26 (w)		19 (w)
Harp seal	7 (o)		9 (w)	
Fin whale			+	
Minke whale	7 (o)	2 (o)	12 (o)	
Sperm whale		5 (o)		
Kittiwake			15 (o)	+
Great black-backed gull				+
Glaucous gull			9 (o)	
Northern fulmar			9 (o)	
Common guillemot				+
Brünnich's guillemot	+	+	15 (o)	
Cormorant			3 (o)	+
Shag			+[a]	+
No. of species analysed	21	27	36	46

[a] Unidentified gadoids (saithe and cod).

mainly in the Barents Sea. Two bird species, kittiwake and Brünnich's guillemot (thick-billed murre), seem to be the major predators, followed by glaucous gull and northern fulmar. Cormorants and shags may also be important predators of cod, since cod or unidentified gadoids (juvenile cod or saithe) were recorded in their diet in considerable amounts in the Barents Sea and North Sea. However, cod has seldom been recorded in the diet of seabirds in the North Sea or Icelandic waters, but gadoids occasionally, e.g., as the prey of gulls in the North Sea and Icelandic waters and kittiwake in the North Sea.

Predation by invertebrates other than cephalopods, is apparently the least studied area of research with respect to predation on cod. The available results strongly indicate that predators such as ctenophores, medusae, crustacean hyperiids, and euphausiids may constitute highly relevant sources of natural mortality during the

early life-stages of cod. Intensified work in this field should be given high priority in marine ecological research during the next decade.

Feeding studies in relation to multispecies considerations have focused on fish, as predators and as prey, as well as top predators such as seals. The findings, summarized in this review, indicate that relevant predators of cod may also be found in the lower taxa, i.e., among medusae and crustaceans, and among seabirds. In view of this, it seems appropriate to broaden the ecological basis of multispecies research.

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Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents Sea, Iceland, and eastern Newfoundland)

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Stomach content data collected from cod caught during offshore resource assessment surveys in three Arcto-boreal ecosystems (the Barents Sea and the shelves off Iceland and eastern Newfoundland) were examined to determine the prevalence of cannibalism, and to identify possible factors associated with variability in prevalence. Cannibalism provides a minor source of food, except for the largest predators. Cannibalism increases with predator length. Most prey are less than 40 cm in length and less than 3 years old. In each region, cannibalism occurs over most of the area surveyed, but is most prevalent where the smallest cod have been found in bottom trawl surveys. The frequency of occurrence of cannibalism recorded in recent years (late 1970s to the present) has usually been low (<1%) in all regions. Much higher values were reported from the Barents Sea in 1949–1960. In the Barents Sea, the frequency of occurrence of cannibalism increased with the abundance of juvenile cod. There was little support for the hypothesis that the frequency of cannibalism increased when the abundance of capelin, the major prey of cod, was low. It can be demonstrated that cod eat large numbers of their young, especially those of ages 0–2, but the mortality rate imposed cannot be calculated without independent estimates of the abundance of young cod. Mortality imposed by cannibalism and competition is estimated without stomach content data for Icelandic cod. This is done by modelling the change in abundance from the pelagic 0-group stage, as measured by pelagic trawl surveys, to age 3, as estimated by VPA.

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Introduction

Cannibalism is a common phenomenon in animals (Fox, 1975; Polis, 1981), and has been found in at least 36 families of teleost fish (Smith and Reay, 1991). Among the Gadidae, it has been reported in cod (*Gadus morhua*) from the Gulf of St Lawrence (Waiwood and Majkowski, 1984), the Flemish Cap (Lilly, 1987), northeastern Newfoundland (Lilly, 1991), Greenland (Hansen, 1949), Iceland (Pálsson, 1983), the Barents Sea (Mehl, 1989, 1991), the North Sea (Daan, 1973), and the Baltic Sea (Arntz, 1978). Predation on conspecifics is generally a minor source of food for cod, a notable exception being the cod of landlocked Ogac Lake on Baffin Island. For this stock, the lack of alternate prey of suitable size makes cannibalism a vital source of energy and a major determinant of population size structure (Patriquin, 1967).

In other stocks, the major interest for stock dynamics is the importance of cannibalism in influencing recruitment to the fishery. This is part of the broader question of whether mortality at the juvenile stage is sufficiently high and variable to affect recruitment (Sissenwine, 1984; Lilly, 1987). The number of juvenile cod eaten by conspecifics may be influenced by several factors, including the following:

1. The number consumed may increase with the number alive at a specified size (or age) because the frequency of encounters with potential predators will increase (Ponomarenko, 1968).
2. As the abundance of larger fish increases, the probability that each juvenile will encounter a potential cannibal increases. This has been cited as a potential mechanism for a decline in recruitment at high stock levels (Ricker, 1954, 1975), although Ricker (1954, p. 613) was of the opinion that cannibalism will probably not prove to be important in regulating more than a minority of populations.
3. The number of juveniles consumed may vary in accordance with several factors which may be grouped under the term intra-cohort density dependence. As the abundance of juveniles increases, (a) the fish may spread into areas where they are more vulnerable to predation (Ricker, 1954), (b) the duration of the vulnerable phase may increase because of a decrease in growth rate attending competition for resources (Ricker, 1954), (c) the ability of the fish to escape potential predators may be reduced if nutritional condition is low because of competition (Ponomarenko, 1965), and (d) predators may be attracted to the higher prey densities (aggregative numerical response).
4. A shortage of resources (e.g. food, space, cover), due to factors other than intra-specific competition, could result in slower growth, poorer condition or movement into areas of higher vulnerability, with the consequences mentioned above.
5. Shortage of food for older cod may result in increased cannibalism. This has been hypothesized to have occurred in the Barents Sea in 1985–1987 as a result of a decline in the biomass of capelin, the major prey of cod in that area in recent years (Mehl, 1989, 1991).
6. Changes in the physical environment, especially temperature, may cause changes in the distributions of juveniles or older cod, thereby affecting the degree of spatial overlap and the frequency of encounter.

In order to understand the potential impact of cannibalism on year-class strength, it is necessary to distinguish among the above processes and to determine the importance of each. Our first objective is to review and document the extent of cannibalism in the cod inhabiting the Arcto-boreal shelves off southern Labrador and northeastern Newfoundland, around Iceland, and in the Barents Sea and Svalbard area. Analyses will be limited to stomachs collected during resource assessment surveys in offshore waters. Our second objective is to use these data, especially those from the Barents Sea, to test hypotheses 1 and 5 above. We then use data from the Barents Sea to illustrate a method for estimating the quantity and number of cod consumed by cod. Finally, we use abundance estimates from pelagic trawl surveys and virtual population analysis (Icelandic cod) to illustrate a method, independent of stomach content data, for estimating the mortality imposed by cannibalism.

Materials and methods

Sampling

The survey design, stomach sampling protocol, and method of stomach content analysis varied within and among areas (ICES, 1992a). The number of stomachs sampled in the three areas, by year and length group, is given in Tables 1a–c.

In the Newfoundland area, cod were caught during random depth-stratified bottom trawl surveys during November–December 1978 and 1980–1992 on the southern Labrador Shelf and Northeast Newfoundland Shelf (Northwest Atlantic Fisheries Organization Divisions 2J+3K) (Lilly, 1991; Lilly and Davis, 1993). The intent, not always attained, was to collect stomachs from a length-stratified sample of cod from every station. The number and weight of cod and other prey occurring in the stomachs was recorded separately for each predator. The fork length (FL) of each predator and prey was recorded to the nearest centimetre.

In the Iceland area, cod were caught mainly in the north and east during fixed station surveys prior to 1985, and during semi-stratified random surveys starting in 1985 (Pálsson *et al.*, 1989). Stomachs were collected during surveys in March 1979–1992 and September–November 1980–1992. Stomach sampling was stratified with respect to subareas and predator length (Pálsson, 1983; Magnússon and Pálsson, 1989). All stomachs from a specific sample (station and length group) were bulked, and the number and weight of cod and other prey were recorded for each sample, together with the number of stomachs contributing to the sample. The total length (cm) of the predators is provided here as the mid-point of the length group. Lengths are available for individual prey.

In the Barents Sea and Svalbard area, cod were caught at various times of the year during surveys conducted by Norway since 1984 and Russia since 1986 (Mehl, 1989; Mehl and Yaragina, 1992). Stations were fixed, stratified-random, or selected on the basis of acoustic information. Stomachs were collected from a length-stratified sample of cod from each survey stratum. The number and weight of cod and other prey occurring in each individual stomach was recorded for each length group of prey. Lengths (FL, cm) are available for each individual predator, but prey lengths are recorded by mid-point of length group. Stomach content data collected by Russia from 1949 to 1982 and by Norway in 1981 and 1982 have been added to the common Norway (IMR)–Russia (PINRO) database.

Table 1a. NEWFOUNDLAND COD. Number of stomachs analysed by predator length group and year in 1978 and 1980–1992.

	Predator length group (cm)												
	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119	Total
1978	0	0	0	13	143	240	267	212	124	30	4	2	1035
1980	0	2	11	35	142	227	495	489	267	98	25	4	1795
1981	0	0	1	67	173	218	297	324	207	88	23	5	1403
1982	0	41	42	168	416	489	551	608	483	185	68	24	3075
1983	2	32	79	249	317	529	446	590	358	120	31	7	2760
1984	1	19	90	151	425	479	522	510	359	121	39	17	2733
1985	0	5	18	75	474	488	621	433	265	47	7	2	2435
1986	0	14	26	91	327	552	526	368	165	48	4	0	2121
1987	0	14	41	41	256	578	661	360	161	38	10	2	2162
1988	3	87	55	92	301	303	517	342	113	19	0	0	1832
1989	0	75	121	262	451	360	422	312	54	16	0	0	2073
1990	0	28	72	151	391	275	204	134	21	2	0	0	1278
1991	0	3	20	152	448	534	233	140	53	6	0	1	1590
1992	0	2	8	40	327	318	70	12	0	0	0	0	777
Total	6	322	584	1587	4591	5590	5832	4834	2630	818	211	64	27069

Table 1b. ICELANDIC COD. Number of stomachs analysed by predator length group and year in 1979–1992.

	Predator length group (cm)												
	7–9	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119	Total
1979	114	140	154	179	173	149	134	92	45	18	6	1	1	1206
1980	117	101	124	207	244	299	312	333	352	221	194	132	45	2681
1981	93	122	167	233	245	614	605	671	885	635	592	364	116	5342
1982	18	99	149	224	234	385	580	769	890	885	646	273	122	5274
1983	29	76	84	177	229	353	508	575	635	621	385	133	45	3850
1984	22	147	56	85	118	159	256	307	318	303	197	62	23	2053
1985	34	117	111	194	205	320	321	402	399	358	237	133	62	2893
1986	10	143	113	129	157	168	227	251	261	258	203	72	45	2037
1987	7	59	78	122	126	161	242	300	308	308	291	162	116	2280
1988	19	58	61	108	136	258	345	410	449	415	266	149	84	2758
1989	31	59	82	157	155	219	277	325	324	301	195	144	89	2358
1990	34	109	77	160	229	355	420	484	515	406	297	139	99	3324
1991	17	88	62	164	236	345	390	456	451	374	277	116	61	3037
1992	4	78	127	335	425	485	439	497	539	427	338	172	69	3935
Total	549	1396	1445	2474	2912	4270	5056	5872	6371	5530	4124	2052	977	43028

ICELANDIC COD. Number of samples analysed by predator length group and year in 1979–1992.

	Predator length group (cm)												
	7–9	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119	Total
1979	22	23	24	23	25	25	29	31	22	11	5	1	1	242
1980	26	37	51	57	64	53	51	56	69	65	65	59	21	674
1981	21	33	53	71	63	109	92	92	115	108	118	110	56	1041
1982	6	31	47	61	61	70	106	134	159	173	174	94	57	1173
1983	14	25	33	42	53	56	66	82	95	105	98	54	20	743
1984	9	35	20	30	38	39	41	53	56	71	66	27	13	498
1985	11	19	32	36	47	62	64	73	68	71	81	67	31	662
1986	5	31	32	22	35	41	50	61	65	71	64	42	31	550
1987	3	13	14	19	20	25	37	55	57	56	63	52	39	453
1988	5	16	19	36	45	60	74	75	83	93	92	75	48	721
1989	11	22	31	44	55	63	69	80	79	81	74	63	50	722
1990	16	31	37	50	74	99	109	131	143	125	11	82	63	1075
1991	7	31	29	50	72	92	101	122	119	116	11	60	37	955
1992	4	38	50	82	108	119	116	130	137	121	126	76	42	1149
Total	160	385	472	623	760	913	1005	1175	1267	1267	1260	862	509	10658

Table 1c. BARENTS SEA COD. Number of stomachs analysed by predator length group and year in 1949–1960, 1973, 1975, 1980–1982, and 1984–1992.

	Predator length group (cm)												
	7–9	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119	Total
1949	0	0	0	0	0	1	19	62	59	32	11	3	2	189
1950	0	0	0	0	0	1	10	73	72	24	9	3	1	193
1951	0	0	0	0	0	0	0	2	3	12	7	0	1	25
1952	0	0	4	0	1	8	74	242	126	92	55	12	2	616
1953	0	0	0	0	2	150	457	334	115	42	18	6	0	1124
1954	0	0	0	0	0	3	44	75	30	22	7	2	0	183
1955	0	0	0	0	0	0	4	65	77	25	14	3	0	188
1956	0	0	0	2	2	9	67	284	364	175	66	32	4	1005
1957	0	0	2	45	33	56	80	89	75	62	38	30	12	522
1958	0	0	1	7	6	30	29	101	122	85	57	10	5	453
1959	0	0	0	0	2	50	162	411	270	96	37	11	3	1042
1960	0	0	0	0	0	0	4	60	44	37	21	2	3	171
1973	0	0	0	0	0	10	63	51	39	6	3	2	0	174
1975	0	0	0	0	0	74	125	0	0	0	0	0	0	199
1980	11	0	0	0	0	0	106	354	116	15	1	1	4	608
1981	6	8	2	0	1	8	31	87	181	73	4	0	6	407
1982	0	0	0	11	32	194	193	174	143	70	14	1	1	833
1984	3	157	334	335	275	640	747	508	372	245	67	12	32	3727
1985	23	79	251	380	421	664	831	762	433	175	87	28	18	4152
1986	37	213	204	284	333	1111	1210	1344	1040	201	38	15	13	6043
1987	4	44	161	308	329	1005	1590	1165	908	349	60	17	4	5944
1988	3	11	33	145	214	810	1750	1695	607	234	66	19	9	5596
1989	11	109	40	100	207	918	1731	2228	1771	517	115	29	16	7792
1990	9	176	164	213	213	747	1011	1581	2031	1364	437	65	38	8049
1991	2	202	231	199	338	852	829	908	909	922	470	119	15	5996
1992	10	125	152	154	141	294	370	403	367	337	287	183	62	2885
Total	119	1124	1579	2183	2550	7635	11537	13058	10274	5212	1989	605	251	58116

Stomach data analysis

The degree and relative importance of cannibalism was expressed using two indices: (1) percent frequency of occurrence (the number of stomachs containing cod expressed as a percentage of the total number of stomachs in a sample) and (2) percent weight (the weight of cod expressed as a percentage of the total weight of the contents of all stomachs in a sample). Because the stomachs from Iceland were bulked, it was necessary to apply the following correction procedure to estimate the frequency of occurrence on an individual stomach basis. Let p denote the probability of observing cod in an individual stomach. Thus, the probability of a stomach being empty is $1-p$ and the probability is $(1-p)^n$ that a bulk of n stomachs is empty (or does not contain the prey in question). It follows that the probability, H, of occurrence within a bulk is given by $H = 1-(1-p)^n$. This equation can now be inverted to yield $p = 1-(1-H)^{1/n}$, which describes the probability of occurrence in individual stomachs based on observations of occurrence in bulked samples. The input value for H is given in Table 3b. As an input value for n the average number of stomachs in bulked samples has been used, as shown in the following text table:

Year	1979	1980	1981	1982	1983	1984	1985
n	4.9	3.9	5.1	4.5	5.2	4.1	4.4
Year	1986	1987	1988	1989	1990	1991	1992
n	3.7	5.0	3.8	3.3	3.1	3.2	3.4

To determine whether cannibalism was positively associated with the availability of juvenile cod and negatively associated with the availability of major prey, the frequency of occurrence of cannibalism in Barents Sea cod was compared with (i) the year-class strength of cod as measured during pelagic 0-group surveys and (ii) the availability of capelin, as approximated by the capelin biomass estimated during acoustic surveys in autumn and the quantity of capelin in cod stomachs. The latter was expressed as a mean partial fullness index (Fahrig *et al.*, 1993) calculated as:

$$PFI_c = \frac{1}{n}\sum_{j=1}^{n}\frac{W_{cj}}{L_j^3} \times 10^4$$

where W_{cj} is the weight of capelin in fish j, L_j is the length of fish j, and n is the number of fish in the sample.

Estimating consumption of cod by cod

The number of cod-at-age consumed each year by the cod in the Barents Sea was estimated using the method of Mehl (1989, 1991) and Bogstad and Mehl (1992). The consumption (tonnes) by size group j in season 1 (C_{jl}) is given by

$$C_{jl} = \sum_{k,n} R_{jkln} \times XN_{nl} \times XP_{kln} \times (10^6 \times 24 \times 182.5)$$

where R_{jkln} is the ration ($g \times h^{-1}$) of prey size group j for predator age group n in area k and season l (half-year), XN_{nl} is the number of individuals of predator age group n in season l and XP_{kln} is the proportion of individuals of predator age group n in area k and season 1. Ration was estimated from the stomach content data and a model for estimating evacuation rate provided by dos Santos and Jobling (1992), as modified by Bogstad and Mehl (1992). The number of cod-at-age was taken from the Arctic Fisheries Working Group Report (ICES, 1993b). It was assumed that the spawning component is outside the Barents Sea for three months during the first half of the year (Godø, 1989). The quantity (in tonnes) of cod consumed by size group was converted to numbers consumed by age group using the method of Mehl (1989). Mean weight of each prey size group was mainly calculated using $W = c \times l^3$, where c was calculated using survey data in each half year and l was the median length in the size group. For the 0-group, prey weights were in some cases taken directly from stomach content data.

Results

Variability in cannibalism

The relationships between the lengths of cod consumed and the lengths of their predators were similar in the three areas (Figs. 1–3). Predator lengths ranged upward from about 30 cm, and prey lengths ranged upward from about 5 cm, with very few instances of prey larger than 40 cm. The maximum prey size was about 50% of the predator length, and the range of prey size increased with predator size. 0-group cod (<10 cm) were preyed upon in relatively large numbers by a wide size range of predators in Iceland waters and the Barents Sea, but were not common prey off Newfoundland (Fig. 4).

The contribution of cod to the total stomach content weight generally increased with predator size in all three areas (Fig. 5, Tables 2a–c). On average, the contribution was nil or small (≤1%) in cod less than 50 cm and increased to 5.1%, 8.2%, and 8.5% in 100–119 cm cod in the waters of Newfoundland and Iceland, and in the Barents Sea, respectively. Cannibalism in small cod (7–14 cm) was found only occasionally off Iceland.

Occurrences of cannibalism were broadly distributed in each of the areas. In the Newfoundland region, cannibalism was most intensive toward the coast off southern Labrador and northeastern Newfoundland, but was also recorded on some of the offshore banks (Fig. 6). In Icelandic waters, cannibalism occurred most frequently off the northwestern and northern coasts. It was less intense off the eastern coast and recorded only occasionally off the southern coast. The frequency of cannibalism was generally higher close to the coast than in offshore areas, but was not recorded within fjords,

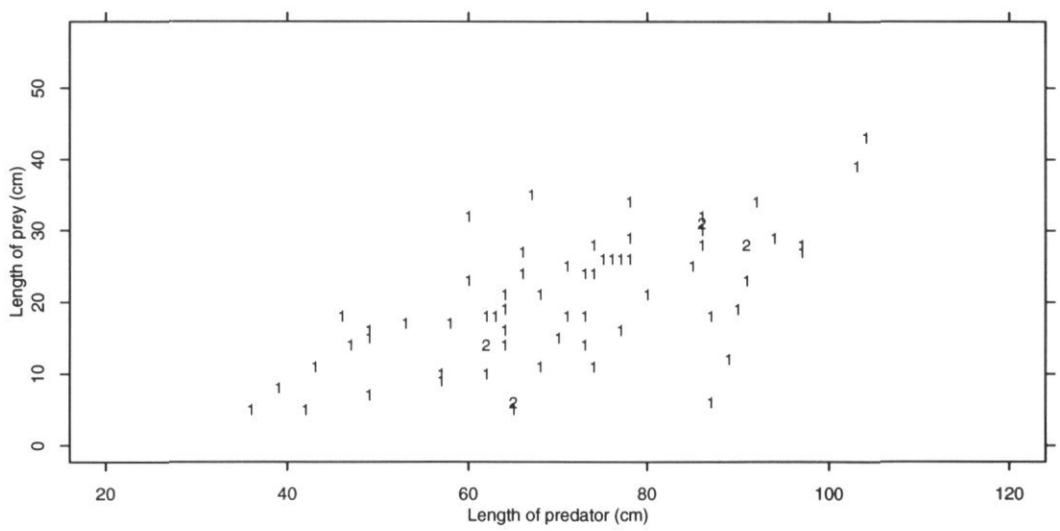


Figure 1. Plot of prey size versus predator size for Newfoundland cod. Number of prey behind each sample are indicated.

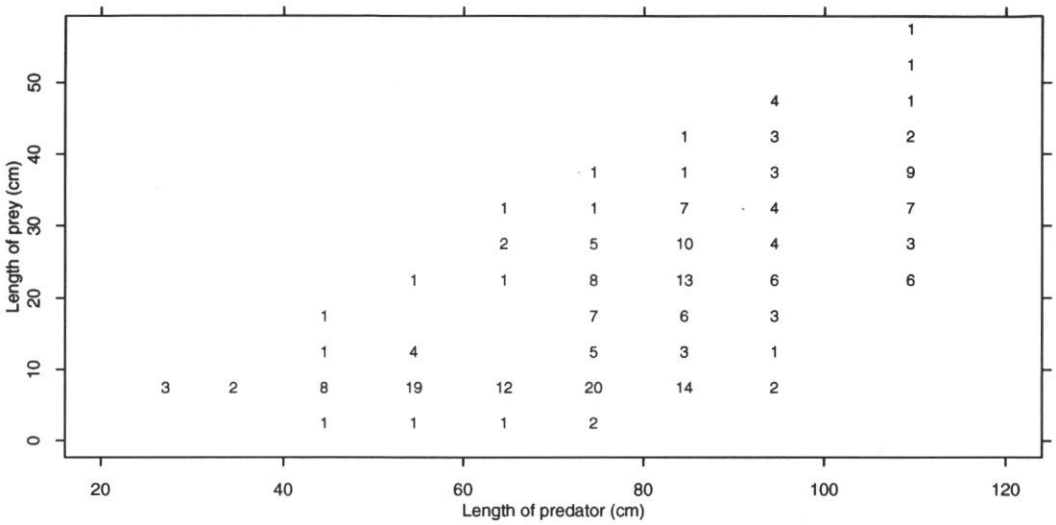


Figure 2. Plot of prey size versus predator size for Icelandic cod. Number of prey behind each sample are indicated.

such as those of the northwestern and northern coasts (Fig. 7). In the Barents Sea area, cannibalism occurred most frequently in the east and in the Svalbard area, mainly within the 200 m isobath (Fig. 8). During the period 1984–1992 cannibalism was recorded in the Barents Sea every year, whereas in the Svalbard area it was observed mainly in years of extensive cannibalism. More than half of the occurrences in the Svalbard area were recorded during 1949–1960.

The frequency of occurrence of cannibalism varied among years in each of the areas (Fig. 9, Tables 3a–c). In the waters off Newfoundland, occurrence was highest in 1983–1984 and 1989–1990. There was a positive correlation between the frequency of occurrence of cannibalism and an index of abundance of juvenile cod ($r = 0.82$; $p < 0.001$; $n = 14$), where the index in year t was calculated as the mean catch (number) per tow of cod aged 1 and 2 in autumn research surveys in NAFO Divisions 2J, 3K, and 3L combined (Bishop *et al.*, 1993). In Icelandic waters, the frequency of occurrence tended to be somewhat higher during 1979–1985 than in more recent years. In the Barents Sea, cannibalism was very

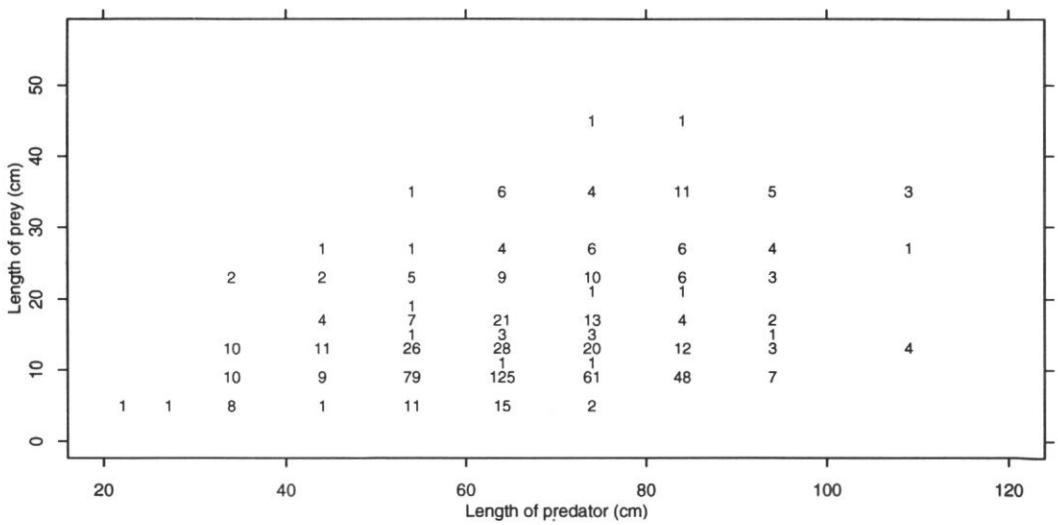


Figure 3. Plot of prey size versus predator size for Barents Sea cod. Number of prey behind each sample are indicated.

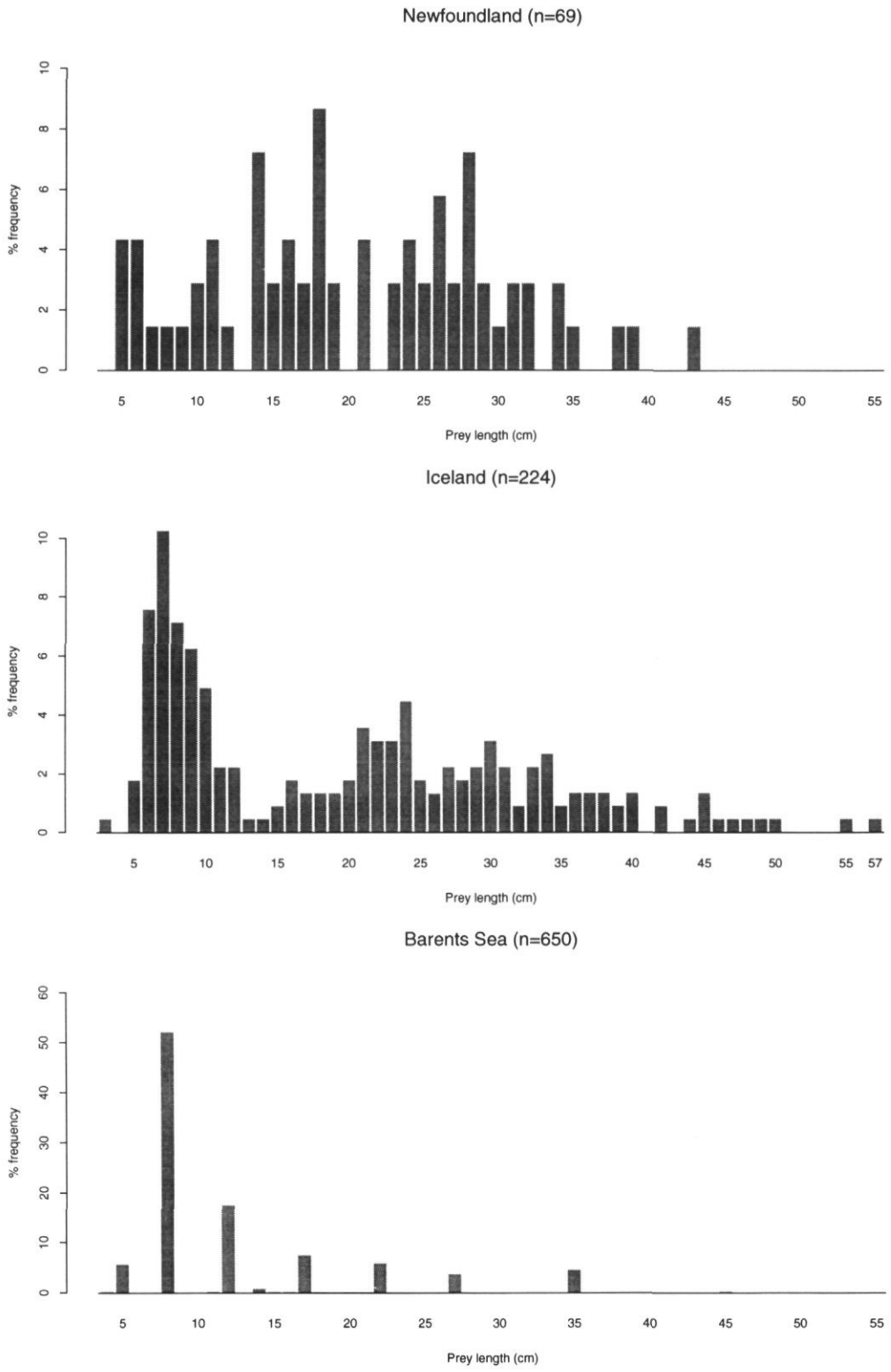


Figure 4. Numerical distribution (%) of cod as prey of cod with respect to prey length.

high in many years during 1949–1960. In more recent years (1984–1992), the frequency of occurrence was relatively low, and at a level similar to that observed off Newfoundland and Iceland. Peaks occurred in 1985–1986 and 1991–1992.

Seasonal variability in cannibalism was investigated in Icelandic waters and in the Barents Sea (Fig. 10). In both areas cannibalism is generally higher and more variable in the autumn than in the winter or spring. This is probably related to the higher abundance and availability of prey shortly after the settlement of the 0-group.

Annual variability in factors which might influence the frequency of occurrence of cannibalism in the Barents Sea is illustrated in Figure 11. During the period 1984–1992 the frequency of occurrence of cannibalism was positively correlated with an index of juvenile abundance, but not negatively correlated with either the biomass of capelin or the quantity of capelin in cod stomachs (Fig. 11, Table 4).

Table 2a. NEWFOUNDLAND COD. Weight percentages of cod in stomach content of cod in 1978 and 1980–1992.

	Predator length group (cm)											
	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119
1978	–	–	–	0.0	0.0	0.0	0.0	0.0	5.2	1.2	0.0	0.0
1980	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0
1981	–	–	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
1982	–	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.6	0.5	3.1	5.3
1983	0.0	0.0	0.0	0.0	0.2	2.0	1.5	0.1	3.3	2.9	0.0	0.0
1984	0.0	0.0	0.0	0.0	0.0	+	0.0	2.2	1.9	0.1	8.5	8.1
1985	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	22.2	0.0
1986	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.3	54.0	–
1987	–	0.0	0.0	0.0	0.0	0.0	0.0	1.1	2.0	7.2	11.2	0.0
1988	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.3	0.0	–	–
1989	–	0.0	0.0	0.0	0.0	0.0	2.3	2.2	1.1	14.9	–	–
1990	–	0.0	0.0	0.0	0.0	0.0	0.4	1.8	16.7	94.1	–	–
1991	–	0.0	0.0	0.0	0.0	0.0	0.0	12.0	15.4	0.0	–	0.0
1992	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	–	–	–
Pooled mean	0.0	0.0	0.0	0.0	0.01	0.2	0.3	1.1	2.0	2.3	4.8	5.1

Table 2b. ICELANDIC COD. Weight percentages of cod in stomach content of cod in 1979–1992.

	Predator length group (cm)												
	7–9	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119
1979	0.0	0.0	0.0	0.0	0.0	0.5	5.6	16.6	39.2	16.8	89.6	0.0	0.0
1980	0.0	0.0	0.0	0.0	3.2	0.0	0.0	1.3	23.2	27.1	0.4	7.1	21.2
1981	0.0	0.0	0.0	0.0	0.0	0.0	1.6	5.7	1.4	31.3	6.8	2.0	30.4
1982	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	1.4	5.4	16.0	8.0	24.5
1983	0.0	0.0	0.0	0.0	0.0	2.1	0.0	1.2	0.7	4.1	30.1	54.5	20.6
1984	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.6	0.0	14.2	19.0	7.3	40.1
1985	0.0	0.0	0.0	0.0	22.7	0.0	5.3	8.0	7.6	9.3	6.1	4.7	13.2
1986	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.6	2.6	7.0	0.0
1987	0.0	0.0	0.0	0.0	0.0	5.7	0.0	1.8	8.4	3.9	19.3	0.0	0.0
1988	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.6	0.2	6.8	15.0	41.1	0.1
1989	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	3.7	2.3	3.5	14.0	12.5
1990	80.1	35.8	0.0	0.0	0.0	3.0	0.0	4.6	0.0	7.6	19.0	9.6	22.7
1991	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.8	8.6	10.1	17.0	11.0
1992	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.9	0.0	0.4	5.4	3.9	10.6
Pooled mean	1.0	1.0	0	0	0.4	0.1	0.3	0.6	1.0	2.2	4.7	6.6	8.2

Table 2c. BARENTS SEA COD. Weight percentages of cod in stomach content of cod in 1949–1960, 1973, 1975, 1980–1982, and 1984–1992.

	Predator length group (cm)												
	7–9	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119
1949	–	–	–	–	–	100.0	1.0	5.0	1.9	8.3	0.2	0.0	80.0
1950	–	–	–	–	–	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
1951	–	–	–	–	–	–	–	0.0	10.0	9.7	3.1	–	0.0
1952	–	–	0.0	–	0.0	17.1	9.2	24.1	10.0	6.5	4.9	2.6	0.0
1953	–	–	–	–	0.0	0.0	0.3	1.0	0.1	8.1	9.0	1.0	–
1954	–	–	–	–	–	0.0	28.7	27.1	0.0	39.6	46.1	0.0	–
1955	–	–	–	–	–	–	0.0	9.1	2.2	10.1	0.0	0.0	–
1956	–	–	–	0.0	0.0	31.4	6.0	7.0	12.9	45.1	15.1	20.1	0.0
1957	–	–	0.0	0.0	5.0	3.9	1.5	2.6	12.4	11.3	6.0	6.8	33.5
1958	–	–	0.0	0.0	0.0	4.3	3.4	33.1	26.7	32.9	30.3	12.8	3.4
1959	–	–	–	–	0.0	3.1	5.9	9.5	22.6	25.1	31.3	84.1	36.1
1960	–	–	–	–	–	–	0.0	8.4	0.0	1.7	2.7	0.0	0.0
1973	–	–	–	–	–	0.0	0.0	0.0	0.0	98.8	99.8	100.0	–
1975	–	–	–	–	–	0.0	0.0	–	–	–	–	–	–
1980	0.0	–	–	–	–	–	0.0	0.0	0.0	42.0	0.0	0.0	0.0
1981	0.0	0.0	0.0	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0
1982	–	–	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1984	0.0	0.0	0.0	0.0	0.0	0.6	0.2	0.2	0.8	7.2	0.0	0.0	3.5
1985	0.0	0.0	0.0	0.1	2.9	0.4	1.6	0.7	0.5	2.9	4.0	14.1	31.4
1986	0.0	0.0	0.0	0.0	0.0	3.5	0.5	2.1	1.7	8.1	26.0	36.2	0.0
1987	0.0	0.0	0.0	0.0	0.0	0.7	0.2	1.1	2.9	2.7	14.0	25.4	0.0
1988	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.7	0.4	2.2	0.0	0.0	0.5
1989	0.0	0.0	0.0	0.0	0.0	0.9	0.2	0.1	0.8	0.1	0.0	0.0	0.5
1990	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.4	0.5	0.1	0.7	0.0	0.0
1991	0.0	0.0	0.0	0.0	0.0	+	0.0	0.2	0.4	+	1.5	3.1	13.3
1992	0.0	0.0	0.0	0.0	1.1	0.7	0.5	0.0	4.3	0.5	0.4	5.8	0.0
Pooled mean	0.0	0.0	0.0	+	0.2	1.1	0.5	1.5	1.8	3.2	4.6	7.3	8.5

Table 3a. NEWFOUNDLANDIC COD. Frequency of occurrence (%) of cannibalism in cod stomachs, based on individual stomachs, in 1978 and 1980–1992.

	Predator length group (cm)											Pooled mean (≥30 cm)
	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119	
1978	–	–	–	0.0	0.0	0.0	0.0	0.0	1.6	3.3	0.0	0.0	0.3
1980	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.1
1981	–	–	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.1
1982	–	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.5	2.9	4.2	0.2
1983	0.0	0.0	0.0	0.0	0.6	0.8	0.5	0.3	1.4	1.7	0.0	0.0	0.7
1984	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.6	0.8	1.7	7.7	5.9	0.6
1985	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	14.3	0.0	0.2
1986	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1	25.0	–	0.1
1987	–	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.6	2.6	10.0	0.0	0.2
1988	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	1.8	0.0	–	–	0.4
1989	–	0.0	0.0	0.0	0.0	0.0	1.2	1.6	1.9	6.3	–	–	0.7
1990	–	0.0	0.0	0.0	0.0	0.0	0.5	1.5	4.8	50.0	–	–	0.5
1991	–	0.0	0.0	0.0	0.0	0.0	0.0	2.1	3.8	0.0	–	0.0	0.4
1992	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	–	–	–	0.0

Table 3b. ICELANDIC COD. Frequency of occurrence (%) of cannibalism in cod stomachs, based on bulked samples, in 1979–1992.

	Predator length group (cm)													Pooled mean (≥30 cm)	Pooled mean corrected
	7–9	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119		
1979	0.0	0.0	0.0	0.0	0.0	8.0	6.9	6.5	13.6	9.1	60.0	0.0	0.0	10.4	2.2
1980	0.0	0.0	0.0	0.0	1.6	0.0	0.0	5.4	4.3	6.2	1.5	6.8	14.3	4.6	1.2
1981	0.0	0.0	0.0	0.0	0.0	0.0	2.2	2.2	1.7	6.5	5.9	3.6	12.5	3.9	0.8
1982	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.6	2.3	5.2	5.0	7.0	2.5	0.6
1983	0.0	0.0	0.0	0.0	0.0	1.8	0.0	4.9	4.2	3.8	10.2	20.4	15.0	6.4	1.3
1984	0.0	0.0	0.0	0.0	0.0	0.0	4.9	1.9	0.0	5.6	6.1	3.7	15.4	3.8	0.9
1985	0.0	0.0	0.0	0.0	2.1	0.0	6.2	4.1	5.9	9.9	6.2	4.5	12.9	5.8	1.3
1986	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	1.6	2.4	0.0	0.7	0.2
1987	0.0	0.0	0.0	0.0	0.0	4.0	0.0	1.8	1.8	1.8	6.3	0.0	0.0	2.1	0.4
1988	0.0	0.0	0.0	0.0	0.0	0.0	4.1	1.3	1.2	4.3	5.4	12.0	2.1	4.0	1.1
1989	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	1.3	2.5	1.4	4.8	4.0	1.8	0.5
1990	6.2	3.2	0.0	0.0	0.0	1.0	0.0	0.8	0.0	0.8	3.5	2.4	7.9	1.6	0.5
1991	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	2.6	8.4	10.0	5.4	3.0	0.9
1992	0.0	0.0	0.0	0.0	0.0	0.0	0.9	1.5	0.0	0.8	3.2	2.6	9.5	1.6	0.5

Table 3c. BARENTS SEA COD. Frequency of occurrence (%) of cannibalism in cod stomachs, based on individual stomachs, in 1949–1960, 1973, 1975, 1980–1982, and 1984–1992.

	Predator length group (cm)													Pooled mean (≥30 cm)
	7–9	10–14	15–19	20–24	25–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–119	
1949	–	–	–	–	–	100.0	5.3	6.5	11.9	12.5	9.1	0.0	50.0	10.1
1950	–	–	–	–	–	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.5
1951	–	–	–	–	–	–	–	0.0	33.3	8.3	28.6	–	0.0	16.0
1952	–	–	0.0	–	0.0	12.5	5.4	12.8	11.9	12.0	9.1	25.0	0.0	11.5
1953	–	–	–	–	0.0	0.0	0.2	1.5	0.9	7.1	11.1	33.3	–	1.2
1954	–	–	–	–	–	0.0	6.8	6.7	0.0	9.1	28.6	0.0	–	6.6
1955	–	–	–	–	–	–	0.0	4.6	5.2	8.0	0.0	0.0	–	4.8
1956	–	–	–	0.0	0.0	11.1	11.9	11.6	12.6	28.0	27.3	18.8	0.0	16.1
1957	–	–	0.0	0.0	3.0	7.1	5.0	4.5	6.7	11.3	2.6	3.3	16.7	6.3
1958	–	–	0.0	0.0	0.0	3.3	13.8	26.7	27.9	20.0	24.6	10.5	40.0	23.9
1959	–	–	–	–	0.0	4.0	4.3	9.7	15.6	14.6	13.5	2.7	33.3	11.2
1960	–	–	–	–	–	–	0.0	18.3	0.0	2.7	9.5	0.0	0.0	8.2
1973	–	–	–	–	–	0.0	0.0	0.0	0.0	16.7	33.3	50.0	–	1.7
1975	–	–	–	–	–	0.0	0.0	–	–	–	–	–	–	0.0
1980	0.0	–	–	–	–	–	0.0	0.0	0.0	0.0	6.7	0.0	0.0	0.2
1981	0.0	0.0	0.0	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0	0.0
1982	–	–	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1984	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.3	1.6	0.0	0.0	3.1	0.3
1985	0.0	0.0	0.0	0.3	0.5	0.7	0.8	0.7	0.5	2.3	2.3	7.1	5.6	0.9
1986	0.0	0.0	0.0	0.0	0.0	0.5	0.6	1.1	1.7	4.0	17.9	26.7	0.0	1.3
1987	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.2	0.7	2.0	11.7	11.8	0.0	0.5
1988	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.4	0.7	0.9	0.0	0.0	11.1	0.3
1989	0.0	0.0	0.0	0.0	0.0	0.4	0.1	0.3	0.3	0.6	0.0	0.0	6.3	0.3
1990	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.3	0.4	0.1	0.7	0.0	0.0	0.3
1991	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.2	0.6	1.3	1.3	0.3	13.3	0.6
1992	0.0	0.0	0.0	0.0	0.7	0.7	0.8	0.0	1.6	0.6	0.3	2.2	0.0	0.8

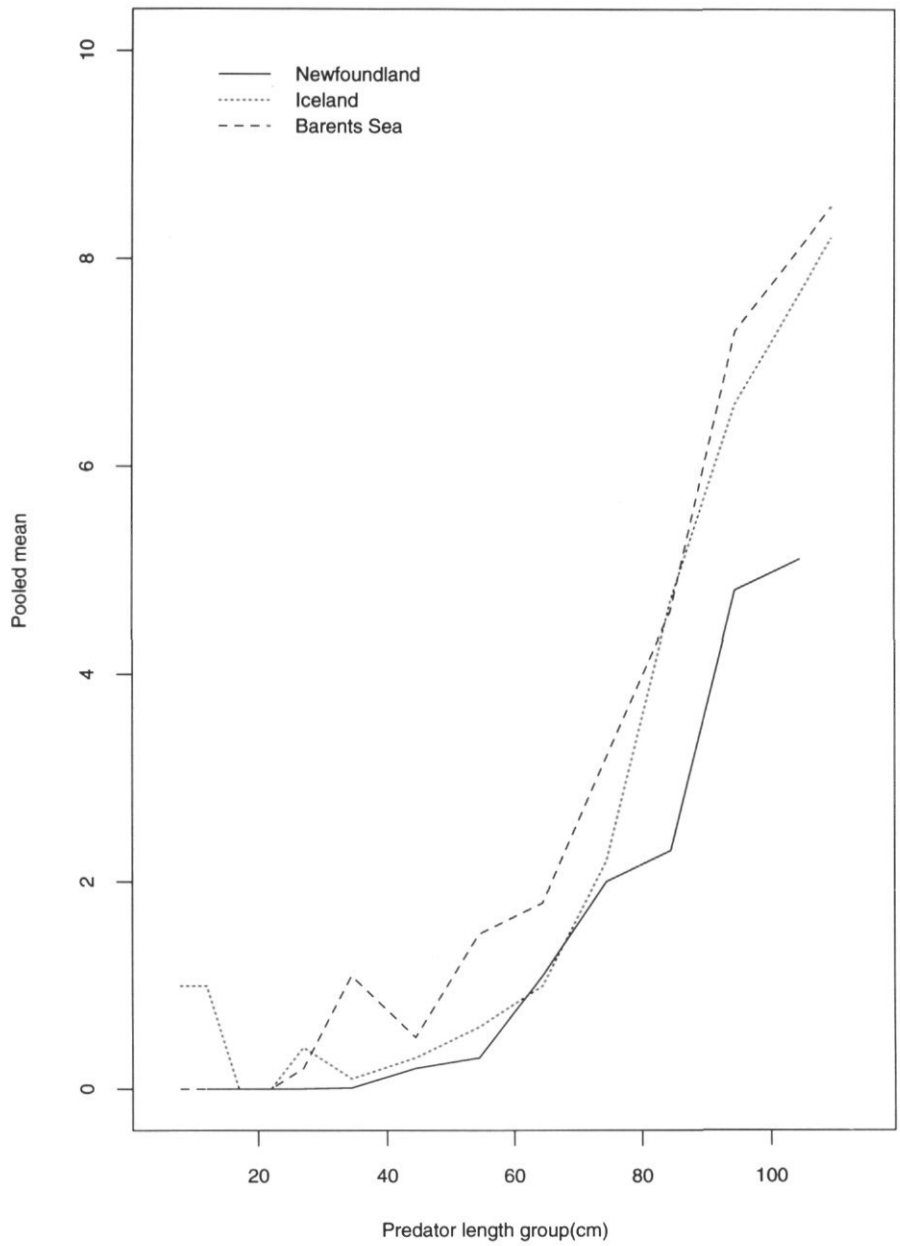


Figure 5. Variation in cannibalism with predator length measured as percentage weight of stomach content (pooled mean).

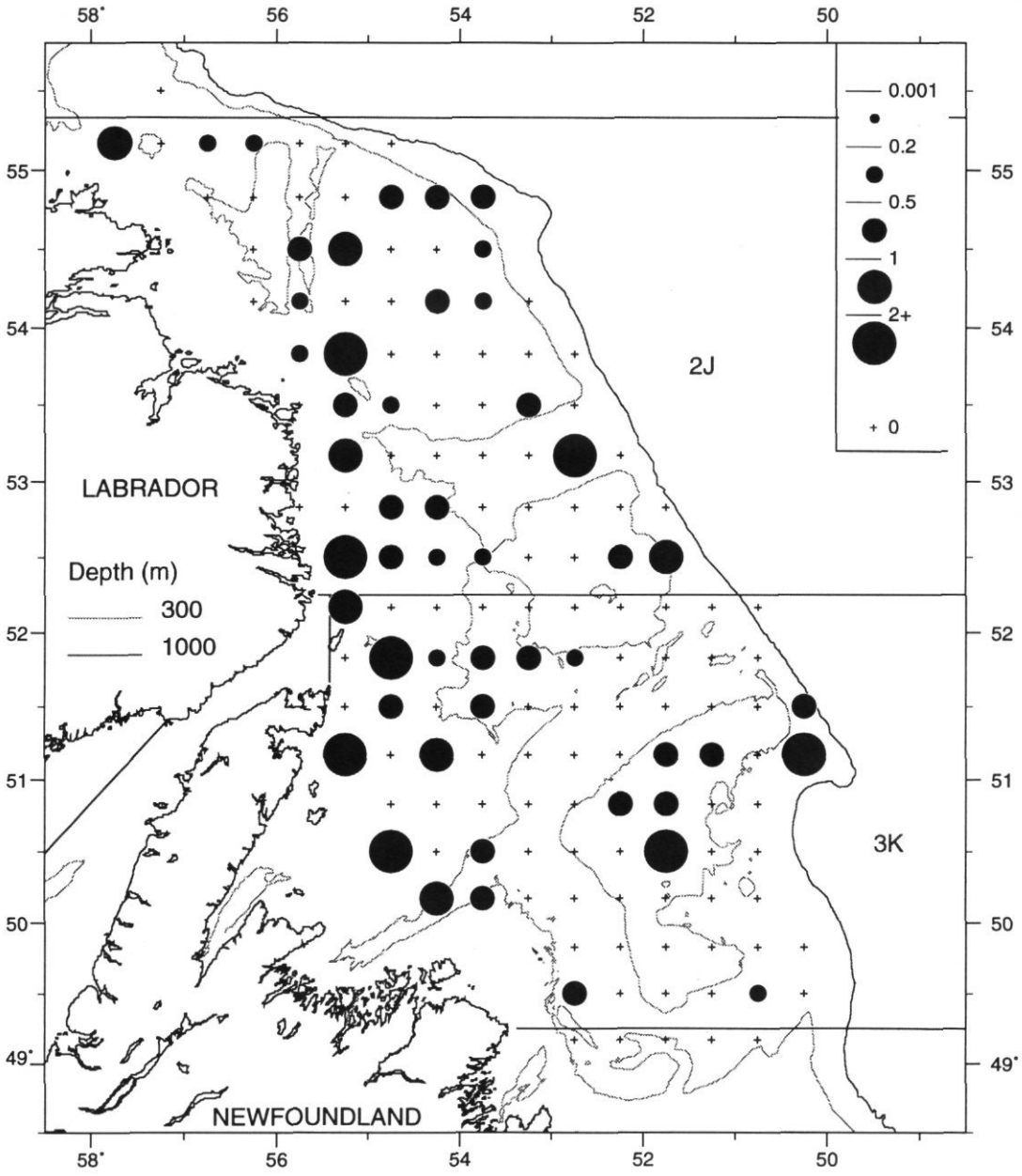


Figure 6. Spatial variation in frequency of occurrence of cannibalism in Newfoundland waters in the autumns of 1978 and 1980–1992. All stomachs collected from cod larger than 29 cm within squares of 20′ latitude and 30′ longitude were pooled. Squares with less than 20 stomachs were excluded. + indicates no occurrence.

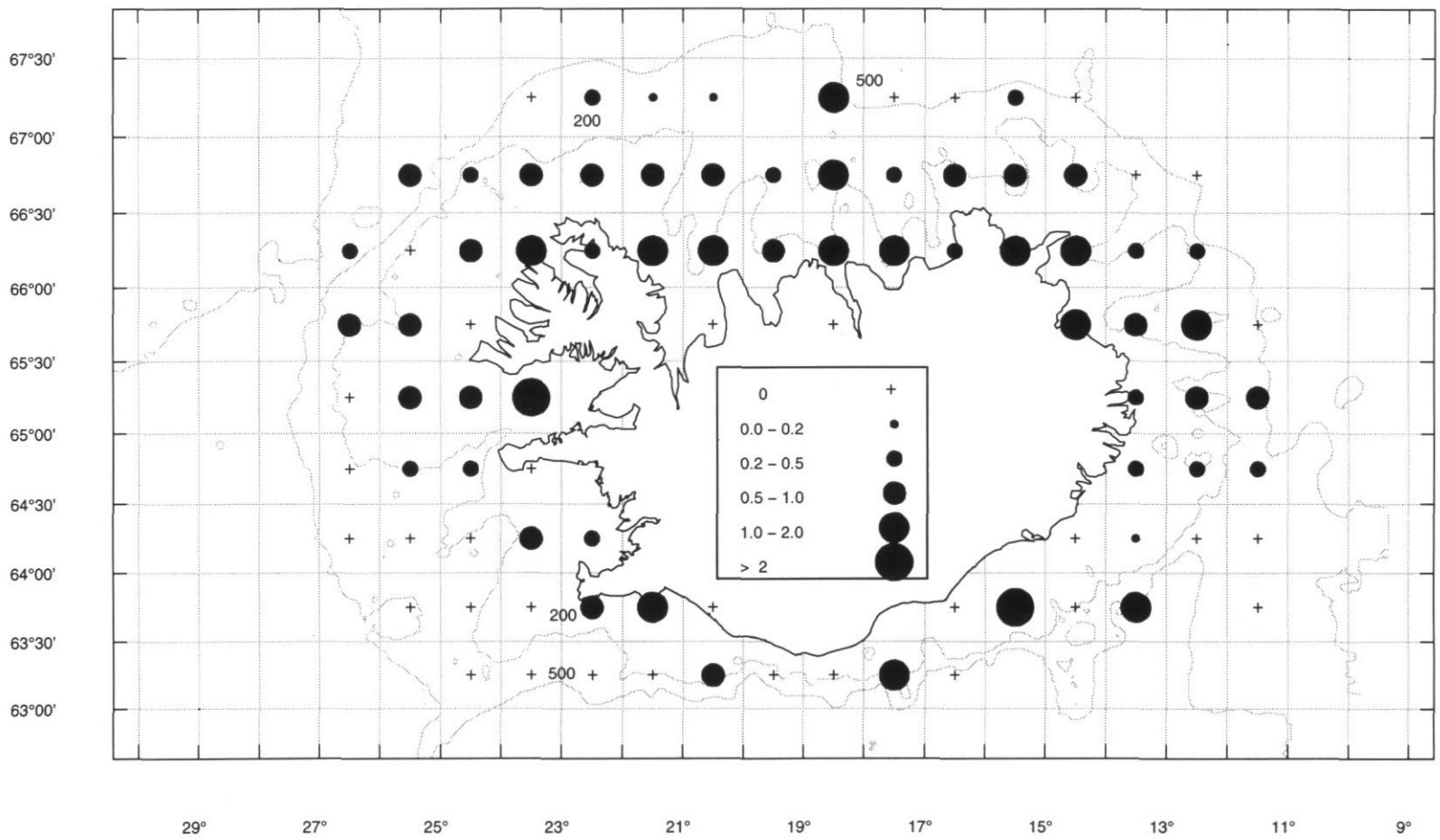


Figure 7. Spatial variation in frequency of occurrence of cannibalism in Icelandic waters 1979–1993. All stomachs collected from cod larger than 29 cm within squares of 30′ latitude and 60′ longitude were pooled. Squares with less than 20 stomachs were excluded. + indicates no occurrence.

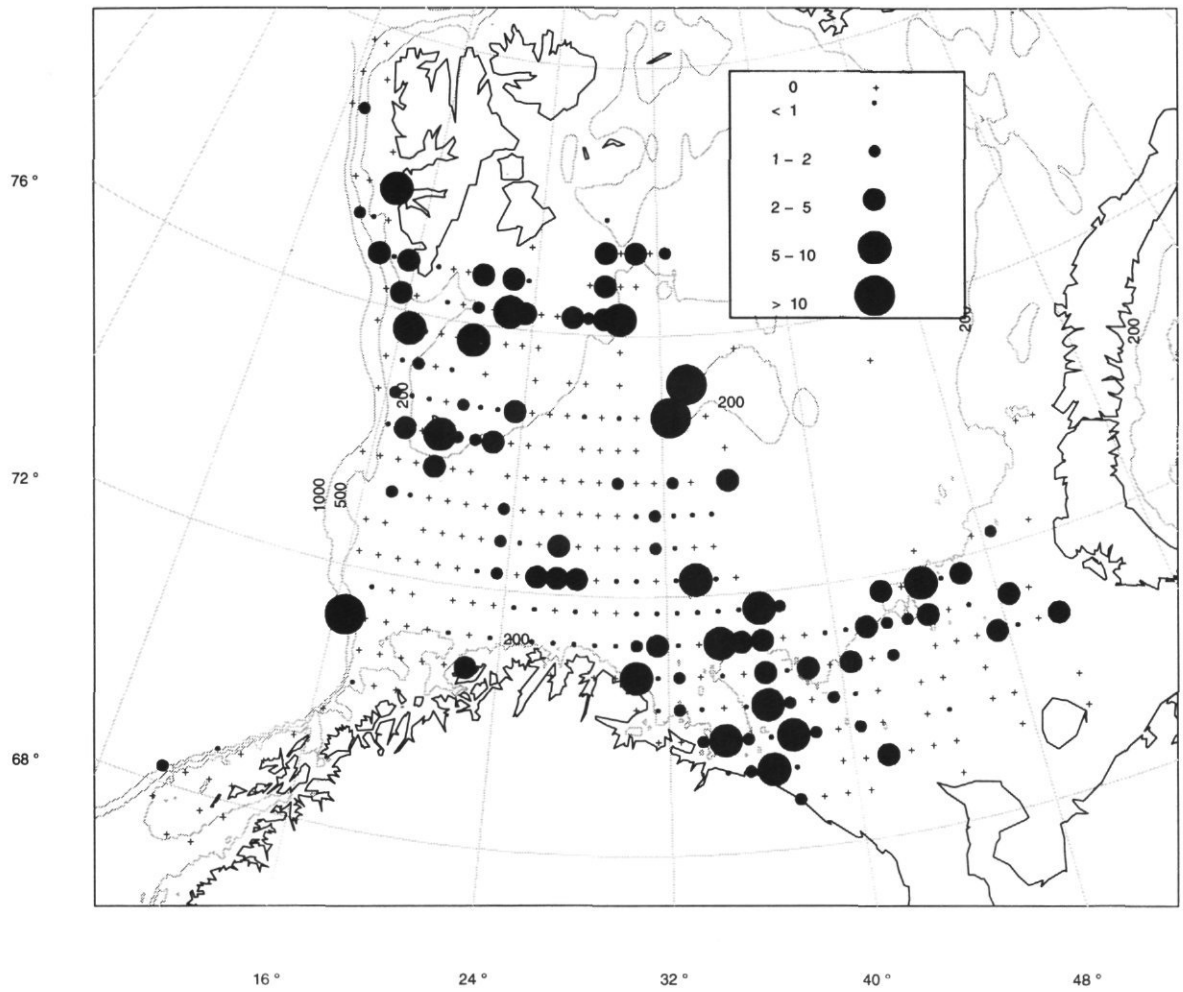


Figure 8. Spatial variation in frequency of occurrence of cannibalism in the Barents Sea 1949–1992. All stomachs collected from cod larger than 29 cm within squares of 30′ latitude and 60′ longitude were pooled. Squares with less than 20 stomachs were excluded. + indicates no occurrence.

Table 4. Correlations between the frequency of occurrence (FO) of cannibalism in cod in the Barents Sea, by half year, and juvenile abundance, capelin biomass, and the mean quantity of capelin in cod stomachs, expressed as a partial fullness index (PFI_c). See Fig. 11. For each pair, the number in parentheses is the probability that the correlation coefficient is zero. n = 9 in all cases.

	Juvenile abundance	Capelin biomass	PFI_c
FO (first half)	0.732 (0.025)	0.041 (0.917)	−0.021 (0.958)
FO (second half)	0.731 (0.025)	0.212 (0.583)	0.334 (0.380)

Consumption of cod by cod in the Barents Sea

Estimation of the contribution of cannibalism to the mortality of juvenile cod requires knowledge of the number of juveniles consumed at age. We used data from the Barents Sea in 1984–1991 to illustrate the magnitude and variability of the total consumption (tonnes) and the consumption (in numbers) of individual age groups (Table 5). The consumption in tonnes increased by a factor of almost 4 from 1984 to 1986 and then decreased to low levels in 1988 and 1989 before increasing again. The estimated consumption in numbers varied greatly among years, especially for the 0-group. Figures for the 1-group seemed to be more stable

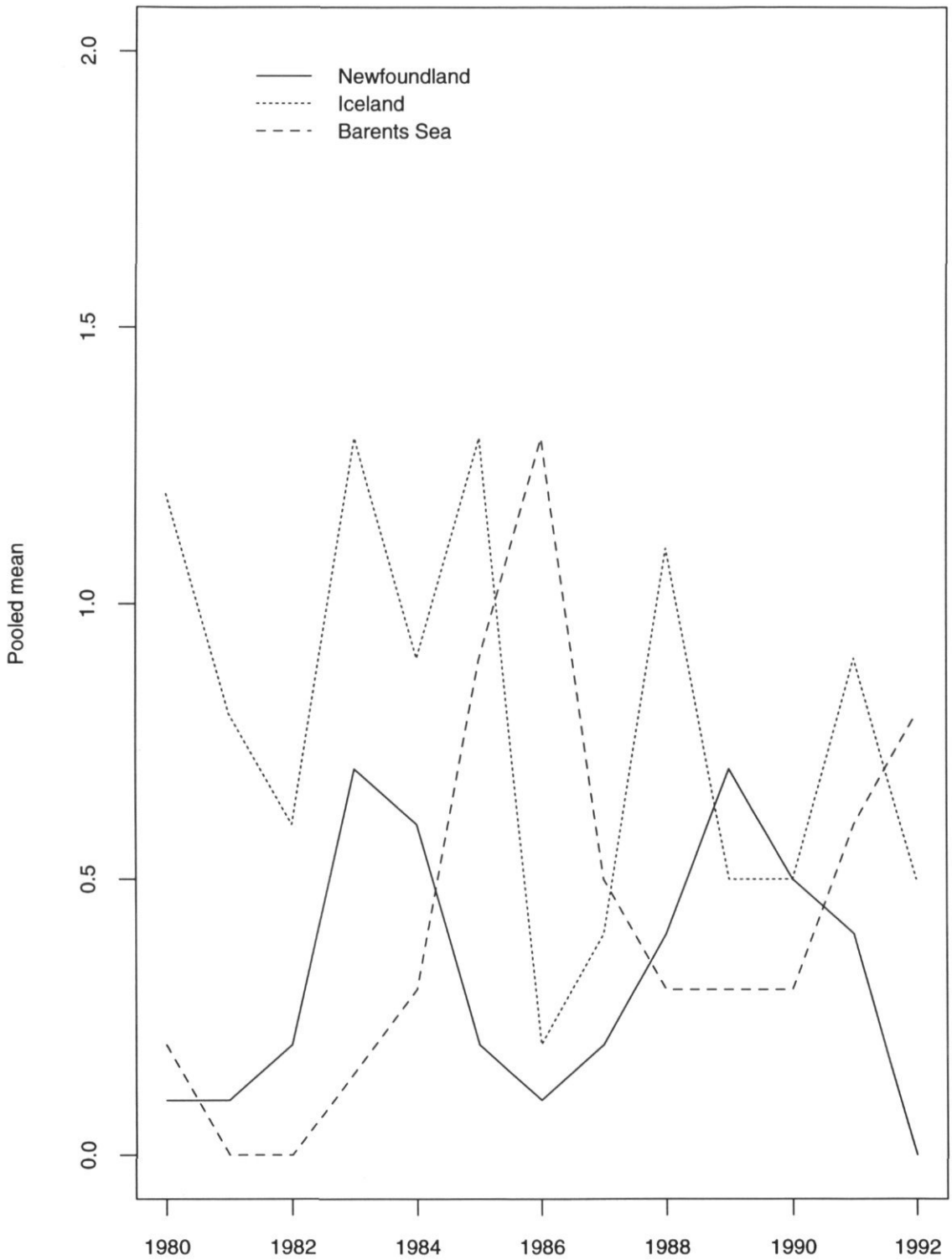


Figure 9. Year-to-year variability of cannibalism measured as percentage occurrence in predator length range 30–119 cm (pooled mean).

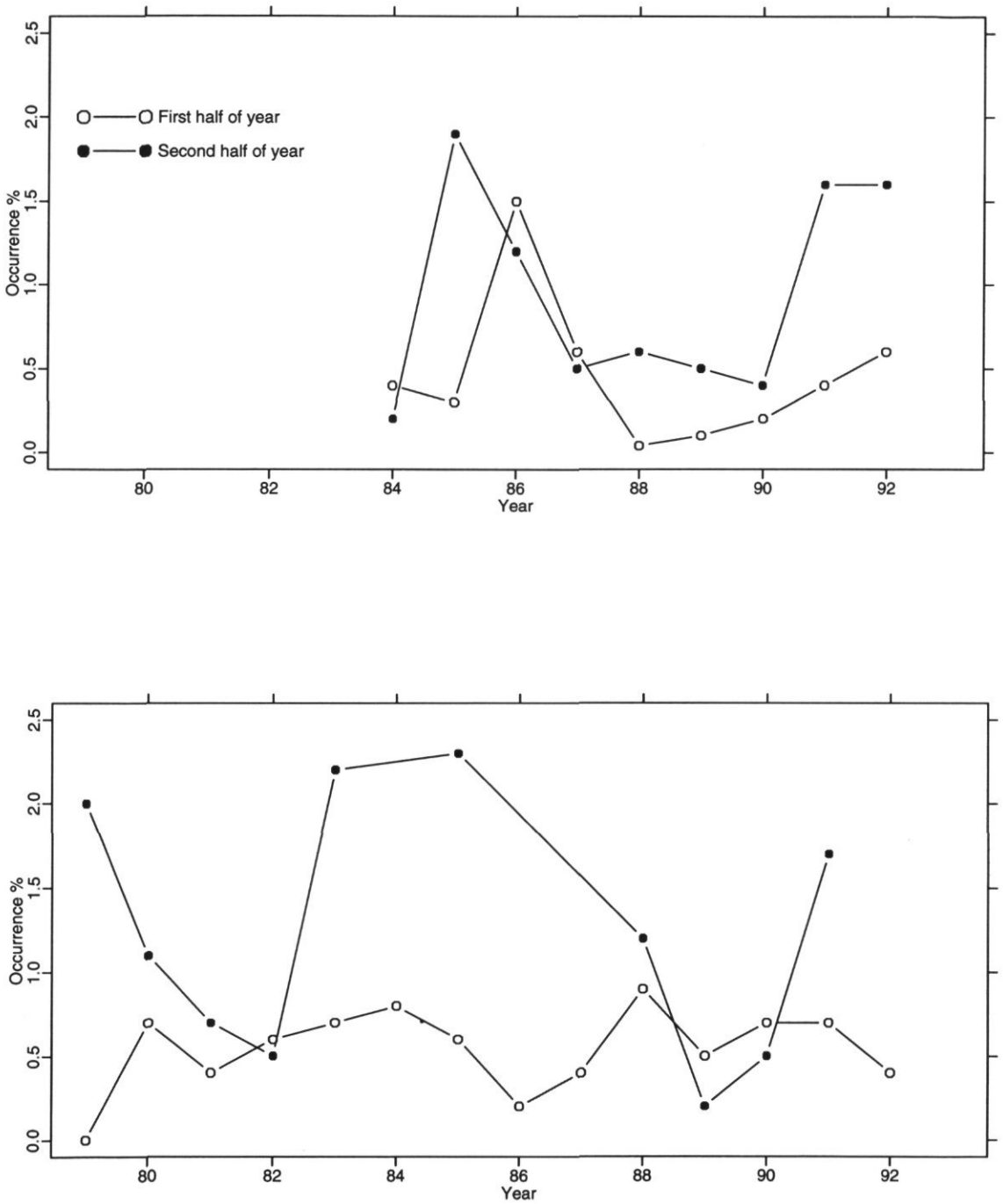


Figure 10. Year-to-year variability of cannibalism with respect to seasons measured as percentage occurrence in predator length range 30–119 cm (pooled mean), by half years in the Barents Sea and in March and autumn (September–December) in Icelandic waters.

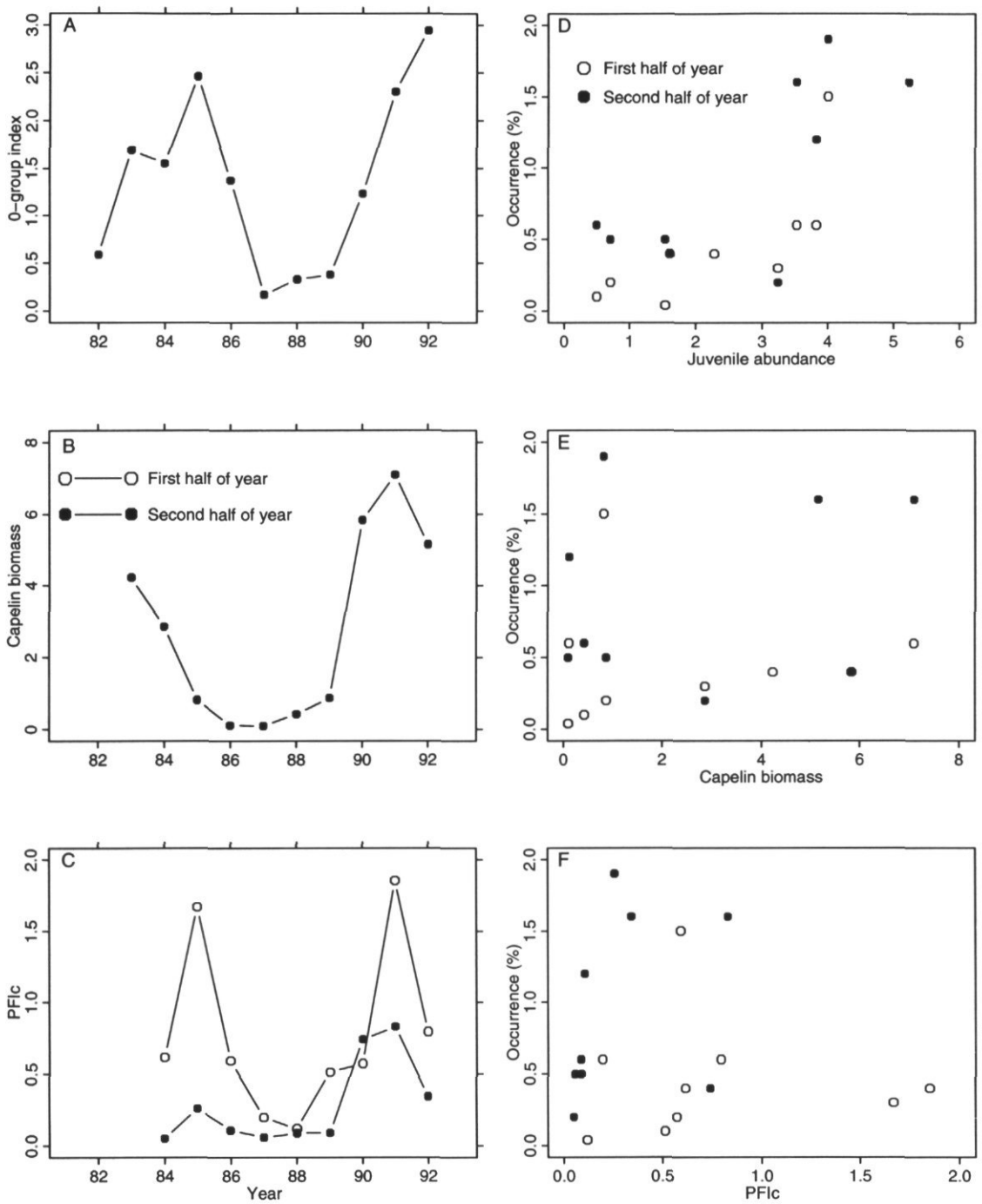


Figure 11. Annual variability in factors which might influence the frequency of occurrence of cannibalism in the Barents Sea. A. Abundance of juvenile cod as determined during pelagic 0-group surveys in late summer (ICES, 1992b). B. Biomass of capelin 1 year and older, as determined during acoustic surveys in the autumn (ICES, 1994). C. Average quantity of capelin in cod stomachs (PFIc), by half year. D. Frequency of occurrence of cannibalism by half year vs. juvenile cod abundance, where an index of juvenile abundance in the first half of year t was calculated as the sum of the indices from pelagic 0-group surveys in years t−1 and t−2, and an index for the second half of the year was calculated as the sum of the indices in years t and t−1. E. Frequency of occurrence by half year vs. capelin biomass, where capelin biomass for the first half of the year was that estimated in the autumn of year t−1 and the biomass for the second half was the estimate from year t. F. Frequency of occurrence versus PFIc, by half year.

Table 5. Consumption of cod by cod (numbers in millions) in the Barents Sea by prey age.

	Prey age group				Total consumption	
	0	I	II	III	(numbers)	(1000 t)
1984	–	504.0	70.0	0.6	574.6	33.2
1985	909.8	294.3	205.1	9.3	1418.5	52.6
1986	61.3	587.2	432.0	372.1	1352.6	125.0
1987	826.7	210.3	350.5	3.6	1391.1	32.8
1988	38.2	566.8	28.3	+	633.3	11.6
1989	1361.4	218.1	0.4	–	1579.9	11.4
1990	–	226.7	50.4	–	277.1	34.5
1991	95.3	246.7	111.9	71.8	543.7	53.6

(200–600 million). In absolute numbers consumed, the 1985 year class seems to have been the most affected (1850 million consumed).

A simple model of predation applied to Icelandic cod

Different models can be used in an attempt to estimate the effect of cannibalism. The following approach is a slight extension of that used by Pope and Woolner (1981) and provides a means of estimating the effect of cannibalism, independent of any evidence from stomach sampling. As will be seen, the actual effects estimated from the model may be due to either cannibalism or competition, since the two effects cannot be distinguished based on the data sets used.

Nilssen *et al.* (1994) constructed a stock and recruitment model for Northeast Arctic cod. They found that the recruitment increases with temperature and with higher spawning stock biomass but declines with increasing juvenile biomass. The form of the spawning stock–recruitment relationship indicates that recruitment increases roughly as the square root of spawning-stock abundance.

The recruitment process in Icelandic waters may be separated into several stages. The first stage can be taken from the time of spawning, mainly in April, to the time of settlement, roughly in September. During this period the eggs and larvae drift from the major spawning areas off the south and west coast clockwise around Iceland to the main nursery areas off the north and east coast. The first measurements of year-class strength are made near the end of the first period, during the 0-group survey in August–September. Later, in March, a groundfish survey is conducted. This survey provides indices of abundance which are used in tuning the VPA estimates.

Cannibalism of eggs and larvae in the southern and western areas has not so far been observed and will not be considered in the analysis. It is, however, well established that cannibalism occurs in the northern and eastern areas and therefore it is reasonable to start a model of cannibalism at the time of the 0-group survey. This separates the pre-recruit (juvenile) period into two parts: the period from spawning to the 0-group survey, and from the time of the 0-group survey until the time of recruitment at age 3 to the fishery.

The original model by Pope and Woolner (1981) connected the VPA estimates of recruitment with other factors, such as spawning stock size, abundance of immature fish and abundance of other species in order to separate out the effects of spawning, cannibalism, and predation.

To investigate further the processes involved, a composite model can be used. Pope and Woolner's approach allows the inclusion of various terms in such a fashion as to first estimate the stock–recruitment function and then add onto that function the effects of different factors, entered basically like M-values. The spatial distribution of adults and juvenile cod in Icelandic waters is such that mature fish would be expected to contribute to the abundance through the usual stock–recruitment curve, whereas there is spatial overlap after 0-group settlement with the older immature fish. A composite model of the two stages can therefore be written as follows:

$$I_0 = \alpha S^{\beta}$$

$$R_3 = \xi I_0^{\eta} e^{\xi J},$$

The first equation describes the period from spawning to settlement (Fig. 12, top) and the second the period from settlement to the 3-group stage (Figure 12, middle). In these equations, I_0 denotes the 0-group index and R_3 the VPA recruitment at age 3. S is the spawning-stock biomass and J an index of the abundance of immature fish (juveniles) which may prey on the year class in question. The various constants need to be estimated by the use of regression.

This provides a means to test separately the processes involved before and after the settlement stage. The first model basically is a Cushing curve (Cushing, 1973). This

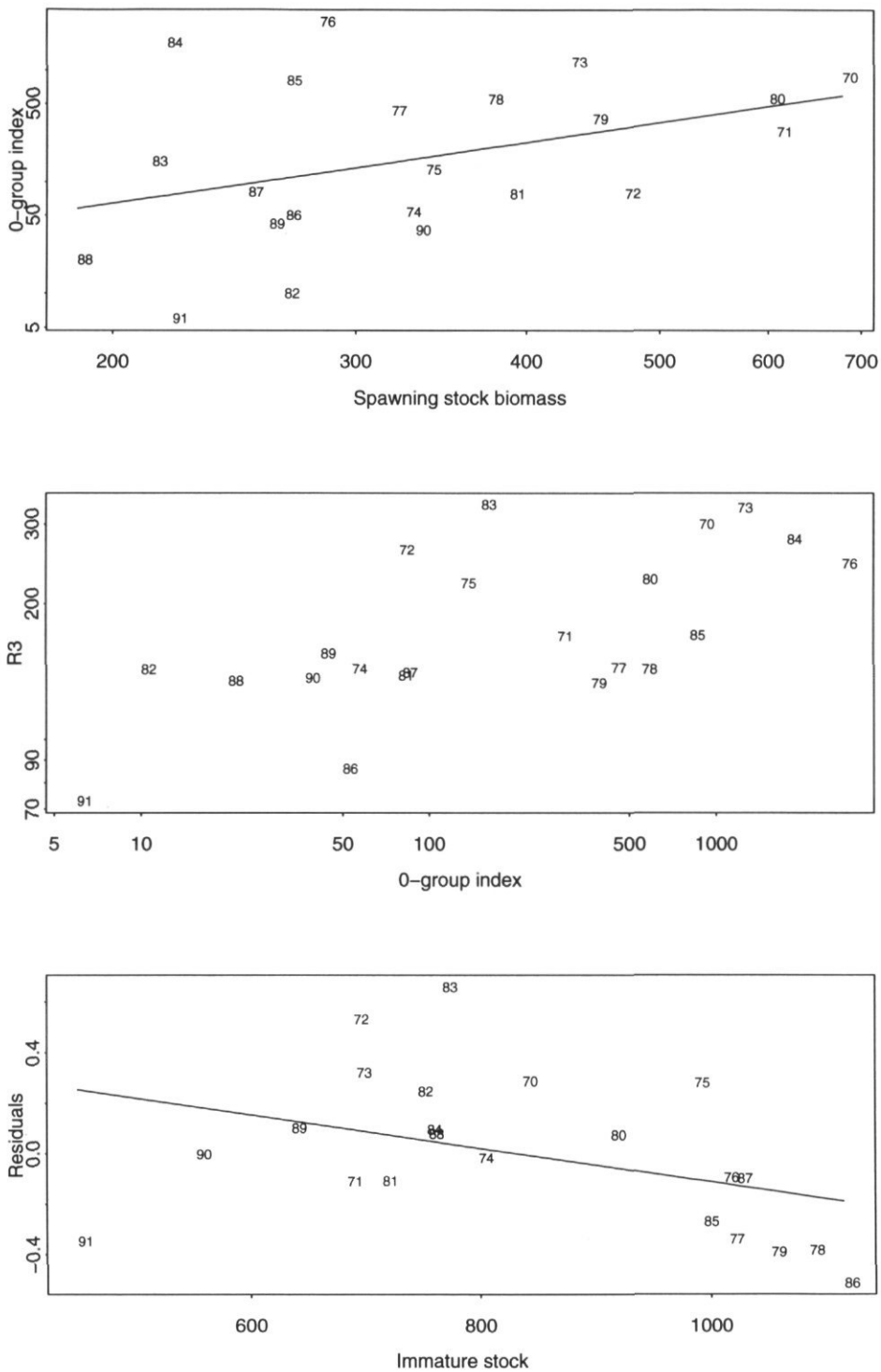


Figure 12. Basis for simple models of predation by Icelandic cod (Table 6). Top: 0-group index versus spawning-stock biomass. Middle: 0-group index versus VPA 3-group. Bottom: Residuals from regression of R_3 on 0-group (I_0) versus immature stock (J).

model can easily be fitted and tested on a log-scale and it is found that the model is marginally significant ($p = 0.07$) which in itself is a very interesting result. It should be noted (as in Pope and Woolner, 1991) that cannibalism by adults during the pre-settlement stage is already in this equation. This particular cannibalism will be incorporated in the regression and it appears in reduced values of the 0-group index with increasing spawning stock size in Figure 12.

The second equation is much more interesting, however. This formulation allows ζJ to appear like an M-value affecting the 0–2 group cod: the second equation first describes how a given 0-group survives to become 3-group in an "average" year, if there were no older year classes (Fig. 12, middle). The $e^{\zeta J}$-term then acts to diminish this in accordance with the size of the older, but immature, year classes (Fig. 12 bottom). In this equation, J is based on VPA values for the abundance of immature cod age 3 and older, but shifted by one year so as to provide an index of the abundance of immature 2+ cod in the year of spawning. Units of measurements are given with the data in Table 6. It should be noted that spurious correlation is not introduced between the variables in the second equation through tuning, since only groundfish survey but not 0-group survey indices are used to tune the VPA.

Other factors can be used in both equations, for example J can be added to the first one and S to the second. Basic regression analysis indicates that no such additions are significant. This gives support to the hypothesis that the effect of the SSB is completely described during the pre-settlement stage and that the effect of cannibalism/competition is mostly a function of the amount of older immature fish on the nursing grounds.

The second equation was linearized by taking logarithms on both sides and fitted to data from the period 1970–1991 (Table 6, ICES, 1993a). The R^2-value from the regression is 0.54 and the parameters in the equation were significantly different from zero:

Parameter	Coefficient of	Value	Std. Error	t value
$\ln(\xi)$		4.8429	0.2972	16.2975
η	ln(I0)	0.2011	0.0424	4.7386
ζ	J	−0.8554	0.3869	−2.2109

Now, the term ζJ, which appears as an M-value, reflects an overall M over the period from the beginning of September in year 0 through December of year 2, i.e., 2.33 years. Since the average of J is 0.831, the point estimate, −0.855, of ζ indicates that M inflicted on 0–2 group cod may be in the order of 0.71 due to cannibalism, as an average value over the years 1970–1991.

It can be deduced that the confidence interval for the ζ-value is roughly from −1.6 to −0.08, corresponding to an average 2.33-year M-value in the range 0.067 to 1.35.

Several important questions immediately come up, one of which is whether the significance of these results is simply due to a few outliers. Regression diagnostics do indeed indicate that there are several highly influential points and outliers. Stepwise deletion of such points is a useful way to consider the sensitivity of the result. The following table summarizes the effects of outlier deletion and also of changes in model assumptions.

Table 6. Input data for a model of the mortality induced by cannibalism in Icelandic cod (SSB = spawning-stock biomass, '000 t, J = juvenile stock, '000 t, R_3 = recruitment at age 3, millions and I_0 = 0-group index).

	SSB	J	R_3	I_0
1970	678.742	837.545	300.418	873
1971	608.973	684.324	169.263	283
1972	472.207	690.300	263.221	79
1973	431.856	692.639	326.284	1191
1974	326.652	799.028	143.285	54
1975	337.628	986.362	221.651	130
1976	282.578	1011.59	245.472	2743
1977	318.643	1016.62	143.982	435
1978	374.998	1086.02	143.163	552
1979	447.179	1053.00	133.346	370
1980	601.718	914.336	226.258	558
1981	389.082	715.310	138.628	78
1982	266.122	746.255	143.084	10
1983	213.546	767.857	331.452	153
1984	219.014	753.965	277.658	1772
1985	267.120	994.235	170.280	812
1986	266.754	1115.12	86.206	50
1987	250.569	1023.62	140.657	81
1988	188.486	755.740	135.000	20
1989	259.479	636.227	155.000	42
1990	331.919	553.647	137.000	37
1991	220.958	451.556	73.000	6

Model $\ln(R_3) = \ln(\xi) + \eta\ln(I_0) + \zeta J$	Years	Coefficients Intercept $\ln(\xi)$	$\ln(I_0)$ η	J ζ
Linear regression	1970–1991	4.843	0.201	−0.855
	Omit 91	5.254	0.174	−1.143
	Omit 90,91	5.478	0.167	−1.342
	Omit 83,90,91	5.352	0.167	−1.229
Least median squares regression	1970–1991	5.954	0.152	−1.796
Robust (M-estimation) regression		4.893	0.197	−0.900
L1 (median absolute residual) regression		4.868	0.180	−0.784
Least trimmed squares regression		4.944	0.233	−1.304
GLM with gamma error and log link		4.954	0.194	−0.904

It is seen that the coefficient of J varies from −1.8 to −0.9, depending on the model assumptions made, corresponding to a 2.33-year average M-value in the range 0.75–1.50. The range may seem somewhat wide, but it should be noted that in all cases the coefficient does have the expected (negative) sign.

The natural mortality due to cannibalism would be expected to be decreasing with respect to age and this decrease may even be expected to be exponential. A simpler approach may be taken, assuming that the 2.33-year value of 0.71 represents the sum of monthly M-values which decrease linearly from the last September as 0-group to zero in January as 3-year-olds. This yields estimates average M due to cannibalism (or competition) as 0.19 during September–December of the 0-group stage, 0.39 as 1-group, and 0.14 as 2-group.

Discussion

In offshore waters of northeastern Newfoundland, Iceland, and the Barents Sea, cannibalism is rare in cod less than 30 cm in length, but becomes more frequent as the cod grow. A comparison between lengths recorded in this study and aging data published elsewhere indicates that many prey are 0-group, especially off Iceland and in the Barents Sea, and that most prey are younger than 3 years. Almost all the cannibals were at least twice the length of their prey and most were more than three times longer. Therefore, most of the cannibalism documented in this study involves intercohort predation. This appears to be the norm among cannibalistic fish (Smith and Reay, 1991). Intracohort cannibalism was recorded only in 0-group cod off Iceland in autumn 1990.

The contribution of cannibalism to the diet of cod, expressed on a percentage weight basis, increased with cod length in all three areas. It was highest in the Barents Sea, lowest off Newfoundland, and intermediate off Iceland, but did not exceed 9% on average even in the largest cod. Cannibalism has been found to account for a larger part of the diet in other gadid species, such as walleye pollock, *Theragra chalcogramma* (Dwyer *et al.*, 1987) and several hakes, *Merluccius* spp. (Lleonart *et al.*, 1985; Clay *et al.*, 1984).

The distribution of cannibalism in three areas is in general agreement with the distribution of small fish as determined by trawl surveys. In the Newfoundland area, cannibalism was high on the coastal shelf off southern Labrador and northeastern Newfoundland, where small cod have been caught most consistently during autumn bottom-trawl surveys (Anderson, 1993). Observations on the outer banks correspond to areas where older (age 2 and 3) cod are common. In the Iceland area, cannibalism was most commonly recorded in the north, which is consistent with Pálsson's (1980) finding that the most important nursery grounds were located off the north and northern northwest coasts. In the Barents Sea, cannibalism occurred most frequently in the east and in the Svalbard area, where overlap between large and small cod is most common. An examination of the distribution of cannibalism by age group of the prey is beyond the scope of this article, but may provide information on ontogenetic shifts in distribution and susceptibility to cannibalism.

The frequency of occurrence of cannibalism increases with the abundance of juvenile cod. In the Newfoundland area, the frequency of occurrence of cannibalism was positively correlated with the catch of young cod in bottom trawl surveys. In the Iceland area, the frequency of occurrence was somewhat higher in 1979–1985 than in more recent years, which is consistent with better recruitment during the earlier period. In the Barents Sea, the frequency of occurrence of cannibalism during the period 1984–1992 was positively correlated with indices of abundance of pelagic 0-group cod. The frequency of occurrence in all three areas was much lower than had been reported from stomach collections in the Barents Sea during the period 1949–1960. This may be related to higher levels of recruitment in the earlier period, but it is also possible that higher values in the earlier period were caused in part by smaller sample sizes from more restricted areas and time periods. Additional research is required before it can be concluded that cannibalism in cod in the Barents Sea was much more common in the 1950s than in more recent years.

The hypothesis that cannibalism in Barents Sea cod increases in years of low abundance of major prey was not supported. A negative correlation was not found between the frequency of occurrence of cannibalism and either the biomass of capelin or the average quantity of capelin found in cod stomachs. This conclusion must be treated with caution because of uncertainties in the calculation of each variable and the shortness of the time-series.

The estimates of the number of cod consumed by cod in the Barents Sea are of the same order of magnitude as the strength of an average year class at age 3 (600 million), as estimated by virtual population analysis (ICES, 1993b). The accuracy and precision of such estimates of consumption are difficult to judge. As noted by many investigators (e.g. Dwyer *et al.*, 1987; Magnússon and Pálsson, 1989; Mehl, 1989; Bowering and Lilly, 1992), there is considerable uncertainty in many of the values entering such calculations, including the stock abundance estimates, the stomach content data, and the parameters of the gastric evacuation model. Of particular concern is the potential variability in the timing of resource assessment surveys relative to the timing of settlement of the 0-group juveniles. Even when the numbers of young cod consumed by older cod can be

reliably estimated, it will be difficult to evaluate the contribution of cannibalism to total natural mortality without measures of absolute abundance over time. In instances where cannibalism is thought to be a major contributor to total natural mortality, it may be included in a virtual population analysis, but some value for the remaining natural mortality must still be assumed (Lleonart *et al.*, 1985).

The data reported in this study are confined to offshore waters covered by bottom trawl surveys. The extent of cannibalism landward of the survey areas is unknown, but might be important. For example, 0-group and 1-group cod are abundant in shallow coastal waters of eastern Newfoundland (Methven and Bajdik, 1994) and older juveniles (ages 2 and 3) are commonly caught and observed (Stevenson *et al.*, 1984; Clark and Green, 1990). Cannibalism has been found in cod near the coast, especially at times other than the few weeks in early summer when capelin are aggregated at the coast to spawn (Templeman, 1965; G. R. Lilly, unpubl. data).

The frequent occurrence of cannibalism on 0-group off Iceland and in the Barents Sea contrasts with the low occurrence found off Newfoundland. This may be related to the degree of overlap between demersal 0-group and larger conspecifics. The high abundance of juvenile cod in shallow coastal waters of eastern Newfoundland, and the lack of evidence for large numbers in adjacent offshore waters, has led to the hypothesis that the nursery area for this stock is inshore (Templeman, 1981). Juvenile cod have been reported in coastal waters elsewhere, such as in Norway (Godø *et al.*, 1989; Olsen and Soldal, 1989; Tveite, 1984) and the British Isles (Hawkins *et al.*, 1985; Riley and Parnell, 1984). In such habitats, the juveniles may be physically separated from larger cod, at least for much of the year, and may be less susceptible to predation. However, there are also observations of abundant juveniles in shelf habitats, such as Georges Bank (Lough *et al.*, 1989), the southern Grand Bank of Newfoundland (S. J. Walsh, Dept. of Fisheries and Oceans, St John's, Newfoundland, Canada, pers. comm.), Flemish Cap (Lilly, 1987), Iceland shelf (Pálsson, 1980), and the Barents Sea (Ponomarenko, 1984). In such areas there may be greater opportunity for cannibalism. Studies of ontogenetic changes in distribution in each stock are vital to understanding the intensity of cannibalism and its potential for influencing recruitment.

Models for the relationship between the abundance of 0-group and the number of recruits as 3-group indicate that there is a positive relationship. Further, the abundance of older, immature fish has a negative effect on the survival. However, the abundance of mature fish does not show a significant effect. This may seem in contrast with the results obtained elsewhere concerning the diet of cod in different length groups, but it is clear that the abundance of the mature fish is much less than of the immatures, and hence relative stomach contents do not reflect the relative mortalities inflicted by the different stock components.

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Predation by Atlantic cod on capelin on the southern Labrador and Northeast Newfoundland shelves during a period of changing spatial distributions

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Lilly, G. R. 1994. Predation by Atlantic cod on capelin on the southern Labrador and Northeast Newfoundland shelves during a period of changing spatial distributions. – ICES mar. Sci. Symp., 198: 600–611.

Catches of cod (*Gadus morhua*) during random depth-stratified bottom-trawl surveys, and the contents of the stomachs of cod sampled during those surveys, were used to study the distribution of cod and the distribution of feeding by cod on capelin (*Mallotus villosus*) on the continental shelf off southern Labrador and eastern Newfoundland (NAFO Divisions 2J, 3K, and 3L) during the autumns of 1978–1992. In 1989 and subsequent years, there occurred a substantial decline in abundance of cod and a reduction in cod distribution. During the same period, the biomass of capelin, as estimated from hydroacoustic surveys in Divisions 2J and 3K, declined to very low levels. Despite the apparent severe decline in capelin biomass, many cod had a relatively high content of capelin in their stomachs, in part because the capelin changed their distribution and occupied the general area where the remaining cod were concentrated. Inspection of the data on a finer spatial scale revealed that in some years cod sampled from large catches had few or no capelin in their stomachs, whereas cod from small catches nearby often had relatively large quantities of capelin in their stomachs. An examination of bottom temperatures during 1978–1992 does not support the postulate that the disappearance of cod from the north and west of Division 2J+3K in 1989–1992 was caused by avoidance of cold water. It remains unclear whether the change in cod distribution was related to the change in capelin distribution.

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Introduction

The stock of cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland in Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J+3KL (Fig. 1) has experienced a substantial decline in biomass and reduction in distribution since 1989 or 1990 (Bishop *et al.*, 1993). Among the numerous factors identified as possible causes for these changes are an apparent decline in the biomass of capelin and a reduction in water temperature (Workshop on Northern Cod, Department of Fisheries and Oceans, Canada, January 1993, unpublished).

Estimates of capelin biomass from hydroacoustic surveys conducted by Canada and Russia during autumn in Divisions 2J+3K declined to very low levels in the early 1990s, with the Canadian series showing a very abrupt drop between 1989 and 1990 (Fig. 2). Many studies (reviewed by Lilly, 1987) have emphasized that capelin is a major prey of cod in this area. During the period 1978–1986, cod in Divisions 2J+3K did not compensate during years of low capelin abundance by preying more intensively on other prey (Lilly, 1991). It has been postulated that the apparent recent reduction in capelin biomass caused a decrease in condition of cod, as happened in the Barents Sea in the late 1980s (Jørgensen, 1992), and that the postulated poor condition might be partly responsible for a high mortality rate in cod.

Water temperatures on the shelf off Labrador and Newfoundland have been below normal for most of the period since 1980, with two unusually cold periods in the mid-1980s and early 1990s (Colbourne *et al.*, 1994). It has been hypothesized that cold water in 1990–1992 may have been responsible, either directly or indirectly, for an increase in cod mortality and a change in cod distribution. deYoung and Rose (1993) and Rose *et al.* (1994) argued that any mortality due directly to cold water would not have influenced population abundance, but

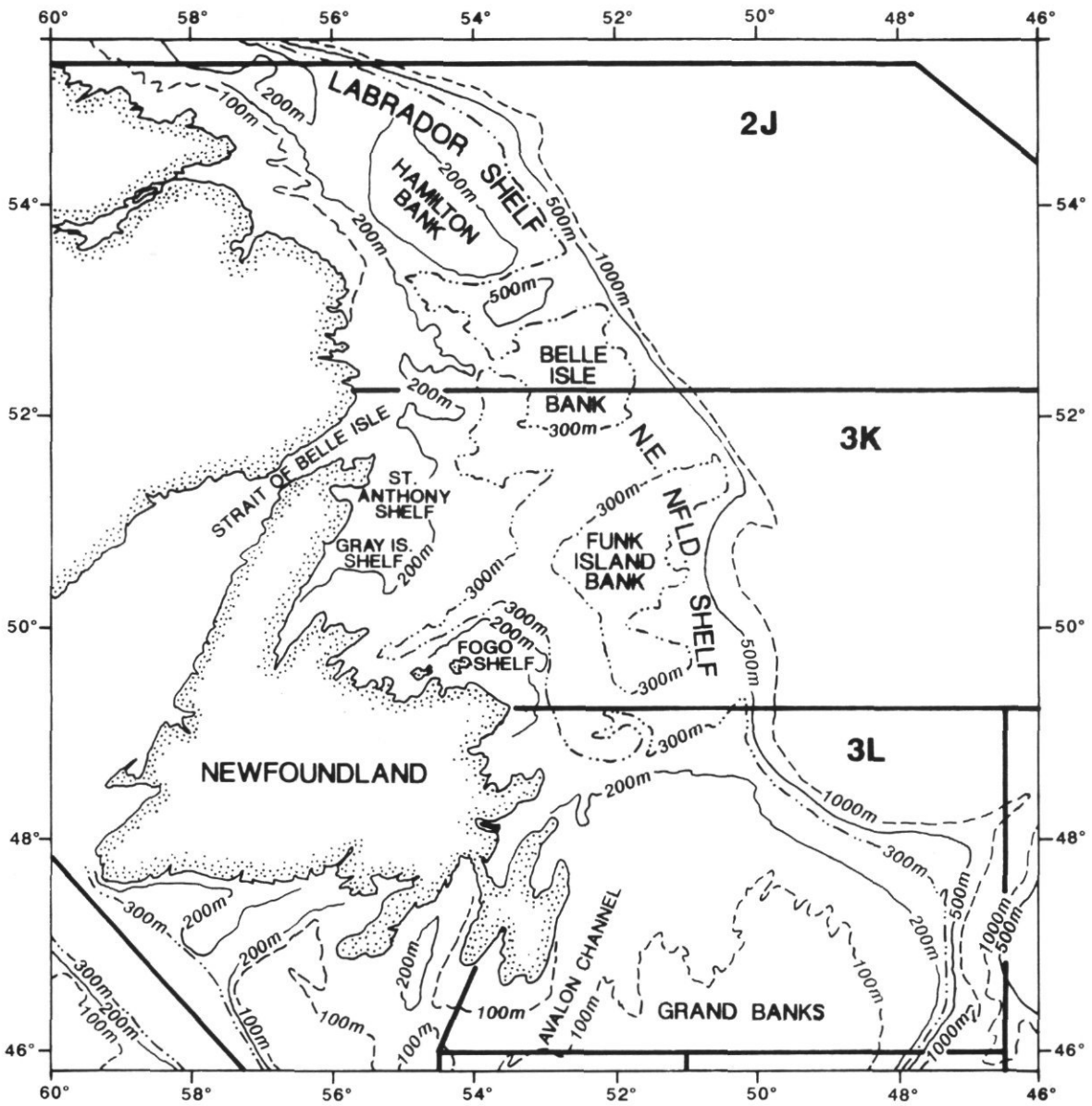


Figure 1. Map of the study area, showing major physiographic features and NAFO Divisions.

that cold water may have had an important indirect effect. They concluded from an analysis of catches in research bottom trawl surveys in autumn and commercial trawl fisheries in winter that cod shift north and south by at least several degrees of latitude in response to changes in water temperature. They suggested that a southward movement during the cold period of the 1990s made the fish more available to fishing activity on the northern Grand Banks. They also rejected the possibility that the reduction in cod distribution in the 1990s was caused by the disappearance of specific populations or substocks within the 2J+3KL cod stock complex.

The first objective of this paper is to examine the geographic patterns in cod distribution and cod predation on capelin during the autumns of 1980–1992 to determine whether the apparent decline in capelin abundance in the 1990s caused a reduction in the feeding by cod on capelin. The second objective is to conduct one specific test of the hypothesis that cod changed their distribution in response to water temperature. Cod

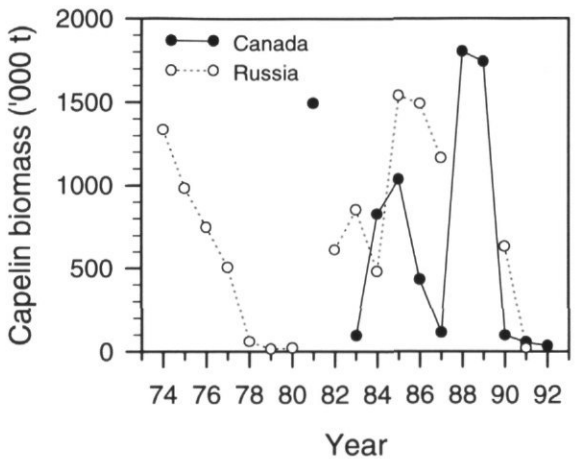


Figure 2. Biomass estimates of capelin from hydroacoustic surveys conducted during autumn in NAFO Divisions 2J+3K by Canada (Miller, 1993) and Russia (Bakanev, 1983, 1992).

catches and bottom water temperatures will be compared in western Division 2J, where the change in cod distribution was first noticed.

Materials and methods

The trawl survey area in NAFO Divisions 2J, 3K, and 3L covers the southern Labrador Shelf, the Northeast Newfoundland Shelf, the northern Grand Bank, and the adjacent continental slope to a maximum depth of 1000 m (Fig. 1). The continental shelf in this area is broad and much of it is deep. Hamilton Bank at the southern end of the Labrador Shelf has an extensive plateau less than 200 m in depth, whereas Belle Isle Bank and Funk Island Bank on the Northeast Newfoundland Shelf have only small areas shallower than 200 m. Grand Bank in the south has an extensive area between 100 and 200 m. Only the northern tip of the plateau (<100 m) lies within the stock area. Depths greater than 400 m occur in the saddles northwest of Hamilton Bank and between Hamilton Bank and Belle Isle Bank, and in basins landward of Belle Isle Bank and Funk Island Bank. The Labrador Current flows southeastward along the shelf and keeps temperatures low. The cold intermediate layer is deepest and coldest toward the coast, and bottom temperatures below 0°C are found at depths of about 100–200 m in late autumn in many years, especially on Grand Bank. Maximum bottom temperatures in the survey area are usually about 4°C.

Cod were caught during random depth-stratified bottom trawl surveys conducted during October–December in Divisions 2J+3K (1978–1992) and Division 3L (1981–1992, excluding 1984). Details regarding ships and gear employed, sampling dates, stratum areas and locations, and changes in survey pattern are provided by Lilly and Davis (1993) and Bishop *et al.* (1993). Tows were made at 3.5 knots for 30 min at each fishing station. Fishing in all Divisions and years was conducted on a 24-h basis.

Stomachs were collected from up to three randomly selected cod per 10-cm length-group per station in 1980–1982 and three per 9-cm length group in 1983–1992. Stomachs were not collected from fish which showed signs of regurgitation, such as food in the mouth or a flaccid stomach. Stomachs were individually tagged and excised, and fixed and preserved in 4% formaldehyde solution in sea water prior to examination of their contents in the laboratory.

Examination involved separation of food items into taxonomic categories. Fish and decapod crustacea were identified to species, but most other groups were assigned to higher order taxa. Items in each taxon were placed briefly on absorbent paper to remove excess liquid, and then counted and weighed to the nearest 0.1 g.

The quantity of capelin in the stomachs of the cod from a specified sample was expressed as a mean partial fullness index (Fahrig *et al.*, 1993):

$$PFI_c = \frac{1}{n}\sum_{j=1}^{n}\frac{W_{cj}}{L_j^3} \times 10^4$$

where W_{cj} is the weight (g) of capelin in fish j, L_j is the length (cm) of fish j, and n is the number of fish in the sample. Mean total fullness index was calculated as:

$$TFI = \frac{1}{n}\sum_{j=1}^{n}\frac{W_{tj}}{L_j^3} \times 10^4$$

where W_{tj} is the total weight of prey in fish j. For simplicity, the present analysis was restricted to cod within the 36–71 cm length range, and all cod within this range were pooled. Cod smaller than about 30–35 cm cannot feed on the largest capelin, and cod larger than about 70 cm tend to feed to an increasing extent on groundfish and crabs (Lilly, 1991).

The geographic distributions of cod catches and capelin in cod stomachs (PFI_c) are presented in expanding symbol plots in order to provide visual information on annual changes in the spatial distribution of fishing stations, the among-station variability in cod catch and PFI_c, and the relationship between fish distribution and bathymetry. This presentation permits station-by-station comparison of the cod catch and the quantity of capelin in cod stomachs. To investigate the long-term distribution of cod and the occurrence of capelin in cod stomachs, the arithmetic mean cod catch per tow and the

mean PFI_c were calculated from all stations occurring in areas of 10′ latitude and 20′ longitude during the period 1980–1988. To illustrate among-year variability, cod catch and mean PFI_c were plotted for each individual station in 1984–1986 and 1989–1992.

Results

Distributions

During the period 1980–1988, relatively large catches of cod occurred in several areas: (1) from the northern limit of the survey to the coastal shelf off northern Newfoundland, especially the northern tip of Hamilton Bank and near the isthmus leading to Belle Isle Bank; (2) the outer trough between Belle Isle Bank and Funk Island Bank; (3) the outer trough between Funk Island Bank and Grand Bank, and from there southeastward along the northeastern slope of Grand Bank; and (4) the plateau of Grand Bank (Fig. 3). This pattern, with some variations, was apparent in both cold years (e.g. 1984, 1985) and warm years (e.g. 1986) (Fig. 4). During the period 1980–1988, the mean stomach fullness index for capelin in cod stomachs (PFI_c) was moderate to high in two broad regions: (1) northern and western Divisions 2J+3K (Hamilton Bank, western Belle Isle Bank, and the inner shelf off northeastern Newfoundland) and (2) northern Division 3L (northern and northeastern slopes of Grand Banks) (Fig. 3). In many years, such as 1984 and 1985 (Fig. 4), the capelin in Divisions 2J+3K were primarily on Hamilton Bank and along the coastal shelf off southern Labrador and northeastern Newfoundland, whereas in some other years, notably 1986 (Fig. 4) and 1987 (not illustrated), they were more aggregated on the central Northeast Newfoundland Shelf. The average distributions (Fig. 3) reveal that the area of cod concentration from Hamilton Bank to the coastal shelf off northern Newfoundland, and the area along the northeast slope of Grand Bank, both broadly coincide with regions of moderate to high PFI_c values. In contrast, cod concentrations in the outer trough between Belle Isle Bank and Funk Island Bank, and in the outer trough between Funk Island Bank and Grand Bank (especially within Division 3K), experienced low PFI_c values. The cod on the plateau of Grand Bank also fed very little on capelin at this time of year, but they did prey intensively on other species, most notably sand lance (*Ammodytes dubius*) (unpubl. data).

Geographic plots for the years 1989–1992 (Fig. 5) illustrate the recent decline in cod catch and change in cod distribution. In 1989 few cod were caught toward the coast in Divisions 2J and 3K. By 1991 there were no large

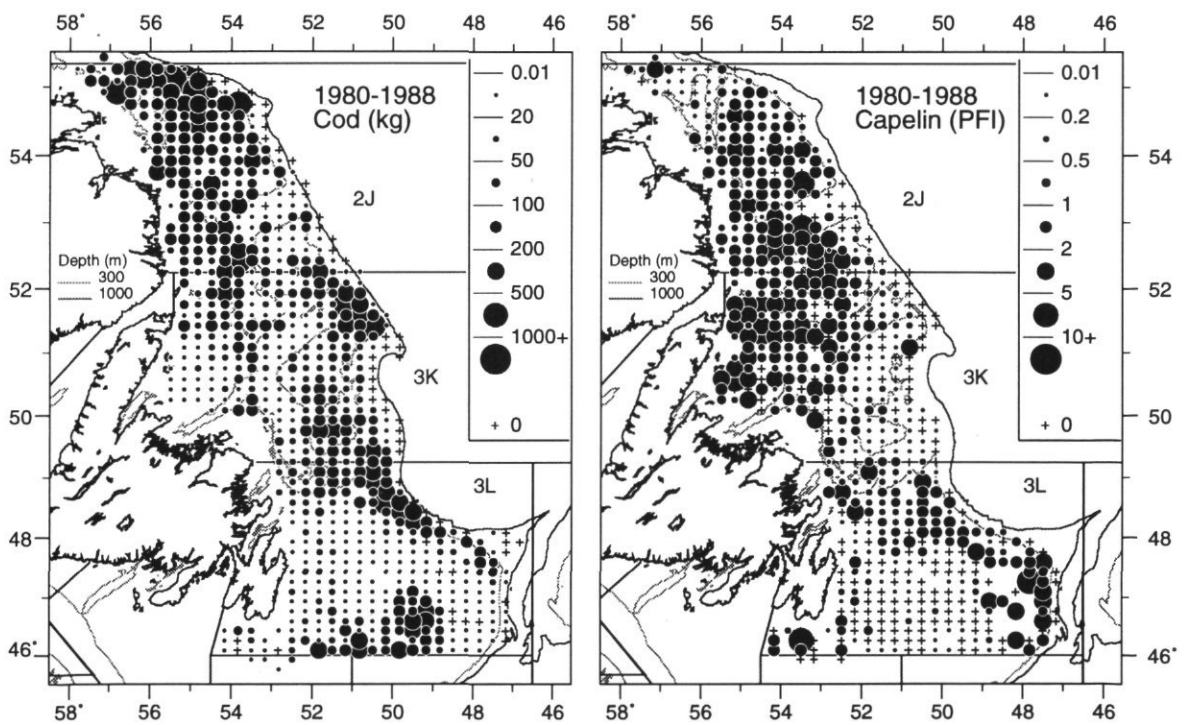


Figure 3. Mean catch of cod (kg/30 min tow) and mean partial fullness index for capelin (PFI_c) in cod stomachs in 1980–1988. The data from all tows in areas of 10′ latitude and 20′ longitude were combined.

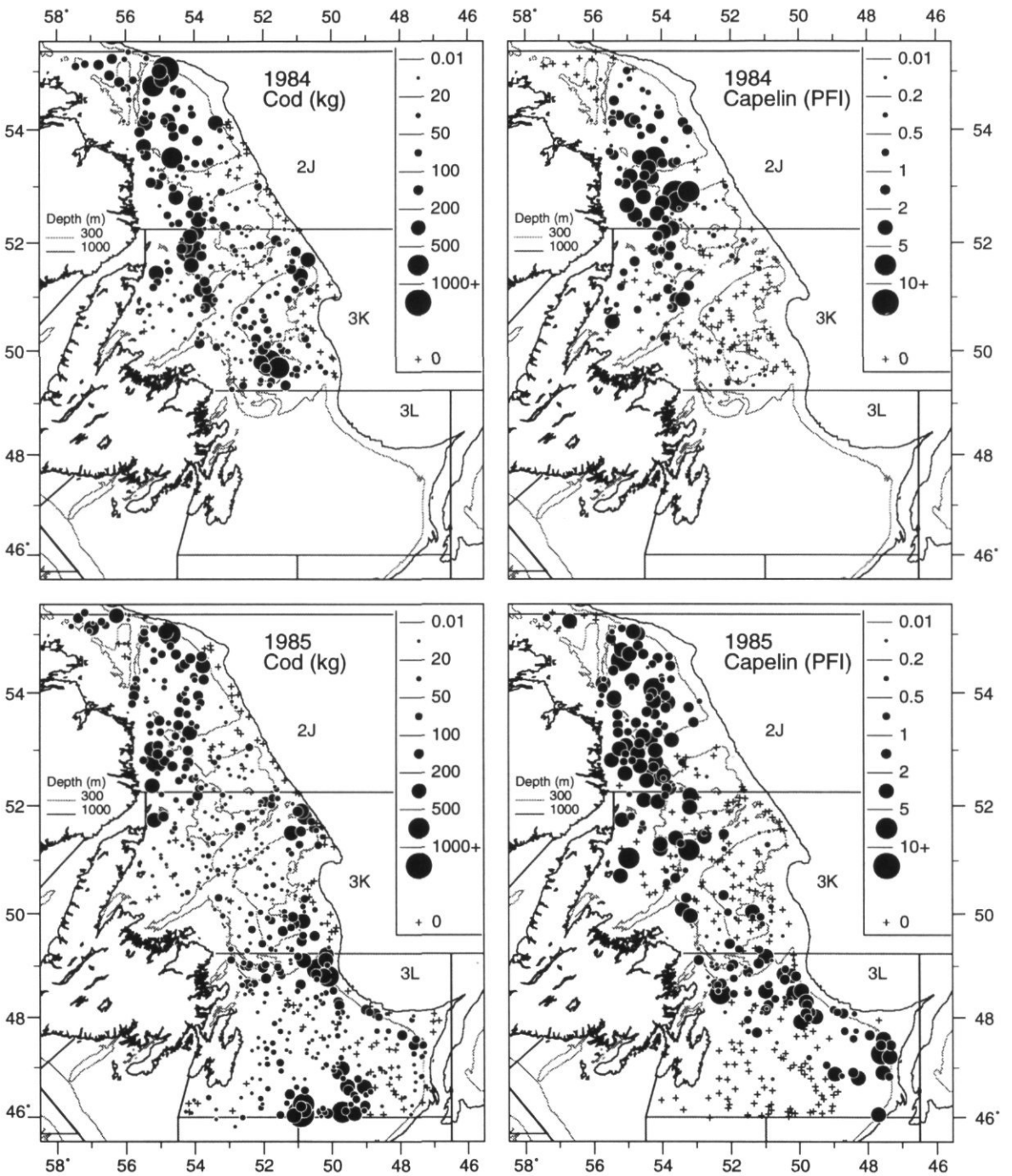


Figure 4. Cod catches (kg/30 min tow) and mean partial fullness indices for capelin (PFI_c) in cod stomachs at each station in 1984–1986. There was no survey in Division 3L in autumn 1984, and the number of stations in Division 3L was unusually high in 1985. The cod biomass index was anomalously high in 1986.

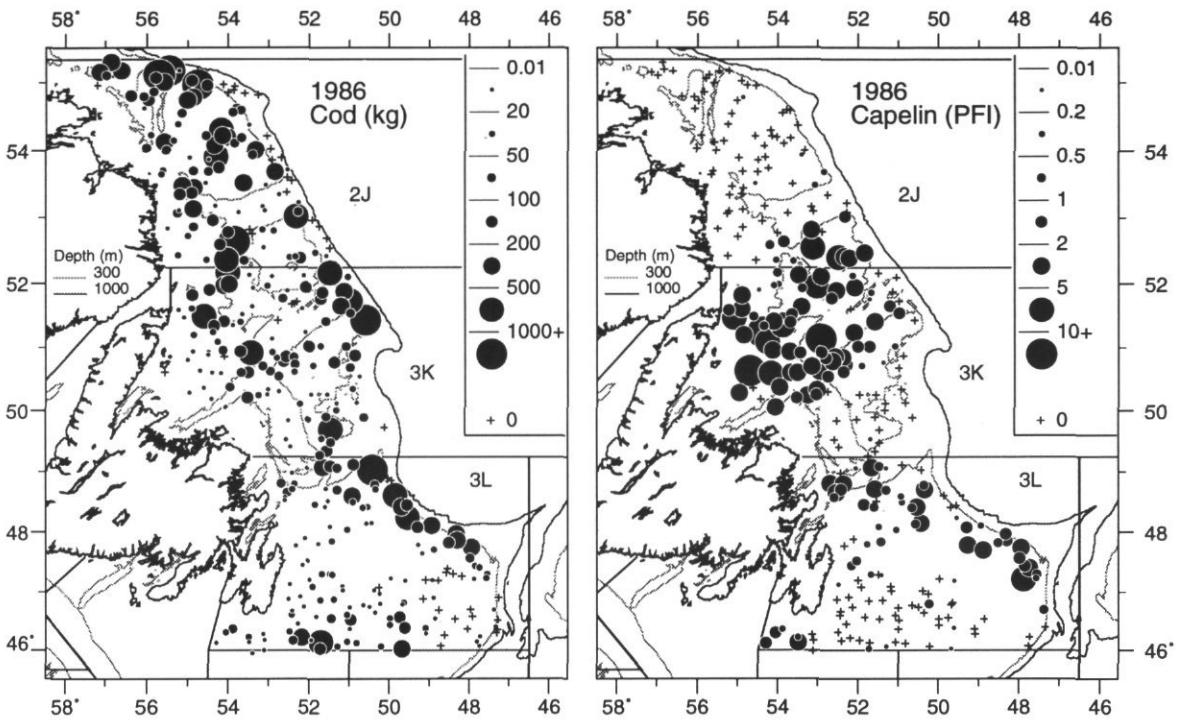


Figure 4. Continued.

catches on Hamilton Bank and the plateau of Grand Bank, and by 1992 good catches were secured only in a small area near the shelf break just south of the Division 3K, 3L boundary. The capelin in Divisions 2J+3K experienced a pronounced shift from the northwest to the southeast during this period. The apparent distinction between a Division 2J+3K group and a Division 3L group (Fig. 3) was less clear in 1990 and absent in 1991 and 1992 (Fig. 5).

Visual comparison of the plots of cod catch and the quantity of capelin in cod stomachs reveals that in 1989 cod preyed intensively on capelin over most of Hamilton Bank, the Northeast Newfoundland Shelf, and the northeastern slope of Grand Bank (Fig. 5). The area of intensive feeding contracted in 1990 and contracted further in 1991 and 1992. It may be inferred from these observations and from the geographic pattern of capelin by-catches during the bottom trawl surveys (Lilly and Davis, 1993) that the capelin not only occupied a smaller area but also moved into that region in which the remaining cod were found, so that in each year most cod were not far from where they could successfully prey on capelin. However, this broad scale overlap between cod distribution and the occurrence of capelin in cod stomachs may be somewhat misleading. Individual cod from large catches tended to have less prey in their stomachs than did cod from small catches (Fig. 6). For example, the cod in the large catches on northeastern Funk Island Bank in 1991 were either not feeding on capelin or had very little capelin in their stomachs, whereas those cod from very small catches a short distance to the southwest had much capelin in their stomachs (Fig. 5). Similarly, the cod taken in several large catches at approximately 49°N in 1992 had very little capelin in their stomachs, even though the cod from smaller catches at similar depths to the north and south were feeding well on capelin.

Distribution and temperature

Was the decline in cod catches in northern and western Division 2J in 1989–1992 caused by a decline in bottom temperatures to a level which could not be tolerated by the cod? Cod in this area are capable of inhabiting very cold water, as is evident from catches on Hamilton Bank and the coastal shelf off southern Labrador in 1985 (Fig. 4). Many of these cod were taken from bottom temperatures below 0°C and even below −1°C, and were found to have moderately large quantities of food (primarily capelin) in their stomachs (Fig. 7). To examine more closely the influence of bottom temperature on cod catch at the time of the annual surveys, I calculated average catches and bottom temperatures in the four shallow (101–200 m) strata in Division 2J in each year

from 1978 to 1992 (Fig. 8). Temperatures were relatively low in 1983–1985, 1987, and 1992, but not in 1988–1991, when cod gradually disappeared from these strata. Records from a mooring on the inner slope of Hamilton Bank (53°50′N 55°30′W; Lazier, 1982) reveal that temperatures at 200 m warm quickly by as much as 1.5–2°C in this area in the autumn. Thus, the temperatures recorded during each survey depend not only on annual differences in temperature but also on the time of the survey relative to the time of the warming. The time of surveying in northwestern Division 2J varied by as much as 30 days during 1978–1992, but the surveys in 1989–1992 were almost identical in time to those in 1983–1984 (Fig. 8). Therefore, differences in time of surveying cannot fully explain the observed differences in temperature. Inspection of temperature records from moorings in 1990–1992 (Narayanan, 1994) reveals that the warming started later in 1992 than in 1990 and 1991, and that the water was indeed colder prior to the surveys in both 1990 and 1991. However, temperatures at the mooring site did not drop lower in 1990–1992 than in 1983–1985 (Narayanan, 1994 and Fig. 16 of Narayanan *et al.*, 1992; note offset of 0.5 y in the time axis of this figure). Thus, temperature records from the bottom trawl surveys and the mooring on western Hamilton Bank do not support the postulate that northern and western Division 2J was too cold for cod in 1989–1992.

Discussion

The dramatic decline in abundance and distribution of cod off southern Labrador and eastern Newfoundland in 1989–1992 occurred at approximately the same time as a decline in water temperature and an apparent decline in the biomass of capelin. Determination of whether these factors contributed to the changes in the cod stock is hampered by difficulties in distinguishing among-year variability from within-year variability. During the late autumn, when the research surveys are conducted, many of the cod are thought to be migrating across the shelf from summer feeding grounds in shallow coastal waters to overwintering areas on the outer shelf and upper slope (Akenhead *et al.*, 1982), capelin migrate southward along the shelf from the Hamilton Bank area into central Division 3K (Carscadden and Atkinson, 1986), and the temperature of water near bottom on Hamilton Bank and the coastal shelf off northeastern Newfoundland becomes warmer. There may be annual variability in the timing of each of these events. Additional uncertainty is added by the long time (at least 6 weeks) required to conduct each survey and annual variability in the timing of the surveys (Myers, 1988). These sources of variability may affect not only the distribution of cod within the survey area but also the proportion of cod outside the survey area (toward the land and to the north and south). There is also the possibility of variable quantities of cod crossing into the survey area from adjacent stocks.

Despite these numerous sources of potential variability, most of the cod caught during the surveys in 1980–1988 were found in four distinct areas. The first major change from this pattern was noted in 1989, when almost no cod were caught on the inner shelf off southern Labrador and northeastern Newfoundland. This is surprising because the coastal fishery with pound nets and gillnets was very successful that year in Division 2J in summer and early autumn (Bishop *et al.*, 1993), especially in the area just north of 53°N (Palmer, 1992). Perhaps the offshore migration was further advanced at the time of the 1989 survey than it had been at the time of previous surveys. An early migration might also explain the offshore distribution in Division 2J in 1990. By 1991 most cod were found in the troughs between Belle Isle Bank and Funk Island Bank and between Funk Island Bank and Grand Bank, and by 1992 they were confined to the latter. Additional study is required to determine whether each of the four areas of relatively high density (Fig. 3) was occupied by a distinct group of cod exhibiting fidelity toward that area in the autumn, and if the observed change in overall distribution was caused by relocation of fish, differences in mortality among individual groups of fish, or a combination of the two.

Cod may change their distribution in response to changes in water temperature (Loeng, 1989), but the present analysis of temperature data does not support the postulate that the disappearance of cod from the north and west of Divisions 2J+3K was directly related to low bottom temperature. Cod in this area are adapted to cold water. Short-term exposure to low temperature is not lethal; cod survive being hauled through the cold intermediate layer on the shelf, with temperatures as low as −1.7°C, during tagging operations. Cod are often found in temperatures well below 0°C, particularly in areas where they find good forage (Lilly, 1982). Hamilton Bank and the coastal shelf off southern Labrador and northeastern Newfoundland have long been known as areas where cod concentrate and feed on capelin in the late summer and autumn. Exploratory surveys in 1952 reported good catches of cod, which had been feeding on capelin, in temperatures as low as −0.9°C (Ancellin, 1953; Templeman, 1953). Annual reports to the International Commission for the Northwest Atlantic Fisheries (ICNAF) (for example, Ruivo and Quartin, 1958; Figueras, 1961; Letaconnoux, 1967) indicate that distant water fleets fished in these areas during the autumn from the late 1950s to the mid-1960s. There are few observations from Canadian research surveys in Division 2J during that period, but in late October 1964 a large catch of cod, which had been feeding well on

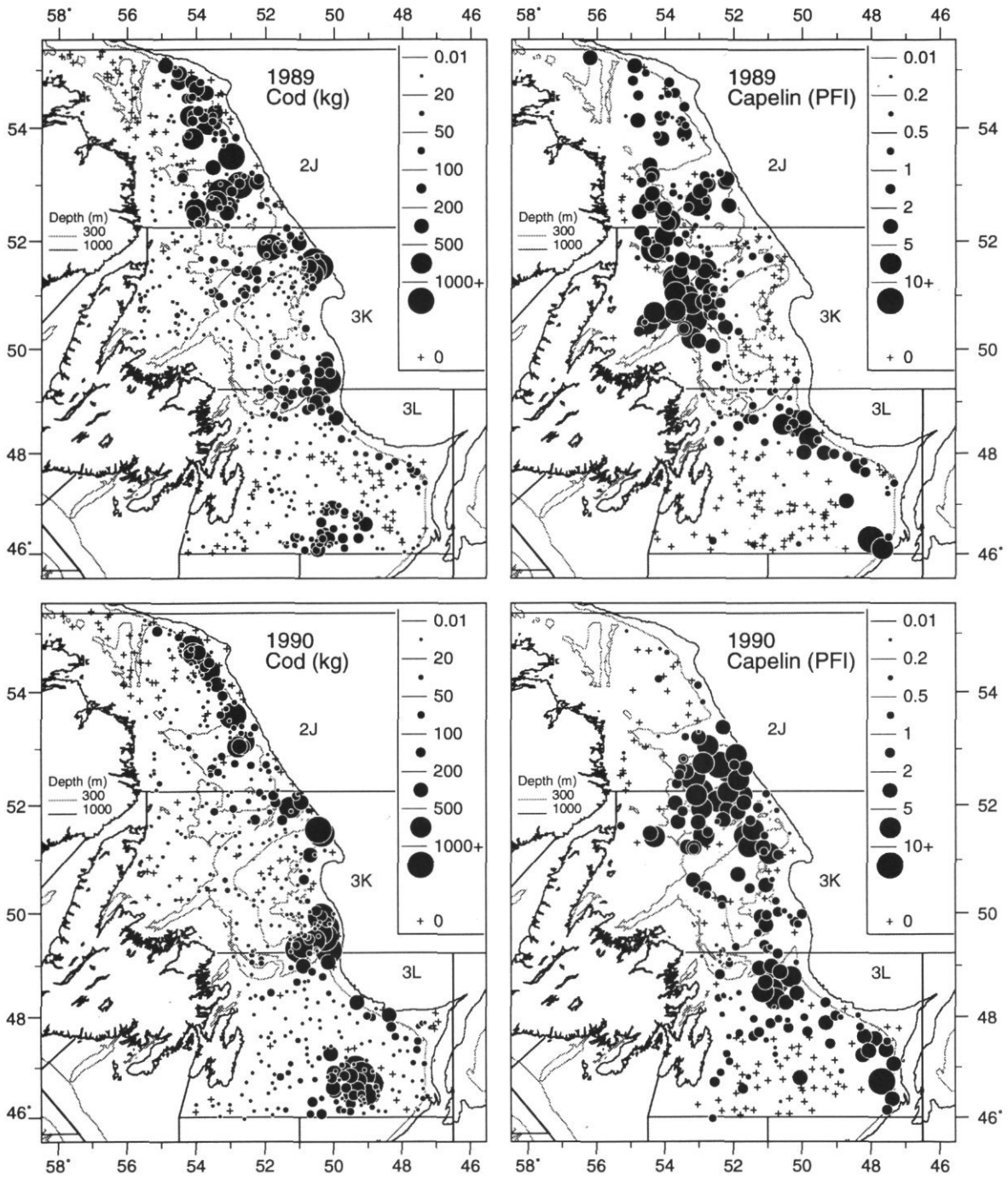


Figure 5. Cod catches (kg/30 min tow) and mean partial fullness indices for capelin (PFI_c) in cod stomachs at each station in 1989–1992.

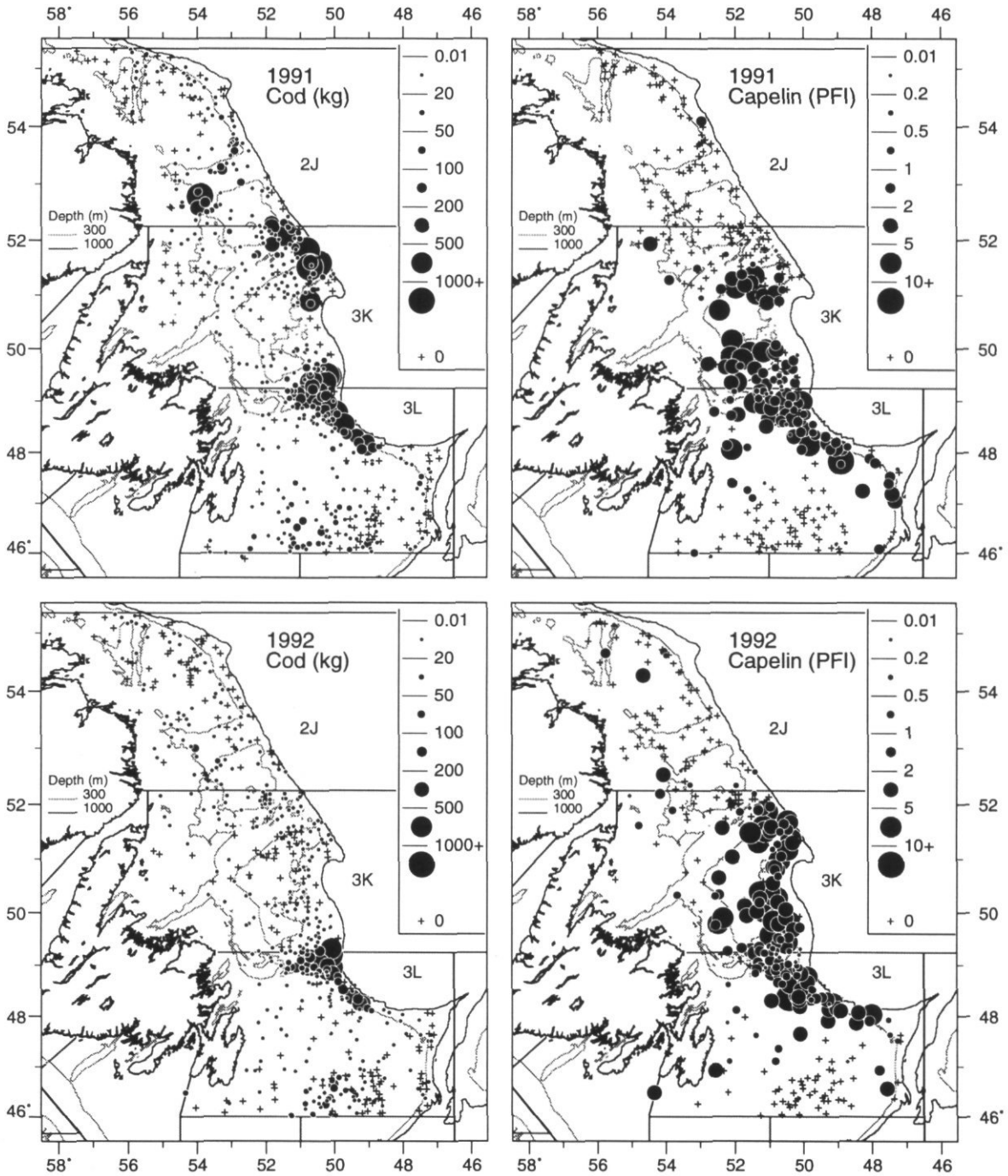


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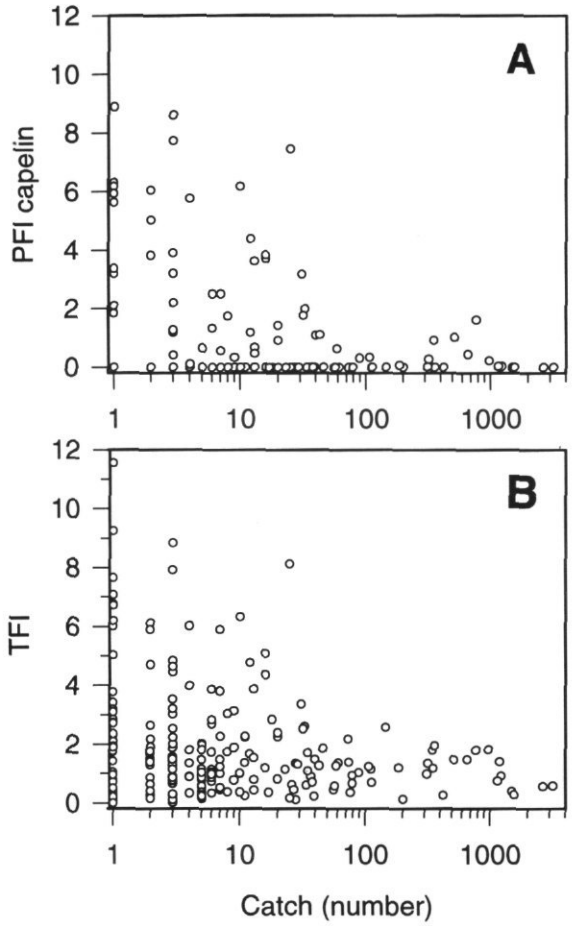


Figure 6. Relationship between the catch (number) of medium-sized (36–71 cm) cod at individual fishing stations in Divisions 2J+3K in autumn 1991 and (A) the mean partial fullness index for capelin (PFI_c) and (B) the mean total fullness index (TFI). Some points are hidden.

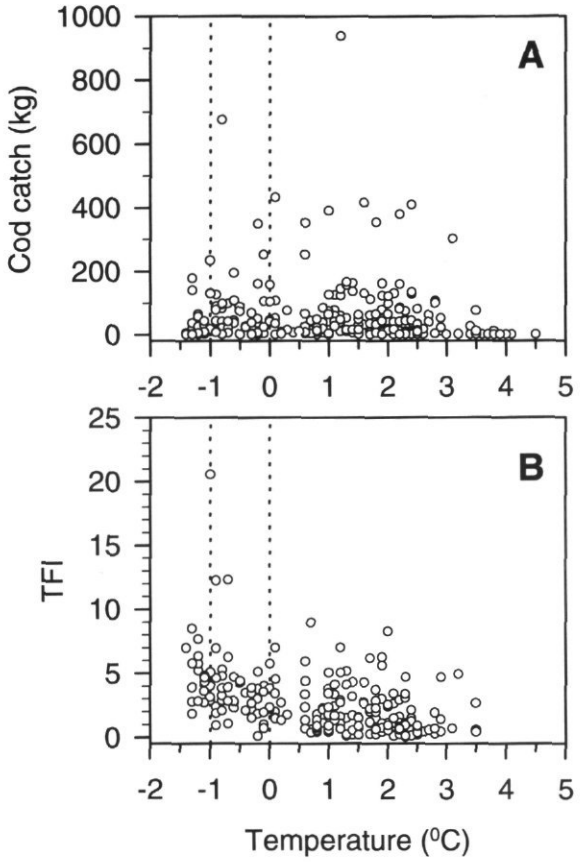


Figure 7. The relationship between the bottom temperature at individual stations in Divisions 2J+3K in 1985 and (A) the catch of cod (kg/30 min tow) and (B) the mean total fullness index (TFI) in a sample of the cod.

capelin, was secured at −0.3°C in the vicinity of 20 trawlers fishing on the coastal shelf off southern Labrador (approximately 52°38′N 54°49′W; unpubl. trip report, RV "A. T. Cameron" trip 94). Although many indices reveal that temperatures were far below normal in 1990–1992, it is not clear that oceanographic conditions off southern Labrador were more severe than during the cold periods of approximately 1972–1975 and 1984–1985 (Colbourne *et al.*, 1994). Cod were still present in northwestern Division 2J in 1985 toward the end of the previous cold period, whereas they started to disappear from that area even before the recent cold period. The progressive disappearance of cod, first from the inner shelf in Division 2J and eventually from almost the entire shelf in Divisions 2J+3KL, may be related to a long-term reduction in temperature, but the evidence for large southward shifts of cod in response to cold water events is not as unequivocal as implied by deYoung and Rose (1993) and Rose *et al.* (1994).

It has been suggested that temperature may be a proxy for other physical or biological variables, and that the southward shift in cod distribution since 1989 may be related to the shift in capelin distribution (deYoung and Rose, 1993; Rose *et al.*, 1994). This possibility deserves additional study, especially for 1991 and 1992. However, it seems unlikely that a change in capelin distribution played a role in the 1984–1985 cod relocation identified in the analyses of deYoung and Rose (1993) and Rose *et al.* (1994). Capelin in Divisions 2J+3K did not have a southeasterly distribution in 1984 and 1985. In addition, cod do not always follow capelin closely; many cod were caught on Hamilton Bank in 1986 and 1990, even though the capelin had already migrated south. If cod relocated southward in the early 1990s in response to the shift in capelin distribution, there still remains the question of why the capelin moved.

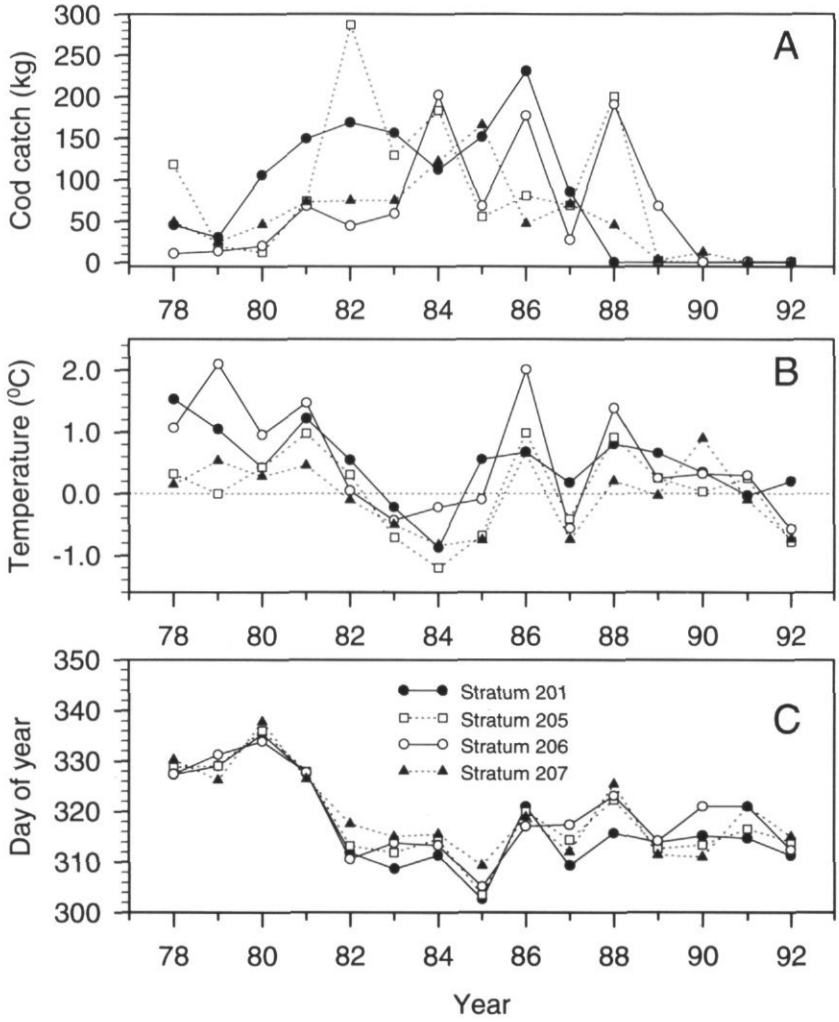


Figure 8. (A) Average cod catches (kg/30 min tow), (B) bottom temperatures, and (C) dates of fishing in four shallow strata (101–200 m) in Division 2J in 1978–1992. Stratum 201 is on Harrison Bank to the northwest of Hamilton Bank, strata 205 and 206 are primarily on Hamilton Bank, and stratum 207 is on the coastal shelf off southern Labrador (see Doubleday, 1982).

The present analysis of stomach contents does not support the postulate that the cod were finding less prey in recent years than they had in the past. Only in Division 2J did the stomach fullness decline. The two areas of high density remaining in Divisions 3K and 3L in 1991 are not sites where the cod historically found good foraging on capelin, but this changed in the 1990s as capelin moved into the southeastern part of the Northeast Newfoundland Shelf from their historic distributions to the north and west. Many cod experienced good feeding on capelin in 1990–1992, despite the impression from hydroacoustic surveys that capelin abundance was low. However, cod taken in most large catches in recent years were feeding poorly, so the present results must be considered preliminary. The tentative conclusion that the overall feeding level of cod had not declined in 1990–1992, except for the very few cod remaining in Division 2J, is supported by analyses of the condition (somatic and liver indices) of cod collected during the autumn surveys (Bishop and Baird, 1993). Only in Division 2J in 1991 and 1992 did average condition drop below levels recorded in the late 1970s and early 1980s.

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Feeding of cod (*Gadus morhua callarias* L.) in the Central Baltic in relation to environmental changes

D. Uzars

Uzars D. 1994. Feeding of cod (*Gadus morhua callarias* L.) in the Central Baltic in relation to environmental changes. – ICES mar. Sci. Symp., 198: 612–623.

Feeding peculiarities are analyzed in relation to general knowledge about the behaviour of cod using stomach content data for the period 1963–1990. The environmental conditions, cod biomass, and food abundance were very variable over this period. The first two decades up to the beginning of the 1980s were characterized by relatively favourable hydrographic conditions in the deepwater layers. Cod inhabited mainly the near-bottom water layers. The diet of cod was fairly diverse but was dominated by benthic prey. Cod biomass, diet composition, and availability of food were stable. Since the 1980s environmental and biological equilibrium in the Central Baltic have been disturbed because of current stagnation. The area suitable for the survival of benthic animals has diminished. Cod have reacted to the unfavourable conditions by changing their distribution and feeding. Young cod have been concentrated mainly in shallow waters, but adult cod have inhabited intermediate water layers. Pelagic prey, crustaceans and sprat, have provided the bulk of the diet. The results indicate that changes in diet are directly linked to changes in the behaviour of cod.

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Introduction

Cod is an important component in the Baltic ecosystem inhabiting deep and shallow waters. As a predator, it imposes a significant natural mortality on prey species and may limit their biomass. According to MSVPA assessment, biomass of food eaten by the eastern Baltic population of cod varies between 1.7 and 0.16 million tonnes, depending on the stock size (ICES, 1994). Fluctuations in prey abundance may also be caused by factors such as environmental conditions. Variable hydrographic processes as well as enhanced eutrophication in offshore areas have influenced benthic and pelagic communities in different ways (Hansson, 1985). Frequently occurring hypoxia in bottom-water layers has resulted in the emigration or elimination of benthic animals. In contrast, conditions in the intermediate layers were favourable during the same time. Intense influxes of the high-salinity waters from the Kattegat and slight increases of nutrients in the 1950s, 1960s, and 1970s (Fonselius, 1969; Matthäus, 1973; Kalejs, 1976) positively affected the abundance and survival of benthic organisms in the deepwater layers. Cod inhabited near-bottom layers in the deeps and coastal areas in those periods (Lablaika, 1967; Tiews, 1974). Feeding studies of cod in the Gotland Basin and Gdańsk Basin as well as in coastal areas of the Southern Baltic in the 1960s (Spasski and Merezinskaja, 1956; Stryzewska, 1962; Chrzan, 1962) have shown that food consisted of the benthic invertebrates Mesidotea (*Mesidotea entomon*), mysids (*Mysis mixta*), amphipods (*Pontoporea femorata, P. affinis*), and polychaetes (*Harmothoe sarsi*), as well as herring (*Clupea harengus m.*). According to Zmudzinski (1971), biomass of *Mesidotea, Pontoporeia,* and *Harmothoe* increased in the Southern Baltic during this period. The abundance of benthic animals in the Eastern Baltic was also high (Jarvekulg, 1979). The importance of the sprat (*Sprattus sprattus*) in the food increased in the 1970s (Zalachowski, 1977), possibly owing to an increased abundance of sprat in the early 1970s as well as to a shift in behaviour of the cod in forming pelagic concentrations during spawning.

In the 1980s the environmental conditions in the Central Baltic deteriorated (Kalejs and Ojaveer, 1989). A continuous stagnation and salinity decrease in deepwater layers not only affected cod reproduction and biomass negatively, but also changed population structure, feeding and, behaviour (Uzars *et al.*, 1991). Hypoxia in the deep layers forced cod up from the bottom to the midwater layers. Stock size of pelagic fish herring and sprat increased, by the late 1980s, achieving very high levels (ICES, 1993a).

In this paper, I describe the ecological responses of cod when exposed to variations in hydrographic conditions and to hypoxia in the Central Baltic. Changes in feeding and behaviour during the years investigated represent evidence of the adaptational abilities of certain life stages of Baltic cod to variable conditions.

Materials and methods

Over 35 000 stomach contents were studied from cod caught during research vessel bottom-trawl surveys and, beginning in the late 1980s, also pelagic trawl surveys. Figure 1 shows the sampling areas of the cod stomachs in 1963–1990. The stomachs were examined individually and food items were determined to species, counted, and weighed. The cod were grouped into two length classes: 20–30 cm and larger than 30 cm. Stomach content was expressed as percentage composition (by weight) of each major prey item in relation to size class and depth. The food composition was determined for the first and second halves of the year separately because of the variation in spatial distribution of the cod. Moreover, feeding peculiarities were analysed for different periods in relation to different hydrographical conditions and biomasses of cod. On the basis of the major hydrographic events in the Baltic Sea (HELCOM 1990; Kalejs and Yula, 1991) in combination with the fluctuations in stock size (Ojaveer *et al.*, 1975; Veldre and Polivajko, 1975; ICES, 1993a,b; Plikshs *et al.*, 1993), the

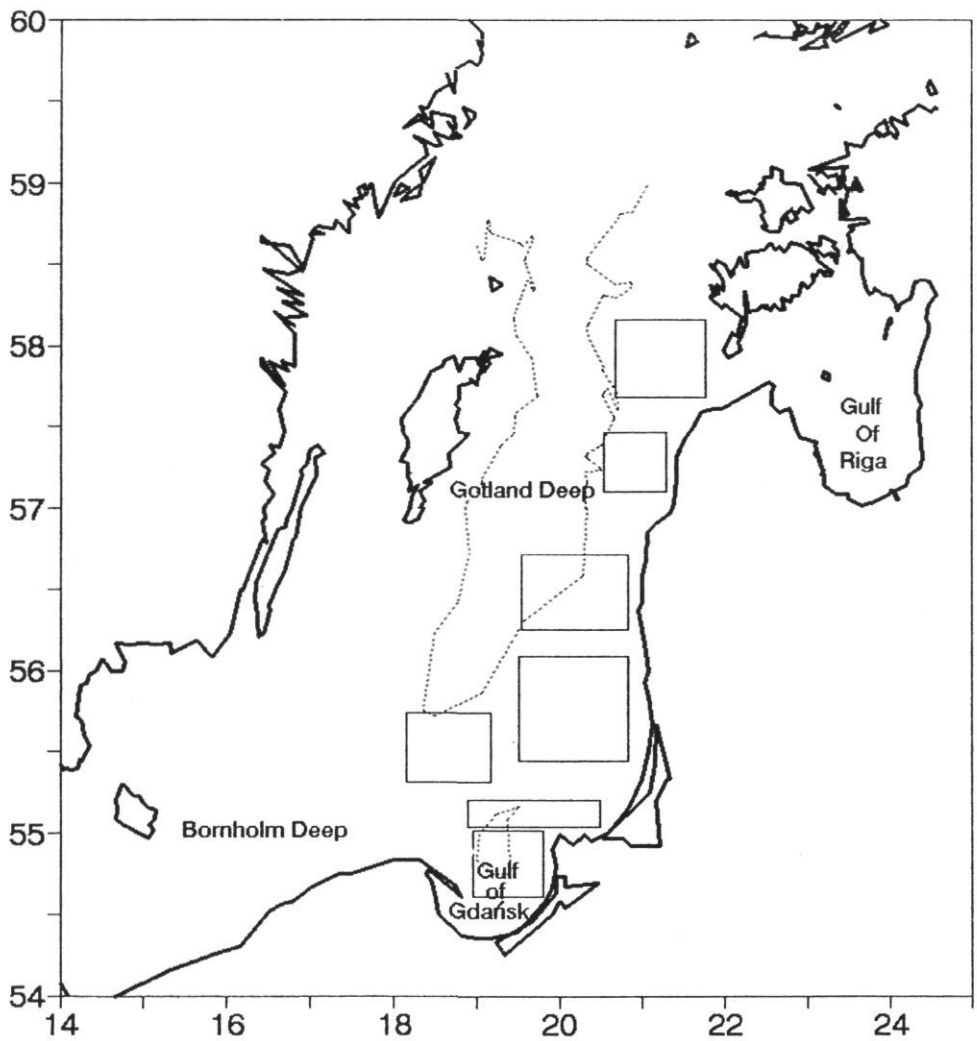


Figure 1. Stomach sampling areas in the Baltic Sea.

total period of investigation was subdivided into the following time periods:

- 1963–1975. Hydrographical conditions in the Baltic Sea were characterized by an intense inflow of water from the North Sea, and short-time stagnation below the halocline. The recruitment and biomass of cod were relatively stable. Pelagic fish stock varied in size. During 1963–1970 the abundances of herring and sprat were low, but in the early 1970s they increased.
- 1976–1979. Oxygen supply and salinity in near-bottom layers were favourable. Biomass of cod increased sharply due to the appearance of very strong year classes (Lablaika *et al.*, 1989). Stock size of the pelagic fish decreased at the end of the 1970s and remained at a low level until 1987.
- 1980–1985. From 1980 onwards stagnation processes developed in the deeper bottom-water layers due to reduced inflow of saline water. The biomass of cod was high.
- 1986–1990. The hydrographical situation remained unchanged but the biomass of cod began to decrease after 1986.

Results

Young cod

Variation in food composition by depths

Figure 2 summarizes the data on food composition of young cod (length classes 20–30 cm) by depth during the first half of the year. In 1963–1975 cod were distributed in the bottom-water layers throughout the Central Baltic. During the first half of the year young fish inhabited both shallow and deep areas (Netzel, 1974; Lablaika and Uzars, 1982). Distribution of young cod during this period of the year depends to a great degree on the severity of the winter. In cold years young cod migrate to offshore deeps to overwinter. In mild winters they are usually found in coastal areas. Variations in the weight percentages of the major food items by depths in cod stomachs are considerable. At depths of 30–70 m, cod feed on both *Mesidotea* and mysids (about 60–70% of the total food), followed by *Pontoporeia*, herring, and *Harmothoe*. At depths of 80–120 m *Harmothoe* constitutes about 50% of the food, but herring, sprat and *Mesidotea* are also found in stomachs.

In 1976–1979 the abundance of young cod achieved its maximum. However, the food composition does not reflect significant changes compared to the earlier period. Only the occurrence of sprat and *Pontoporeia* was somewhat higher.

In 1980–1985, when abundance of young cod decreased gradually, the spatial distribution and migrations during the first half of the year were limited by low oxygen and salinity levels in bottom waters of the deeps. The increasing amount of *Mesidotea* and mysids and decrease in *Harmothoe* indicate a shallow distribution of the cod. *Pontoporeia* sp., which occurred down to 80 m, also diminished as food. A decrease in macrobenthos during the period 1979–1988 below the halocline (70–80 m) in the Gdańsk Deep and the Gotland basin has been reported by Warzocha (HELCOM, 1990). In the deepest part, fauna has been absent or at best very poor.

In 1989–1990 stagnation continued in the whole Baltic. The abundance of young cod was low both in coastal waters and in the Deeps. Formerly highly productive young cod nursery grounds in Ventspils and Klaipeda were sparsely inhabited during this period (Kondratovitch and Lablaika, 1989). Pelagic mysids dominated as a benthic animals (*Harmothoe, Pontoporeia,* and *Mesidotea*) occurred rarely in cod stomachs.

Seasonal variation in food composition

Figures 3 and 4 indicate differences in food composition during the first and second halves of the year. In the first half of the year, owing to the distribution of young cod over a wide area characterized by a large depth range, the prey spectrum is fairly diverse. The diet includes benthic species *Harmothoe, Mesidotea, Pontoporeia* as well as mysids and herring which formed near-bottom concentrations, while sprat inhabited midwater layers.

Over the period 1963–1979 the proportions of the different prey species were relatively stable, which is probably related to favourable conditions with respect to salinity and oxygen supply in the deeper basins over this long period. Only the fraction of fish in the food increased: herring in 1970–1975 and sprat in 1970–1979; a relatively high abundance of sprat in the food of young cod was related to stock size of sprat, as well as to cod distribution in the deeps during the winter–spring period.

After 1980 the diet changed abruptly from *Harmothoe* and sprat to mysids and *Mesidotea*, and this situation persisted up to recent years. Benthic organisms like *Harmothoe* and *Pontoporeia*, which are distributed in deeper and warmer waters, were rarely represented. This reflects a restricted distribution of young cod due to stagnation of the deeper waters and low temperatures in coastal areas during winter and spring in the 1980s. In the late 1980s the abundance of benthic *Mesidotea* in stomachs was also reduced.

In the second half of the year young cod usually inhabit bottom-water layers along the southern and eastern coasts of the Baltic Sea. Between 1963 and 1975 mysids formed the major part of the diet (about 50%). In 1976–1979 the proportion of mysids in the food decreased by at least a factor of 2 compared to the former

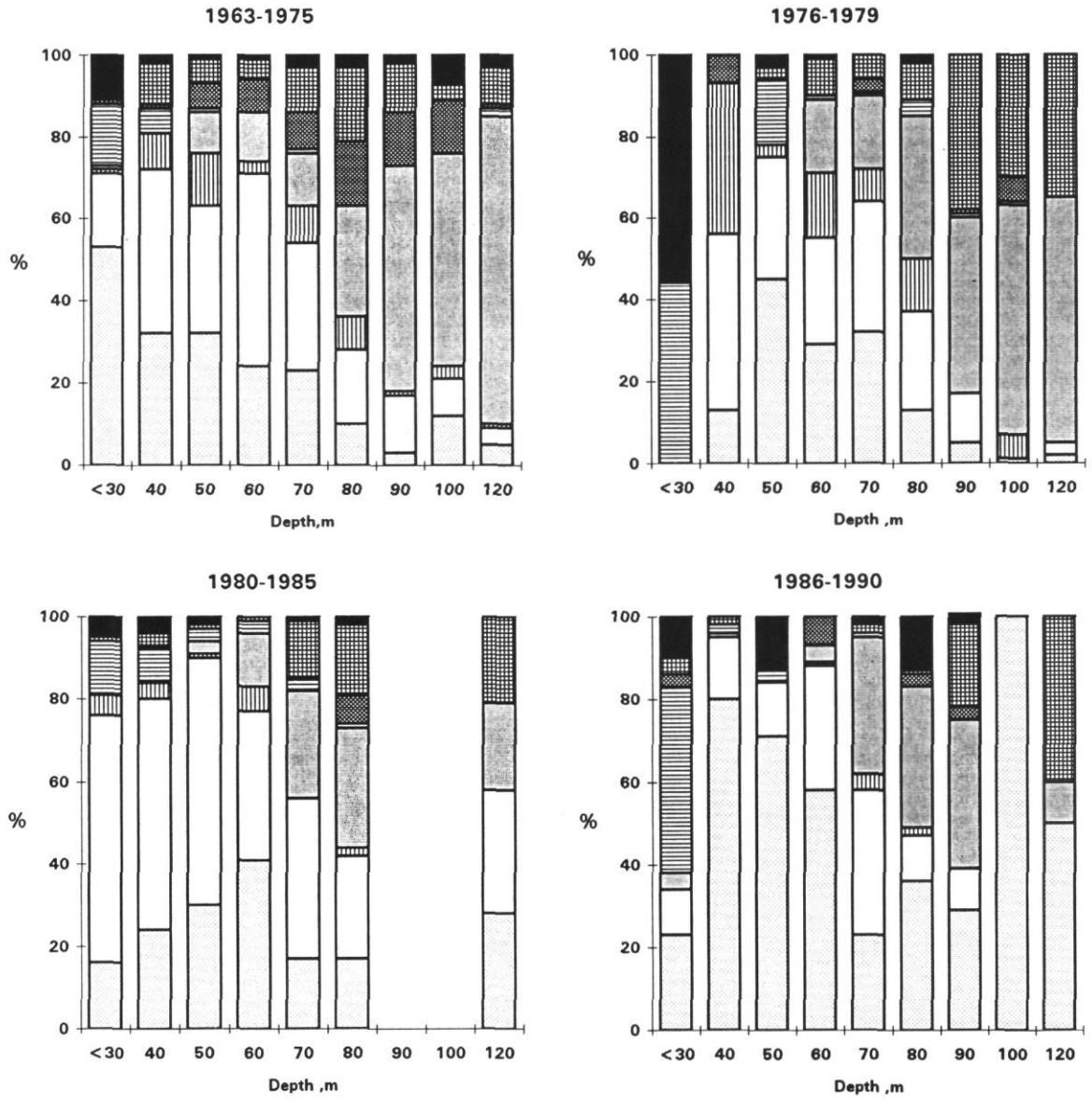


Figure 2. Variation by depths of food composition (in % by weight) of cod in length class 20–30 cm in the first half of the year in the Central Baltic.

period, which coincided with the sharp increase in recruitment. Cod predated more intensively on *Harmothoe* and *Pontoporeia*. In the 1980s the proportion of mysids rose synchronously with the development of weak year classes of cod. This suggests that the abundance of mysids may have been reduced by the increased abundance of young cod. The contribution of mysids recovered in the early 1980s to the level observed in the early 1970s. In the late 1980s, mysids constituted more than 70% of food. The benthic polychaeta and crustacea became more rare, while the *Pomatoschistus* sp. and *Crangon* sp., which are characteristic of brackish waters, were met more frequently.

Cod >30 cm

Variation in food composition by depths

During the first half of the year, prespawning cod congregate in a limited area on the banks near the deeps, but spawners migrate to the Gotland and Gdańsk spawning

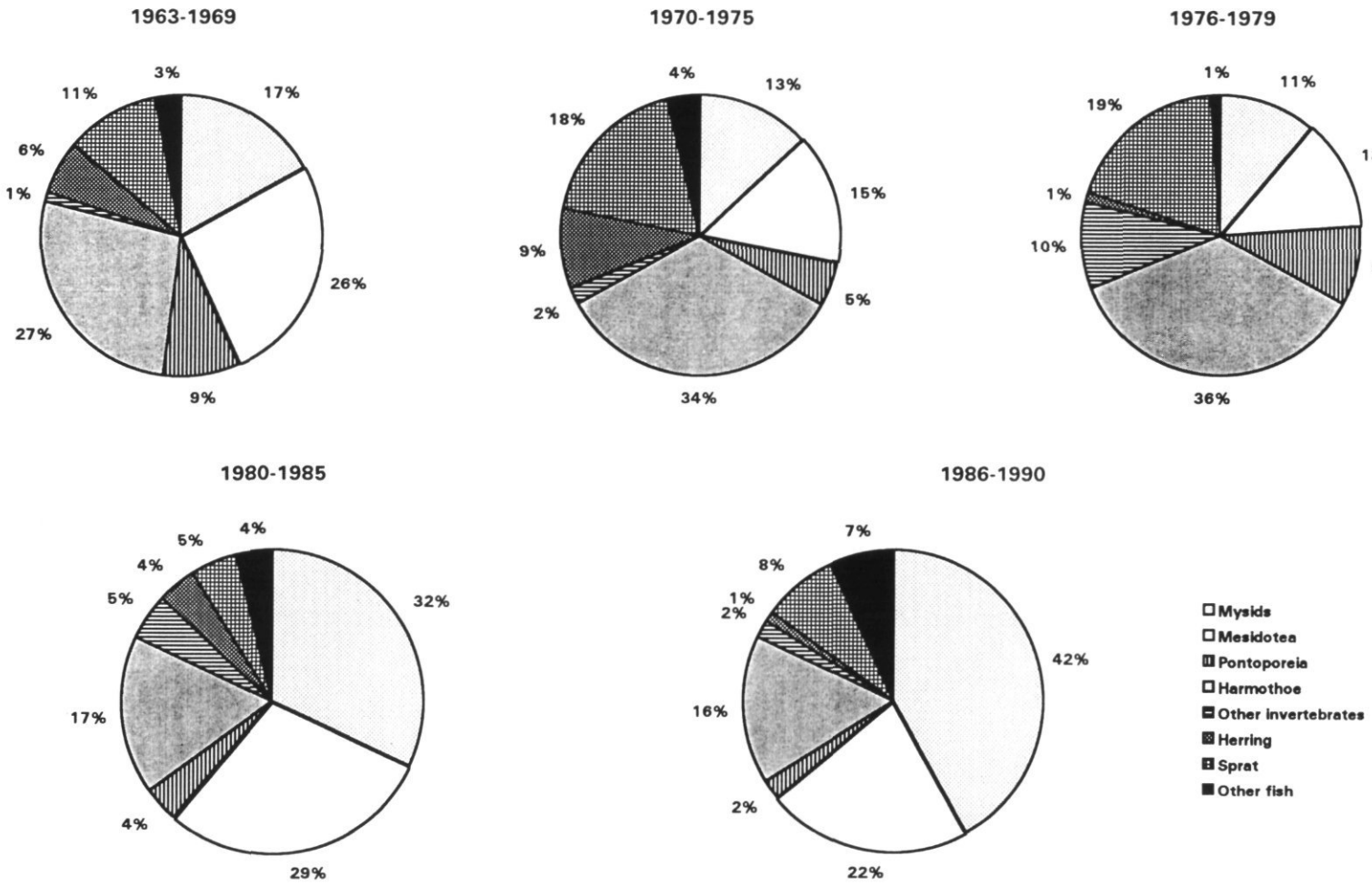


Figure 3. Food composition (in % by weight) of cod in length 20–30 cm at the first half of the year in the Central Baltic.

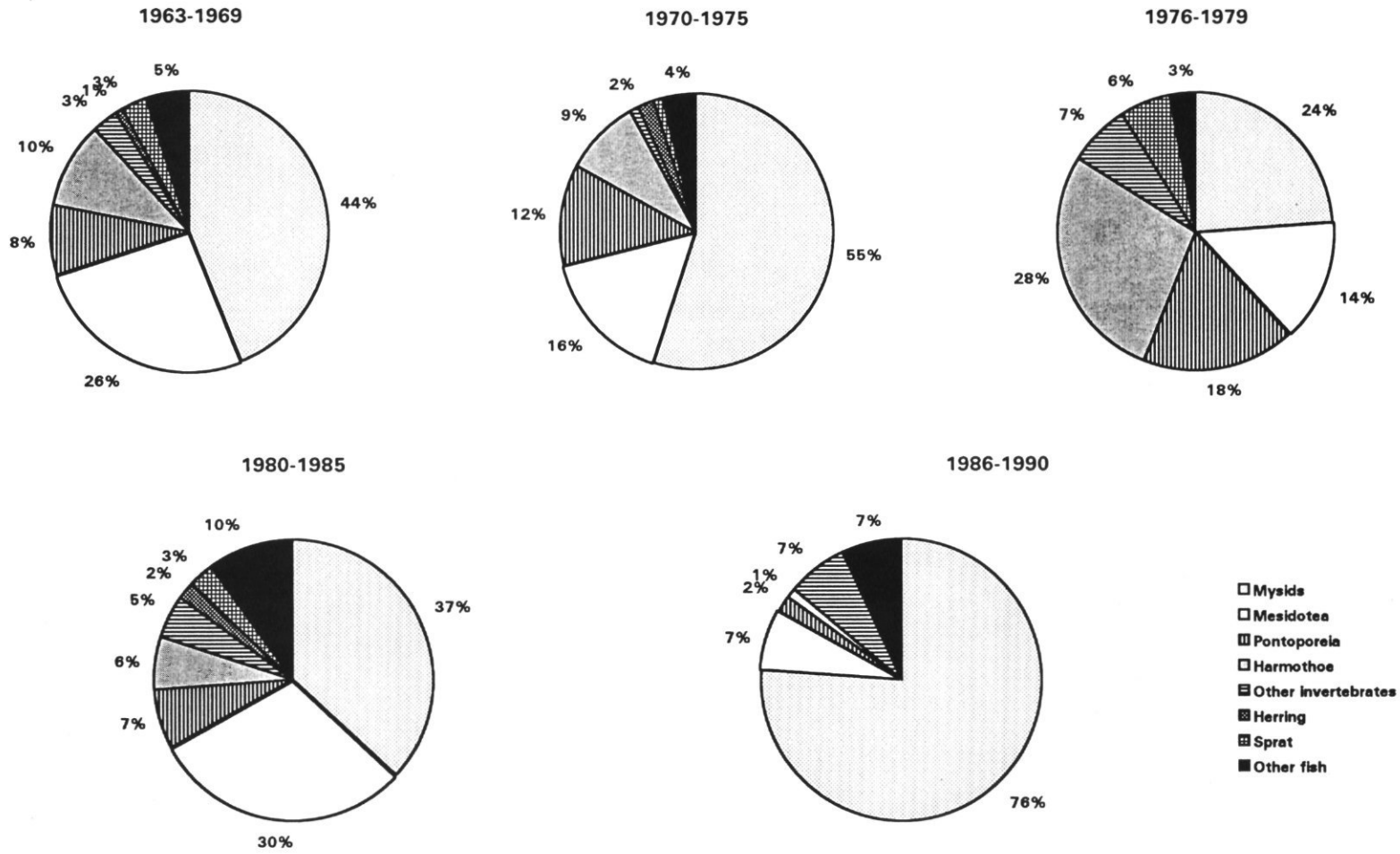


Figure 4. Food composition (in % by weight) of cod in length 20–30 cm at the second half of the year in the Central Baltic.

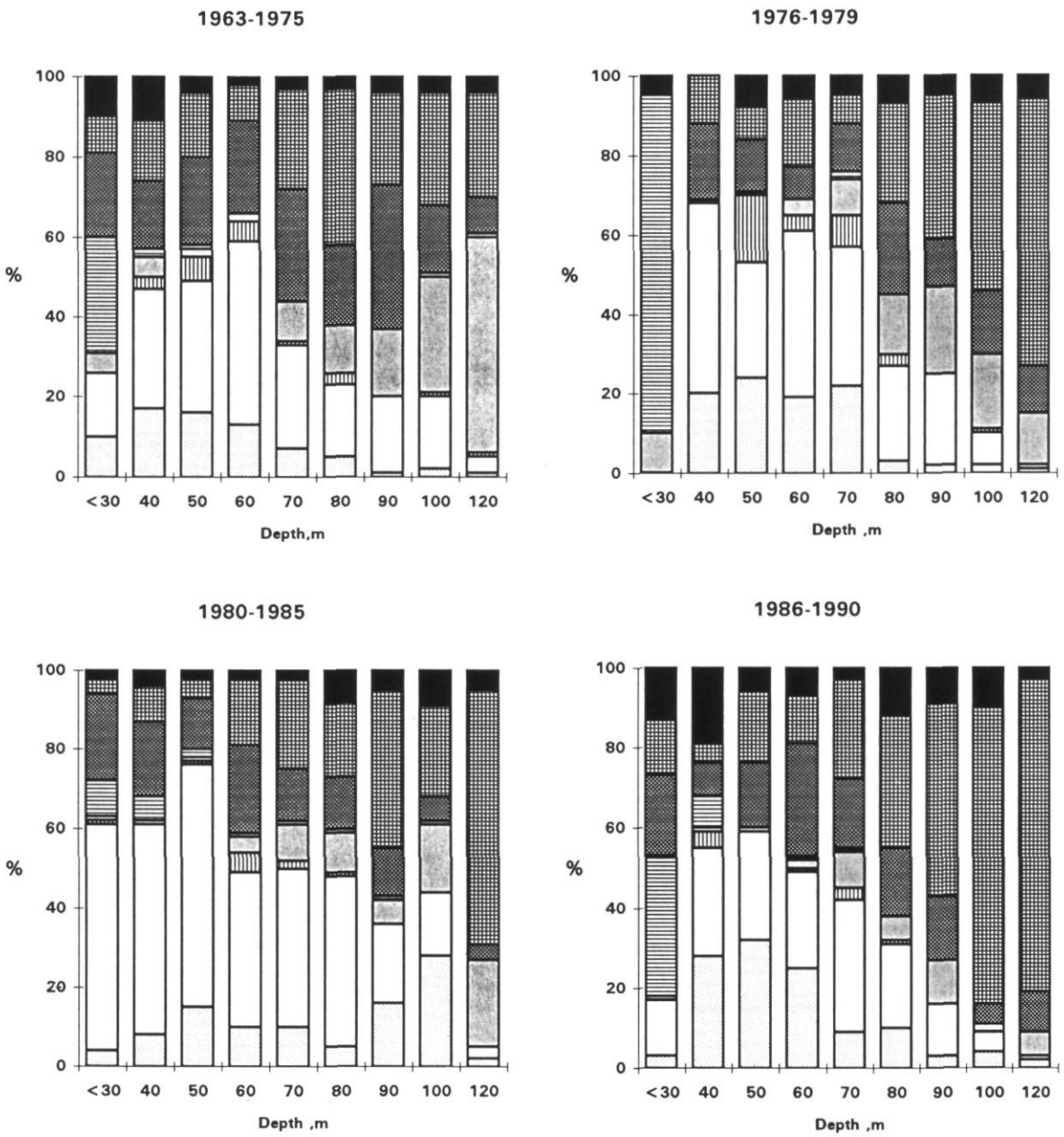


Figure 5. Variation by depths of food composition (in % by weight) of cod over 30 cm in length in first half of the year in the Central Baltic.

grounds. The distribution during this period of the year depends on the oxygen and salinity conditions on the spawning grounds (Lablaika and Lishev, 1964; Bagge, 1981).

Because of the better environmental conditions in the 1960s and early 1970s adult cod were distributed near the bottom in the Central Baltic. *Mesidotea* and herring dominated in the food over a wide range of depths (Fig. 5). Sprat and *Harmothoe* were found only at greater depths.

During the period 1976–1979 cod formed mainly bottom concentrations, but during spawning pelagic concentrations occurred too. *Mesidotea* dominated in the shallow water. The contribution of herring in the diet declined, compared to 1963–1975, by a factor of about 2. This concurs with a diminishing herring biomass in the

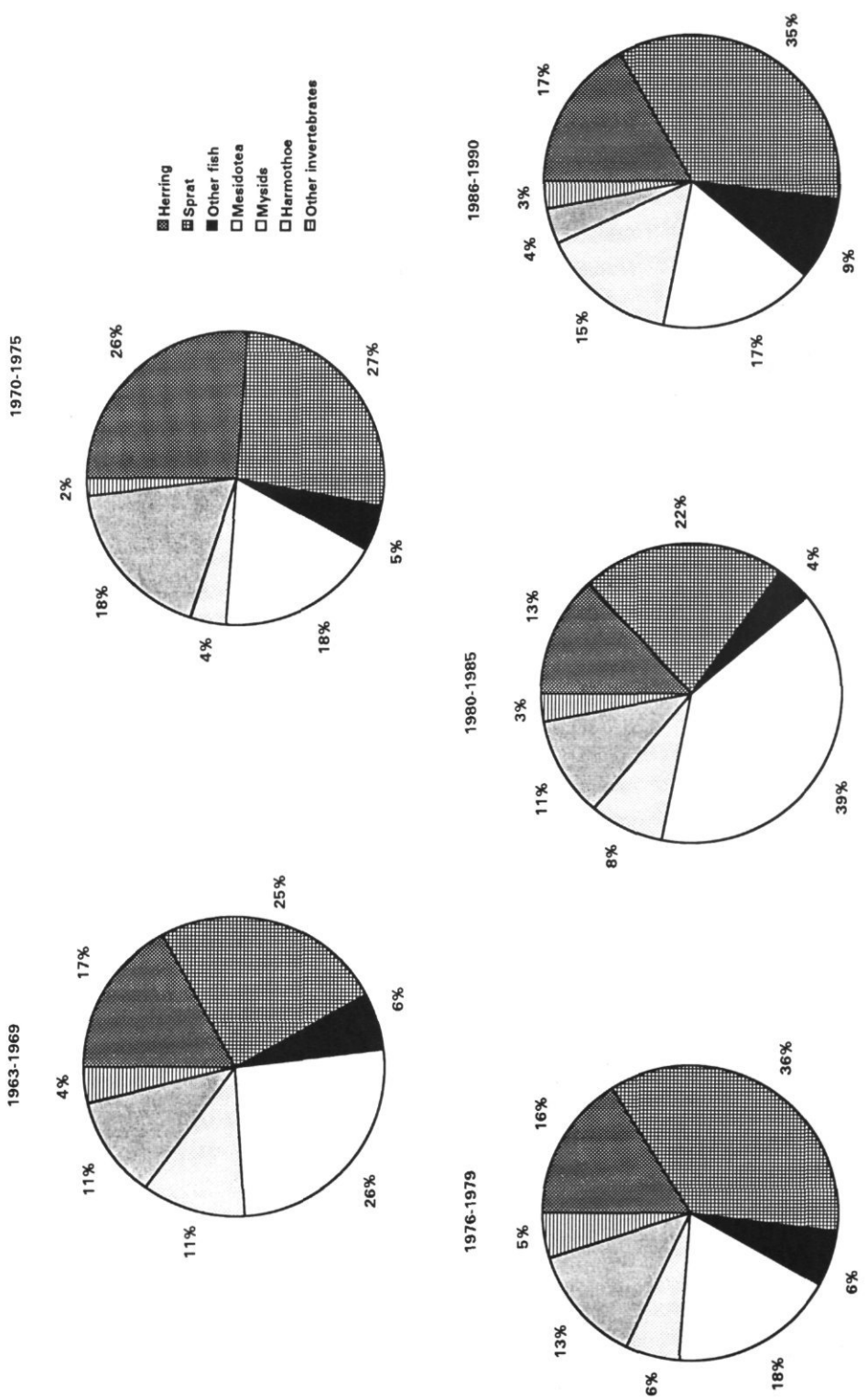


Figure 6. Food composition (in % by weight) of cod over 30 cm in length at the first half of the year in the Central Baltic.

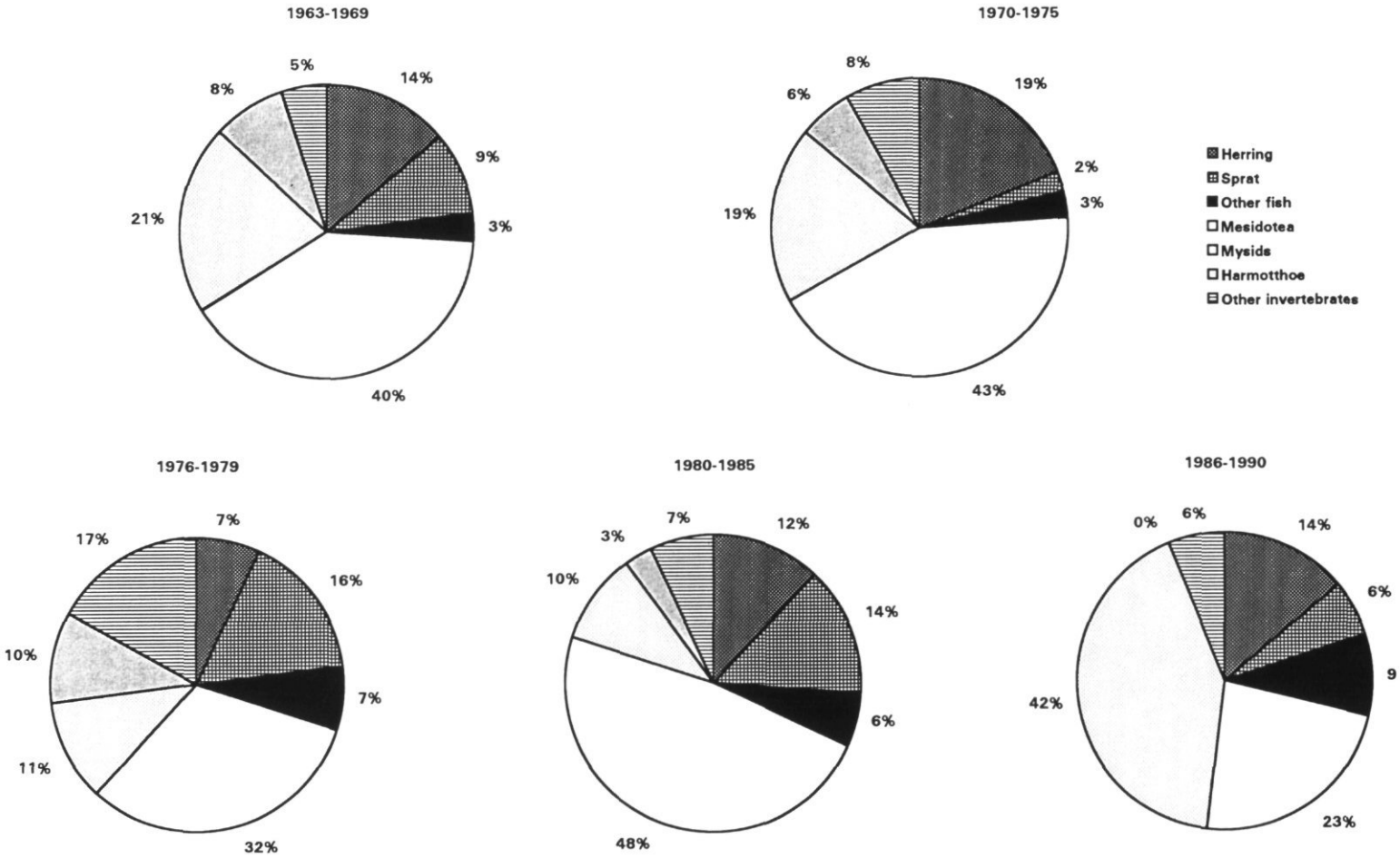


Figure 7. Food composition (in % by weight) of cod over 30 cm in length at the second half of the year in the Central Baltic.

late 1970s in the Eastern Baltic (Ojaveer, 1990). At depths of 100–120 m *Harmothoe* was replaced by a significant increase of sprat constituting up to 50–70% of the stomach content.

In 1980–1985 stock size of cod in the Central Baltic was the highest ever observed, with 4 to 6-year-olds prevailing (Baranova, 1989). Isolated concentrations were found at the bottom in the vicinity of the Gotland and Gdańsk Deeps, but the share of pelagic cod increased with depth. *Mesidotea* appeared in unusually high values (about 40–60%) in the food at depths 30 to 80 m. In deeper areas sprat was more dominant. Apparently, the 80 m contour separated two zones: a shallow water zone dominated by crustacea and herring, and a deep water zone inhabited by polychaetes and sprat.

The prolonged stagnation has had a major impact on the reproduction and ecology of adults in 1986–1990. Environmental conditions were extremely unfavourable in the Gotland Basin and cod were found mainly in intermediate water layers on the spawning grounds. Pelagic concentrations were rare and found only in the Southern Gotland Deep (Plikshs and Kalejs, 1990). At greater depths cod preyed largely on sprat; the contribution of other food items was negligible. At depths less than 70 m, mysids and herring were relatively more important. The fraction of *Mesidotea* was the lowest during the period investigated.

Seasonal variation in food composition

Figures 6 and 7 show the food composition during the first and second halves of the year. In the first half of the year adults fed mainly on fish. Clupeids and other fishes, including sand goby (*Pomatoschistus* sp.), cod, and fourbeard rockling (*Enchelyopus cimbrius*), constituted together approximately 50% of diet. In addition, cod consumed *Mesidotea* and *Harmothoe*.

In the 1960s and early 1970s, the density of the food of cod was quite high. The food items herring, sprat, and *Mesidotea* constituted about 20% and *Harmothoe* from 11 to 18% of the diet. In the early 1970s, compared to 1963–1969, the proportion of herring increased, possibly due to the occurrence of strong year classes (Kalejs and Ojaveer, 1989). In the late 1970s, it was mainly sprat that predominated in the food, because of a changed vertical distribution of cod.

During the early 1980s, substantial changes in both cod biomass and the biomass of pelagic fish prey were observed: the cod biomass increased greatly, but the recruitment and biomass of herring and sprat decreased. The spawning stock size of sprat dropped to the lowest level in the Gotland Basin (Elvertowski, 1982; Shvetsov, 1982). Possibly as a result of the low abundance of fish, cod predated on *Mesidotea,* which constituted about 40% of the diet. The negative influence of the stagnation and low salinity in the late 1980s affected the cod in particular, the stock size of herring and sprat in the Central Baltic increasing significantly in the same period. Sprat was predominant (about 35%) in the food of cod. The proportion of mysids increased relatively too, while *Mesidotea* and other invertebrates contributed little to the diet. In the second half of the year, cod were concentrated at depths less than 80 m in the coastal areas. The diet appeared to have been relatively stable over the entire period. *Mesidotea* was dominant in the food during most of the years and fish was less important than in the first half of the year. Over the period 1963–1975 herring was the most important fish prey, but later sprat became more important.

During 1986–1990 some significant changes in the feeding ecology in coastal waters were observed. Cod switched to a macroplanktonic diet, mysids constituting over 40% of the food. *Mesidotea* declined in the food of cod in 1986–1990 by at least a factor of 2 compared with the period 1963–1985 and the 1950s as reported by Chran (1962) and Strzyzewska (1962).

Discussion

The diet of cod includes different prey categories of benthic species (*Harmothoe, Mesidotea, Pontoporeia*), inhabitants of near-bottom layers (herring and mysids), as well as pelagic species (sprat). The proportion of different food items in young and adult cod diet was fairly stable during the prolonged period 1963–1979. Young cod consumed small food items–polychaetes at greater depths, but crustacea in shallow waters. During the prespawning and spawning periods, mature cod fed more intensively on fish, which could be related to greater demands of energy during gonadal growth. Sprat and herring were dominant in the food during 1970–1975, especially herring, possibly because of the increased stock size. Invertebrates were important as food (about 70% by weight) in the second half of the year.

Since the 1980s environmental and biological conditions in the Central Baltic have gradually changed. When the stock size of cod in 1980–1984 reached its peak owing to the development of extremely abundant year classes in the late 1970s, the recruitment and biomass of herring and sprat populations decreased. One of the main reasons causing the reduction in pelagic fish stocks, besides environment, may obviously have been a high predation mortality. Anomalously low salinity and oxygen concentrations in the bottom waters negatively affected the distribution and biomass of the bottom fauna. Oxygen values of 1 ml l^{-1} were measured at depths of about 100 m (Kalejs and Yula, 1991). Apparently, the area suitable for survival of benthic animals had diminished. Cod reacted to the unfavourable en-

vironment by making spatial and vertical migrations to the areas where living conditions were better. Young cod migrated to shallow water where they fed on crustacea. The main food of young fish in shallow waters was mysids the whole year around. The proportion of other benthic organisms in the food, particularly *Harmothoe*, was low, although it was intensively utilized during the first half of the year in former years. Mature cod migrated during spawning to the intermediate water layers and remained there for feeding and spawning. The prespawning cod in the pelagic zone fed mainly on sprat. Besides sprats, *Enchelyopus cimbrius* and *Platichthys flesus* were found in the stomachs relatively frequently, which may be related to an increased biomass, particularly of the flounder, but most likely to changed availability. On the feeding grounds, cod of more than 30 cm in length switched to macroplanktonic diet, with mysids prevailing. The main food component, *Mesidotea*, which constituted about 40–50% of the adult cod diet in 1963–1985 declined in the late 1980s by a factor of nearly 2. The sharp decline in principal benthic food items has possibly been the background to the shift to alternate benthic food. Found in cod stomachs were invertebrates like *Crangon* sp., *Gammarus locusta* as well as fish *Pomatoschistus* sp., *Osmerus eperlanus, Ammodytes tobianus* and *Zoarces viviparus*, which lives in coastal waters, but because of the low salinity their area had expanded. Extremely unfavourable conditions at greater depths caused adaptational flexibility of the benthic fauna. The changes in the distribution and the shifts to very restricted and inappropriate diets indicate the ability of cod at different stages of life (2 years old and more) to adapt to stagnation. The reduced proportion of benthic animals in the food of cod might be related to their elimination in the deeps. The depths strata unfavourable for survival of the deep sea benthic fauna have expanded to the inshore in the last decade.

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Growth of juvenile Arcto-Norwegian and Norwegian coastal cod reared under similar conditions (Abstract)

Terje Svåsand, Knut E. Jørstad, and Håkon Otterå

Life history characteristics of fish populations are often influenced by genetic factors as well as by environmental parameters. Few studies have compared different cod stocks under identical environmental conditions, which could provide important knowledge towards our understanding fish stock fluctuations as a result of environmental variations (ICES, 1990; Blom, 1991). The main objectives of this study were to compare growth and

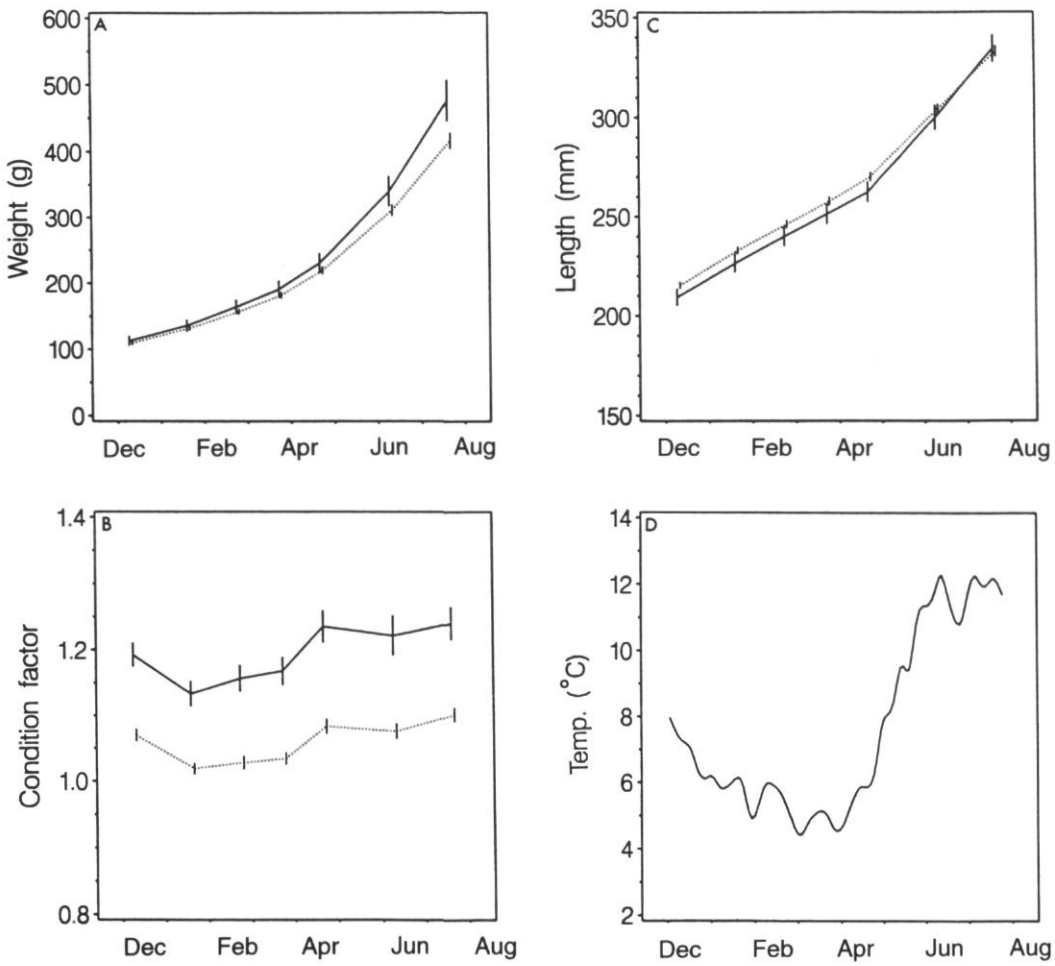


Figure 1. Comparisons of live weight (A), condition factor (B), and total length (C) at different dates of Arcto-Norwegian (. . . .) and Norwegian coastal cod (——). Means and 95% confidence intervals of means are given for each sampling period (December 1992–July 1993). The temperature during the investigation is also shown (D).

maturation of offspring from a migratory cod population (Arcto-Norwegian cod) and a non-migratory cod population (Norwegian coastal cod) under artificial rearing. The first results, comparing growth in the juvenile period, are presented in this contribution.

Offspring from seven family groups of Arcto-Norwegian cod and a genetically tagged Norwegian coastal cod broodstock were raised from the egg stage in the same rearing environments (van der Meeren *et al.*, 1994). At metamorphosis, the offspring groups were pooled together and raised as a single group under standard farming conditions. At the beginning of December 1992, 466 cod were measured for length, weighed, and individually tagged. At the end of April 1993 all fish were genotyped, and each fish could be identified as either Norwegian coastal cod (NC) or Arcto-Norwegian cod (AN). After that, growth was measured at about one-month intervals.

Of the 466 cod initially tagged in December 1992, 436 (93.6%) survived to April 1993, when they were genotyped. Of the surviving cod, 74 (17%) were classified as NC and 362 (83%) as AN. Only seven tags were lost during this period. The main results are shown in Figure 1. The mean weight of the AN group was not significantly different from the NC group from the beginning of the experiment to April 1993. From June the NC group was significantly heavier than the AN group (Fig. 1A). The mean condition factor of the NC group was significantly higher than for the NA group during the whole period (Fig. 1B). In the period December 1992 to April 1993 the mean length of the AN group was significantly larger than the NC group. In June and July the mean lengths were similar (Fig. 1C).

The results so far clearly demonstrate stock-specific differences in growth performance under identical environmental conditions. In contrast to earlier studies (Godø and Moksness, 1987), the comparison involved cod offspring of identical age that have experienced the same environmental conditions and food regimes (van der Meeren *et al.*, 1994). The experiment will be continued with monthly measurements of length, weight, and condition factor, and an important aim will be to compare the onset of maturation between the two groups.

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Survival of eggs and yolk-sac larvae of Baltic cod (*Gadus morhua* L.) at low oxygen levels in different salinities

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Nissling, A. 1994. Survival of eggs and yolk-sac larvae of Baltic cod (*Gadus morhua* L.) at low oxygen levels in different salinities. – ICES mar. Sci. Symp., 198: 626–631.

In the Baltic Sea, successful spawning of cod is restricted to the deep basins, the Bornholm, Gdańsk, and Gotland basins, with salinities of 10–17. Deep water is exchanged mainly during periods of inflow of saline water from the North Sea. These inflows are irregular and stagnant waters prevail for long periods accompanied by unfavourable oxygen conditions. Consequently, cod eggs occur regularly at low oxygen levels. In this study, batches of eggs (2, 4, and 7 days old) and larvae (newly hatched and 4 days old) were exposed to low oxygen concentrations – 1.0–3.5 mg O_2/l – at two salinities – 11 and 15 – and compared with survival in controls at 100% oxygen saturation in short-term experiments. Egg survival decreased with decreasing oxygen concentration, with no difference in tolerance between egg stages. Egg survival at low oxygen levels was clearly affected by salinity, with significantly higher survival at 15 ppt than at 11 ppt. This implies that egg survival at low oxygen levels differs between the spawning grounds of Baltic cod. It is higher in the Bornholm Basin with higher salinities, 13–17, than in the Gdańsk and Gotland basins, with 10–13. For both larval stages, a marked decrease in tolerance to low oxygen levels was evident between 3.0 and 2.5 mg O_2/l irrespective of salinity, suggesting that the limit for survival of Baltic cod larvae is at about 2.5–3.0 mg O_2/l.

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Introduction

Successful spawning of Baltic cod is restricted to the Baltic deep basins – the Bornholm, Gdańsk, and Gotland basins. In the Baltic deep basins there is a halocline at 50–70 m depth with a denser more saline (10–17 ppt) deep water which is only partly mixed with the less saline (6–8 ppt) surface water. The deep water is exchanged mainly during occasions of inflow of saline water from the North Sea. These inflows are irregular, however, and during periods between inflows stagnant conditions prevail with a decrease in the salinity and oxygen content of the water. These varying conditions have a profound impact on the reproductive success of fishes with pelagic eggs. In the Baltic, cod eggs often occur in layers with low oxygen content (see Lebedek, 1978; Wieland, 1989), as determined by their buoyancy.

The year-class strength of Baltic cod is thought to be established during the embryonic period and apparently determined by the thickness of the spawning layer (Grauman, 1973), i.e., the layer with 11 ppt salinity or more (Westin and Nissling, 1991) and sufficient oxygen content for egg and larval development.

The last two major inflows of saline water to the Baltic Sea occurred in the winters 1975–1976 and 1976–1977 (Fonselius, 1988) and resulted in favourable spawning conditions. Consequently, an increase in the Baltic cod stock followed and high catches were reported from the late 1970s until the mid-1980s [450 000 t in the early 1980s (Hansson and Rudstam, 1990)]. However, since stagnant water has prevailed in the deep basins from the late 1970s, there has been a dramatic decrease in the Baltic cod stock, with poor catches reported since the mid-1980s [about 75 000 t reported in 1992 (P.-O. Larsson, pers. comm.)].

The metabolic rate of fish embryos is independent of the water oxygen content until a certain critical level is reached, below which metabolism becomes dependent on ambient oxygen concentrations (Rombough, 1986). Any deviation from normal oxygen uptake will influence development and survival negatively (Serigstad, 1987). Metabolic rate in fishes is highly influenced by temperature, since temperature controls the rate of different biochemical reactions, and by salinity, which affects osmoregulation. Consequently, oxygen requirements of eggs and larvae are affected by temperature [see Schur-

mann and Steffensen, 1992 (juvenile cod); Alderdice and Forrester, 1971 (Pacific cod eggs); Almatar, 1984 (herring and plaice larvae)] and possibly by salinity (see Alderdice and Forrester, 1971; Almatar, 1984).

The aim of the present investigation was to study the tolerance of Baltic cod eggs and larvae to low oxygen concentrations at prevailing salinities of the Baltic deep basins. In short-term experiments (48 h), eggs (three different stages) and yolk-sac larvae (two stages) were incubated at low oxygen levels; 1.0–2.8 (for eggs) and 1.5–3.5 (for larvae) mg O_2/l at 7°C at 11 and 15 ppt and compared with survival in controls at 100% oxygen saturation.

Materials and methods

Spawning cod were caught in gillnets at 50–90 m depth off Gotland (58°N19°E) in the middle of the Baltic Sea. Eggs and semen were obtained by stripping. Fertilization was carried out in water at 7°C and 17 ppt prepared from filtered (0.2 μm cartridge filter) sea water (7 ppt) and synthetic sea salt (hw Marinemix). Eggs at three different stages of development (2, 4, and 7 days old) and larvae at two stages [newly hatched and 4 days old (onset of first feeding)] were incubated. Water of different oxygen concentrations was obtained by bubbling with nitrogen gas to the nearest 0.1 mg O_2/l (WTW Oximeter 196). In all incubations, filtered water was treated with antibiotics [Mycostatin (2500 IU/l), Streptomycin (0.05 g/l), and Doctacillin (0.2 g/l)]. Treated water was transferred to the incubation flasks by means of a tube before the eggs and larvae were added. Prior to incubation the eggs and larvae were kept in water at 7°C and 17 ppt salinity.

Batches of eggs and larvae were incubated at five oxygen concentrations, ranging between 1.0 and 2.8 mg O_2/l for eggs and 1.5 and 3.5 mg O_2/l for larvae, at two different salinities; 11 and 15 at 7°C. As controls, incubations at 100% oxygen saturation (10–11 mg O_2/l) in respective salinities were used. Each treatment, containing 125–150 eggs or 10–15 larvae, was incubated for 48 h in a 500 ml flask with conical stopper to prevent air bubbles at the start of incubation. The water was mixed gently three times a day by rotating the flask to prevent microstratification of oxygen. Each set of incubation, i.e., 12 flasks, was performed in replicates with batches from different females as follows: 6 replicates for 2 and 4 days old eggs; 2 replicates for 7 days old eggs; 5 and 6 replicates for newly hatched and 4 days old larvae, respectively. The flasks were placed on their side and the eggs developed at the bottom of 11 ppt, since Baltic cod eggs are non-buoyant at 11 ppt (see Nissling and Westin, 1991); because of positive buoyancy they developed at the top at 15 ppt. At the end of the incubations egg

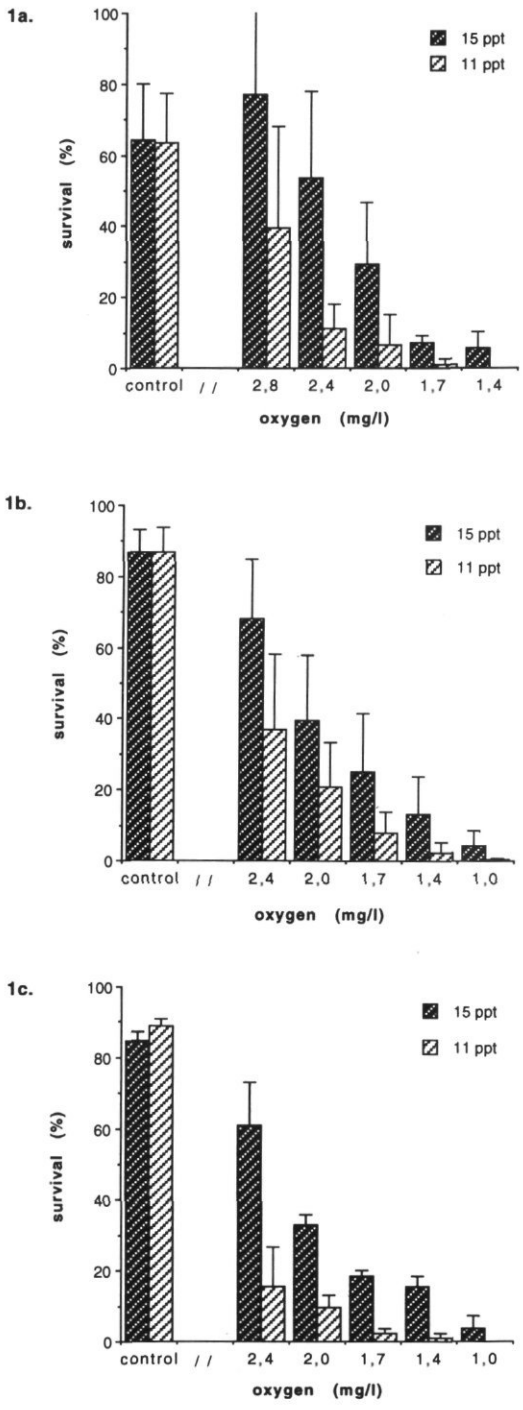


Figure 1. Survival of Baltic cod eggs incubated at low oxygen levels for 48 h at 7°C with salinities of 11 and 15. Survival in controls is given as absolute survival and survival at low oxygen concentrations is given as relative survival, i.e. as percentage of survival in controls. (a) 2 days old eggs (six replicates), (b) 4 days old eggs (six replicates), (c) 7 days old eggs (two replicates). Standard deviation shown at top of bars.

Table 1. Oxygen concentrations (mg O_2/l) at the start and end of exposure of Baltic cod eggs (2 and 4 days old) (six replicates) and larvae (4 days old) (one larval group) to low oxygen levels. Each experiment was carried out at 7°C with a salinity of 11 for 48 h.

Eggs			Larvae	
Start of incubation (mg O_2/l)	End of incubation (mg O_2/l)		Start of incubation (mg O_2/l)	End of incubation (mg O_2/l)
	2 days old	4 days old		2 days old
10–11 (control)	9.0 ± 0.6	9.3 ± 0.4	10–11 (control)	9.6
2.8	2.6 ± 0.1	–	3.5	3.4
2.4	2.3 ± 0.1	2.3 ± 0.1	3.0	3.0
2.0	2.0 ± 0.1	1.9 ± 0.1	2.5	2.5
1.7	1.6 ± 0.1	1.6 ± 0.1	2.0	2.0
1.4	1.4 ± 0	1.4 ± 0	1.5	1.5
1.0	–	1.1 ± 0.1	–	–

survival and larval condition were checked. White eggs (dimpled) and eggs which had ceased in development were considered dead and larval condition was judged as follows: dead, moribund (partly white), alive but inactive (did not react when touched), or active (swimming). In order to exclude differences in survival due to differences in egg quality caused by maternal effects and stage during the spawning period (see Kjesbu, 1989; Kjesbu *et al.*, 1991; Solemdal *et al.*, 1991), egg survival was calculated in relation to survival in the controls (survival in the controls treated as 100% survival) and given as a percentage of survival in the controls. To check the consumption of oxygen during the incubation, oxygen concentrations at the end of incubations at 11 ppt were measured.

To examine whether transference from a high salinity (17) to lower salinities (11 and 15) influenced egg survival at low oxygen concentrations, two egg batches were fertilized and incubated at respective salinity until start of exposure, i.e., day 3 (one batch) and day 5 (one batch), and then incubated at low oxygen concentrations at 7°C for 48 h as above.

Results

Table 1 gives the oxygen concentrations at the end of incubations for 2 and 4-day-old eggs and one larval group. The measurements revealed a small decrease in oxygen content during the 48 h incubation. The highest decrease occurred in the controls, while the decrease was low at low oxygen levels. The decreases in oxygen content seem to be related to egg survival, i.e., the higher the survival the higher the oxygen consumption (cp. with Fig. 1).

Egg survival and larval condition after incubation at low oxygen concentrations at 11 and 15 ppt are shown in Figures 1a–c and 2a–d, respectively. Egg survival decreased with decreasing oxygen concentrations at all developmental stages studied, with no apparent difference in tolerance to low oxygen levels between egg stages. Compared with controls (100% oxygen saturation) there was a decrease in egg survival at 2.8 mg O_2/l and only a few eggs survived at 1.0 mg O_2/l. However, egg survival differed between salinities and was significantly higher at 15 ppt than at 11 ppt, $p < 0.001$ (sign test of paired observations) for both 2 and 4-day-old eggs (the numbers of incubations of 7-day-old eggs were too low for a sign test) at low oxygen concentrations, while no difference in survival occurred between controls at 11 and 15 ppt.

Table 2 gives egg survival at low oxygen concentrations at 11 and 15 ppt for two egg batches incubated at the same salinities from fertilization until the start of exposure to low oxygen concentrations. Egg survival was higher at 15 ppt than at 11 ppt for both 3 and 5-day-old eggs. These results suggest that the difference in egg survival between salinities was not caused by the transference of eggs from a higher salinity (17 ppt) at the start of exposure.

In short-term incubations of larvae at low oxygen concentrations at 11 and 15 ppt, no differences in tolerance to low oxygen concentrations were apparent be-

Table 2. Survival of Baltic cod eggs (3 and 5 days old) fertilized and incubated with salinities of 11 and 15 and exposed to low oxygen levels for 48 h at 7°C at identical salinities.

	3 days old		5 days old	
Oxygen (mg O_2/l)	11 ppt	15 ppt	11 ppt	15 ppt
10–11 (control)	96.5	95.5	73.6	70.4
2.4	34.5	67.8	22.5	58.8
2.0	16.1	36.1	5.0	20.7
1.7	3.5	31.8	4.1	9.4
1.4	0	–	1.1	7.5
1.0	0	7.2	–	–

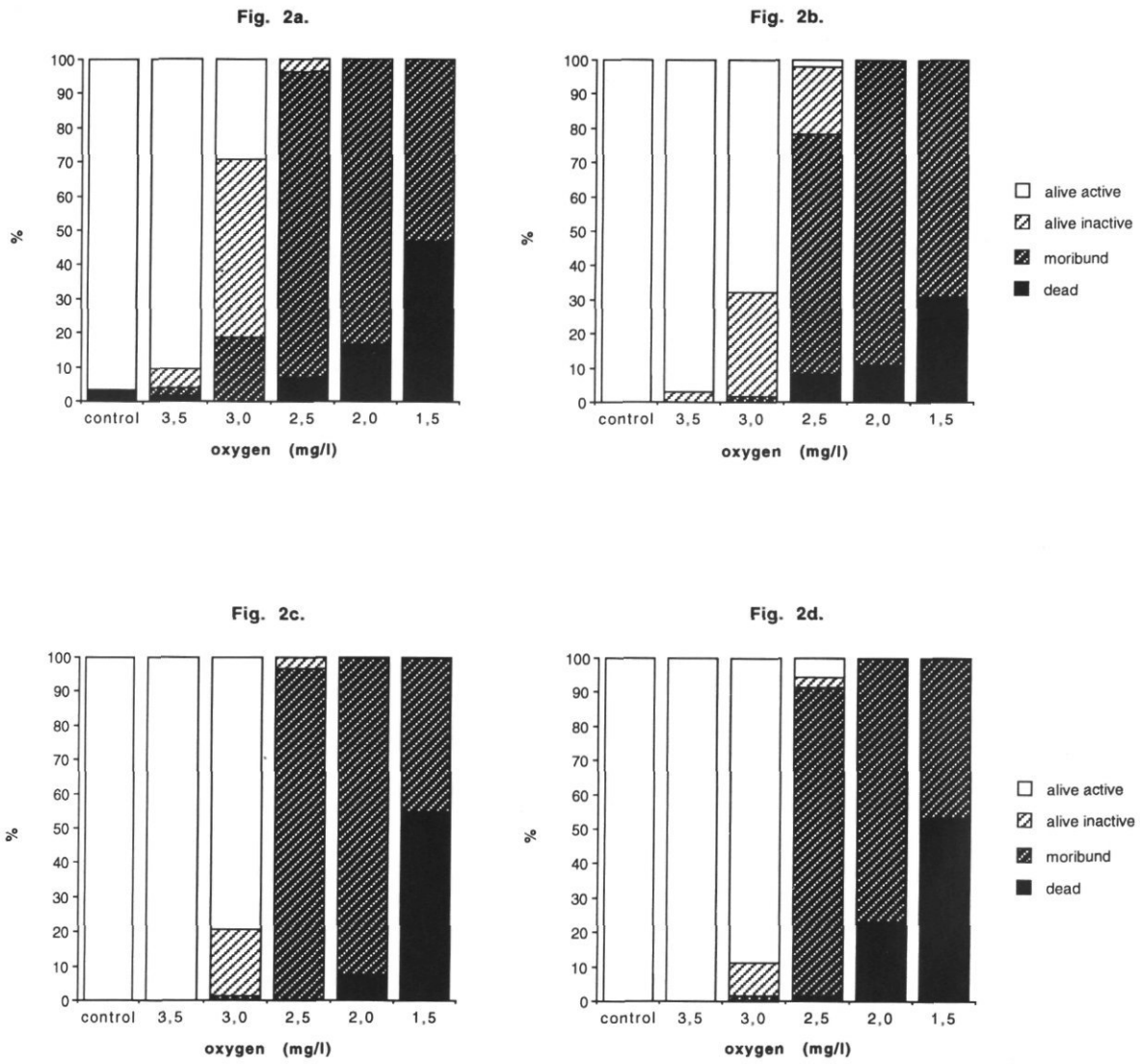


Figure 2. Condition of Baltic cod larvae incubated at low oxygen levels for 48 h at 7°C. (a) Newly hatched larvae incubated with a salinity of 11 (five replicates), (b) newly hatched larvae incubated with a salinity of 15 (five replicates), (c) 4 days old larvae incubated with a salinity of 11 (six replicates), (d) 4 days old larvae incubated with a salinity of 15 (six replicates).

tween larval stages or between incubation salinities. For both newly hatched larvae and larvae at the onset of feeding the majority of larvae were alive and active at 3.5 mg O_2/l, with inactive and moribund larvae beginning to appear at 3.0 mg O_2/l. For both larval stages there was a marked decrease in tolerance to low oxygen concentrations between 3.0 and 2.5 mg O_2/l. Incubations at 3.0 mg O_2/l displayed high survival, whereas incubations at 2.5 mg O_2/l or lower revealed dead or moribund larvae with only a few surviving larvae at 2.5 mg O_2/l.

Discussion

Surveys in the Baltic deep basins have shown that adult cod may occur in layers with oxygen content as low as 1.4–2.9 mg O_2/l (see Berner and Schemainda, 1957, 1958; Tiews, 1970) and that cod eggs are regularly found at low oxygen levels; 1.7–5.4 mg O_2/l (Lebedek, 1978), 2.6–5.4 mg O_2/l (Wieland, 1989) with high mortalities reported during the egg stage period; 79–98.8% (Grauman, 1973), 99.8% (Wieland, 1987). The critical oxygen

level for successful development of Baltic cod eggs has been suggested as being 1.4 mg O_2/l (Grauman, 1973); >2.9 mg O_2/l (Kosior and Netzel, 1989), but experimental data are scarce. (Oxygen levels reported in ml O_2/l are recalculated to mg O_2/l).

The present study shows that cod eggs may survive at low oxygen levels for at least two days, but that survival is greatly affected at oxygen concentrations of 1.0–2.8 mg O_2/l. Since cod eggs are regularly found at oxygen levels of this magnitude, these results suggest that low oxygen levels in the Baltic deep basins may cause high egg mortalities. As concluded by Wieland, from investigations on cod egg distribution in the Bornholm Basin, vertical occurrence of eggs is not only controlled by egg buoyancy. In addition to water density, the vertical occurrence of eggs is also influenced by oxygen levels as a result of high egg mortality at low oxygen concentrations. Cod eggs were most abundant at depths of 60–75 m at oxygen levels of 2.6–6.9 mg O_2/l, but eggs also occurred deeper, at oxygen concentrations of less than 1.4 mg O_2/l (Wieland, 1987, 1989).

According to several investigations on marine fish embryos the uptake rate of oxygen increases during development from fertilization to hatching and absorption of the yolk sac [Serigstad, 1987 (cod); Davenport and Lönning, 1980 (cod); Finn *et al.*, 1991 (halibut)], and is also influenced by larval activity level (Davenport and Lönning, 1980; Serigstad, 1987), i.e., an increase of oxygen demand during development. However, in this study no differences in tolerance to low oxygen levels among egg stages or between two larval stages were observed. For both larval stages a marked decrease in tolerance to low oxygen concentrations was evident between 3.0 and 2.5 mg O_2/l, with only a few surviving larvae at 2.5 mg O_2/l. Accordingly, this suggests that the limit for survival of Baltic cod larvae is at about 2.5–3.0 mg O_2/l.

Incubation of eggs and larvae at two different salinities showed that larval condition was not affected by salinity at low oxygen levels, whereas egg survival at low oxygen concentrations was significantly higher at 15 ppt than at 11 ppt. Hence, the higher mortality of eggs at low oxygen levels at 11 ppt compared to 15 ppt, whereas no differences in egg mortality occurred between controls (100% oxygen saturation), suggests that cod eggs are more vulnerable to oxygen deficit at extreme salinities. Further, this investigation indicates that Baltic cod are less affected by extremes in salinity as larvae than at the egg stage.

Although a long-term experiment is required to estimate overall egg mortality from fertilization to hatching at a certain oxygen level, the present investigation indicates a significant difference in total egg mortality between 11 and 15 ppt. For instance, if egg mortality at 48 h of exposure at 2.4 mg O_2/l (egg mortality at the three egg stages pooled for 11 and 15 ppt) is extrapolated, it results in an overall mortality (egg development time 13–15 days at 7°C) of about >99.99 and 97% at 11 and 15 ppt, respectively. This indicates a considerable difference in spawning success with salinity for a given oxygen concentration.

The inflows of saline oxygen rich water from the North Sea are irregular and as a consequence conditions for successful spawning vary greatly between years, but also between spawning areas. Because of the relative distance from the North Sea, the most favourable conditions, generally higher oxygen concentrations and more saline water (13–17 ppt compared with 10–13 ppt in the Gdańsk and Gotland basins), occur in the Bornholm Basin, which is more regularly influenced by influxes of water from the North Sea than are the Gdańsk and Gotland basins, where stagnant periods are more pronounced. Consequently, egg survival is higher in the Bornholm Basin than in the Gdańsk and Gotland basins, owing to more favourable oxygen conditions but also, as this study implies, because of higher salinity, since eggs are less vulnerable to oxygen depletion at 15 ppt than at 11 ppt.

Acknowledgments

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ICES mar. Sci. Symp., 198: 632. 1994

Effects of temperature and density on growth, survival, and cannibalism of juvenile cod (*Gadus morhua* L.) (Abstract)

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Growth, survival, and cannibalism of cod with an initial weight of about 2 g were studied in the laboratory for 8 weeks using a balanced 2 × 3 factorial design. The juveniles (n = 3300) were hand-graded and randomly allocated to three environmental temperatures (6, 10, and 14°C) and two densities (50 and 500 fish in 500-litre tanks). Two replicates were used within each treatment. The juveniles were allowed 2 weeks of acclimatization to conditions before the experiment started. Dry feed was supplied in excess every 10 min, and a continuous photoperiod was used. Surviving fish in all of the 12 tanks were counted and individually weighed every second week. Survival averaged 95.1, 89.6, and 90.6% at 6, 10, and 14°C respectively after 8 weeks. Survival was slightly higher among the cod fry in the low density group (95.3%) than in those in the high density group (91.4%). All cannibalism, with one exception, occurred in the high density group. This constituted 4.9 and 0.3% of the total respectively. Daily growth rate (DGR) averaged 2.0, 3.1, and 3.8% at 6, 10, and 14°C, respectively, but no clear density effect in DGR was noticed. The fish at 14°C were on average 56% larger in wet weight than the fish at 10°C, which again were 104% larger than the fish at 6°C at the end of the experiment. A temperature preferendum for juvenile cod (5.5 g) was estimated at 13.7°C. Estimated Q_{10} for cod was 3.0 and 1.7 at temperatures between 6 and 10°C and 10 and 14°C with respect to DGR. The max:min weight ratio was larger in the groups with 500 fish than in the tanks with 50 fish, 5.6–17.8 vs. 3.5–11.3. Differences in max:min ratios may thus partly explain the higher losses due to cannibalism in the high density groups in this experiment. A significant interaction between temperature and density was found with respect to growth rate. At 6 and 10°C, DGR was highest in the high density group, while at 14°C the growth was highest in the low density group. Significant interactions between temperature and density on growth point to the importance of rearing conditions in temperature studies.

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Growth and survival of cod larvae (*Gadus morhua* L.): comparative enclosure studies of Northeast Arctic cod and coastal cod from western Norway

Terje van der Meeren, Knut E. Jørstad, Per Solemdal, and Olav S. Kjesbu

van der Meeren, T., Jørstad, K. E., Solemdal, P., and Kjesbu, O. S. 1994. Growth and survival of cod larvae (*Gadus morhua* L.): comparative enclosure studies of Northeast Arctic cod and coastal cod from western Norway. – ICES mar. Sci. Symp., 198: 633–645.

To evaluate genetic differences in survival and growth potential under similar environmental and feeding conditions, cod larvae (*Gadus morhua* L.) from two different stocks were reared in 5.2 m^3 plastic bag enclosures. In the enclosures, genetically marked coastal cod larvae were reared along with equal numbers of either Northeast Arctic cod larvae or coastal cod larvae without a genetic marker. The enclosures were floating in a saltwater basin used for the production of zooplankton. Nauplii, juveniles, and adult stages of copepods were collected from the basin and fed to the larval groups in accordance with a theoretical energy model. The different experimental series were terminated between days 36 and 48 post-hatch. Individual larval weights were measured and samples for stock identification by electrophoresis were taken. The results indicate stock-specific difference in growth capability under the given environmental conditions and feeding regimes. Daily weight-specific growth rates for Northeast Arctic cod larvae (13.6–19.7%) were lower than for coastal cod (14.4–22.3%). Growth was density-dependent, with the highest growth rates in enclosures with low survival. No stock-specific difference in survival potential was evident.

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Introduction

The effects of climatic changes on the dynamics and variability of commercially important species, including Atlantic cod (*Gadus morhua* L.), have been of considerable practical and scientific concern (ICES, 1990a). For this reason, a comprehensive modelling work for cod is suggested, which includes the development of both basic physical and biological process models (ICES, 1990a). In all life stages of cod, genetic variation may influence the response to environmental changes. Thus, of particular importance for the biological process models is the extent to which generalizations between stocks can be allowed.

Atlantic cod is distributed over a large geographic area, and many different stocks are recognized and managed as separate units (ICES, 1990b). These stocks differ in various life history characteristics which are possibly influenced by both genetic and environmental factors. Differences in meristic characters and otolith structure in samples of cod from different regions have been known for a long time (Schmidt, 1930; Rollefsen, 1933). Møller (1966, 1968) found genetic differentiation between Northeast Arctic cod and Norwegian coastal cod populations. A low level of genetic variation in tissue enzymes in cod from different regions has been reported (Mork *et al.*, 1985). However, detailed investigations of cod in the Norwegian waters have confirmed Møller's results (Jørstad and Nævdal, 1989; Dahle and Jørstad, 1993).

Genetic variation in a number of important life history characteristics has been discussed for salmonids (Ricker, 1972; Nævdal *et al.*, 1978; Saunders, 1981; Gjerde, 1986). So far, no controlled studies have been carried out to estimate the heritability of important characters in cod. Differences in growth rate have been reported between cod larvae from Scotland and western Norway reared under similar conditions (Gamble and

Houde, 1984). However, such differences were not found in comparisons between juveniles from Norwegian coastal cod and Northeast Arctic cod (Godø and Moksness, 1987).

At the moment, successful rearing of numerous cod fry can only be performed in large enclosures or lagoons (Øiestad *et al.*, 1985; Pedersen *et al.*, 1989; Blom *et al.*, 1991). The development of the mesocosms experimental design (Gamble *et al.*, 1981; Øiestad, 1983; van der Meeren and Næss, 1993; Otterå, 1993) offers a new opportunity to conduct detailed studies of survival and growth in fish larvae. The present work is an implementation of the proposal of comparative growth and survival studies in cod larvae (Blom, 1991) using the mesocosms experimental design. Larvae of the Northeast Arctic cod and coastal cod from western Norway were both reared together in the same enclosure. This ensured that comparison of survival and growth for the two stocks were carried out under similar environmental and nutritional conditions, as recommended for cod (ICES, 1990a).

Materials and methods

Rearing system

The experiments were carried out at Austevoll Aquaculture Research Station situated on the Norwegian west coast at approximately 60°N. Cod larvae were reared in 5.2 m^3 enclosures of black PVC plastic (no. 4659057, Duratex A/S, Denmark), supported by a floating PEH plastic ring tied to a raft system (Fig. 1). The enclosures, 12 and 9 units in the 1992 and 1993 experiments respectively, were placed in a 20 000 m^3 seawater basin used for zooplankton production and temperature stabilization (Naas *et al.*, 1991). The enclosures were initially filled with sea water collected from the fjord outside the basin and filtered through an 80 μm plankton net with the use of an UNIK 900 wheel filter (van der Meeren, 1991a). The same source was also used for water renewal entering the bottom of the bags through a flexible tube (Fig. 1). Flow rate was approximately 10% per day in the first 14 days after larval stocking, after which it increased gradually to 60% on day 40 post-hatch. Temperature, oxygen saturation, and salinity were measured at two depths (0.5 and 2.5 m) in two of the enclosures throughout the experiments. Light was not able to penetrate the plastic wall of the enclosures. Thus, the enclosures were equally illuminated from above by natural light.

Feeding conditions

Zooplankton, mainly nauplii, juvenile, and adult stages of the copepod *Eurytemora affinis* (Poppe), was collected from the basin using an UNIK 900 wheel filter placed on the raft system. The filter concentrated plankton retained on plankton nets of 80 and 250 μm mesh size. Thus two size fractions, 80–250 μm and >250 μm,

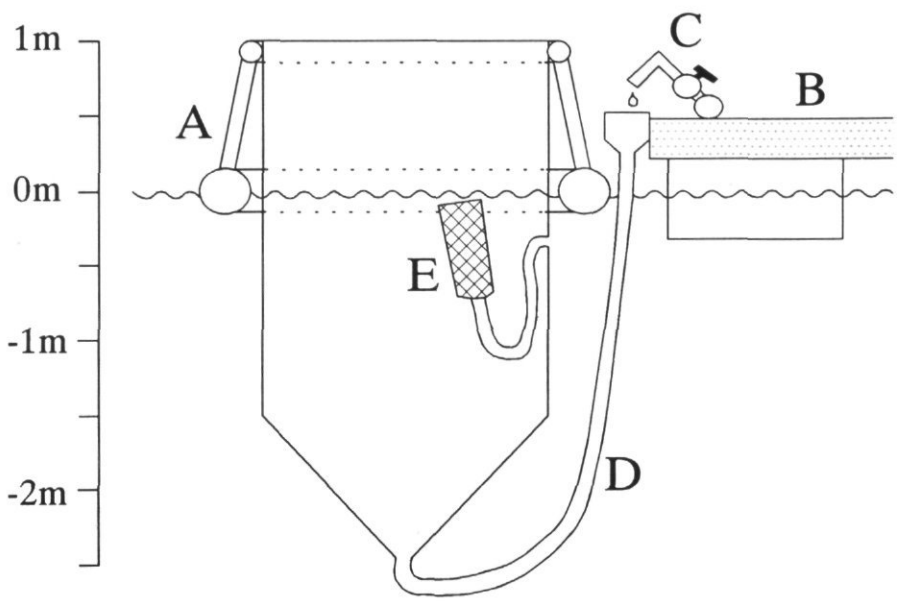


Figure 1. Schematic drawing of a rearing enclosure. A. Floating PEH plastic support ring. B. Raft. C Water supply system with tap. D. Flexible bottom tube for water renewal. E. Sieve with 350 μm plankton net. Scale denotes depth and height from water surface.

were collected. The 80–250 μm fraction was further manually filtered through plankton nets of 120 μm (before day 5) and 150 μm (day 6 to 14). The >250 μm fraction was used after day 36.

All enclosures received equal amounts of food on a daily basis. Feeding was carried out according to calculated food consumption from a theoretical energy model for small fish larvae (van der Meeren, 1991b), with substitution of respiration values for cod (Laurence, 1978). An average specific growth rate of 15% daily increase in weight was used in the calculations. The collected plankton was counted and categorized into four groups: rotifers, copepod nauplii, copepodites, and copepods. To simplify the feeding procedure, values used for average energy content of the different plankton groups was 0.0033, 0.0054, 0.037, and 0.37 J ind^{-1} for rotifers, nauplii, copepodites, and copepods, respectively (calculated from Böttger and Schnack, 1986; Blom *et al.*, 1991; van der Meeren, 1991b).

Biological material and experimental design

Three experiments were carried out, one in 1992 and two in 1993. To evaluate genetic differences in survival and growth potential under similar environmental and feeding conditions, cod larvae from two different stocks were reared together in each of the plastic bag enclosures. The stocks compared were the Northeast Arctic cod and coastal cod from western Norway. Rearing cod larvae of different origin in the same enclosure became possible because of genetic characterization of the parental fishes and the yolk-sac larvae. With the exceptions of hydrographical measurements and the addition of food, the cod larvae were left undisturbed in the enclosures until termination of the experiments.

The 1992 experiment

In 1992, eggs and milt were stripped from wild-caught spawners of the Northeast Arctic cod (NAC) in Lofoten (69°N), and from coastal cod (CC) from Øygarden, western Norway (60°N), kept in captivity less than a year. The procedures for collection of spawning products and subsequent fertilization are described in Solemdal *et al.* (1992). The eggs from Lofoten were sent by air freight and incubated on arrival together with the coastal cod eggs in 12-litre buckets with continuous water flow. Eggs from individual females were kept apart for separate stocking in the enclosures.

The number of batches shed by each single female at the time of egg collection was considered of interest because progressively smaller eggs are produced throughout the spawning season (Kjesbu, 1989). This, together with any likely variations in egg quality, could thus affect larval survival and thereby complicate interpretations of the results if no data on the "stage of spawning" were given. This stage classification refers to the portion of eggs spawned (PES) in relation to the total number of eggs in the ovary (Kjesbu *et al.*, 1990): PES $\leq$ 25% (stage 1), 25% < PES $\leq$ 50% (stage 2), 50% < PES $\leq$ 75% (stage 3), and PES > 75% (stage 4). The technique used relies upon statistics describing the vitellogenic oocyte mode, in particular the standard deviation, but also minimum, maximum, and mean diameter measurements of 50 oocytes in physiological sea water under the binocular microscope (50×). Published data on duration between first and last batch (Kjesbu, 1989) were also taken into consideration in a few cases for the captive fish, i.e., when the eggs were collected some time after the time of oocyte sampling. Oocytes from the CC were sampled by ovarian catheterization (i.e. with-

Table 1. Data on the parental fish and eggs used in the 1992 experiment.

	Fish data (females)				Egg data		
Enclosure no.	Length (cm)	Weight (g)	Condition factor[a]	Stage of spawning	Diameter (mm) (mean ± SD)	Dry weight (μg)	Fertilization (%)
Northeast Arctic cod							
1	72	3400	0.91	2	n.a.	n.a.	98
2	96	9700	1.10	1–2	n.a.	n.a.	97
3	84	7850	1.32	1	1.37 ± 0.01	103	99
4	85	4500	0.73	3–4	1.32 ± 0.02	106	89
5	90	6650	0.91	3	n.a.	n.a.	96
6	95	8550	1.00	3	n.a.	n.a.	98
Coastal cod							
7	56	2350	1.34	2	1.34 ± 0.02	90	70
8	58	2500	1.28	1–2	1.28 ± 0.02	119	98
9	69	4360	1.33	2	1.34 ± 0.02	91	95
10	54	2150	1.37	1–2	1.31 ± 0.02	65	88
11	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a
12	67	3700	1.23	4	1.26 ± 0.02	82	98

[a]Fulton's condition factor (Condition = weight × 100/length^3).
n.a. Data not available.

Table 2. Date of experiment startup and number of cod larvae from the different stocks released in each of the enclosures. Numbers in parentheses denote larval age (days after 100% hatchings) at time of transfer to the enclosures.

Enclosure no.	Date	Arctic cod	Coastal cod	Coastal cod, genetic marked
1992 experiment				
1–6	10 April	500 (1)*		500 (3)**
7–12	10 April		500 (1)*	500 (3)**
1993 experiments				
1–6 (experiment I)	24 March	400 (1)**		400 (1)**
7–9 (experiment II)	7 April	400 (3)**		400 (3)**

*Larvae from single matings (family groups).
**Larvae from a mixed population of several spawners (replicates).

out killing the fish) while the ovary was dissected out in the NAC. Table 1 gives stage of spawning and other stock data.

To evaluate variation between the rearing enclosures, an additional strain of coastal cod larvae with a genetic marker (CCGM) (Jørstad *et al.*, 1987, 1991; Svåsand *et al.*, 1991) was stocked in all enclosures. These larvae were hatched from eggs collected from a naturally spawning broodstock kept in large plastic bags at the Austevoll Aquaculture Research Station (Huse and Jensen, 1983; Holm and Andersen, 1989). The CCGM larvae represented a mixed population of several spawners, in contrast to the other larval groups which were from individual females (Table 2). Numbers of yolk-sac larvae released in the enclosures and age at transfer are detailed in Table 2. Total stocking density in each enclosure was 0.19 larvae per litre. Dry weights of 45 cod larvae from each of the different larval groups were measured with a Mettler M3 Microbalance. Prior to measurement, the larvae were rinsed for a few seconds in fresh water and dried for 24 h at 60°C.

The 1993 experiments

In 1993, eggs were collected from naturally spawning broodstocks of NAC and CCGM only. The NAC broodstock was caught in the Lofoten area during the egg collection cruises in 1992 and transferred to Austevoll prior to spawning for light adaptation and synchronization of the spawning cycle with CCGM. Broodstocks were chosen so as to give as similar size distributions as possible (Fig. 2a–b, Table 3). Daily monitoring of egg diameter throughout the spawning season by means of video taping of 80 eggs and a computer-based image analyser program made it possible to choose egg groups with good overlap in size distribution (Fig. 2c–f, Table 3). About 0.5 litre of eggs were incubated in 70-litre tanks with 0.5 litre per minute water renewal.

Larvae from egg groups collected at two different times in the spawning cycle (Fig. 2c–d) were used in two separate experiments (experiments I and II: Table 2). To ensure good overlap in larval size between the stocks, dry weight distribution was determined from a sample of approximately 60 larvae when hatching was completed (Fig. 2g, Table 3). The procedure for dry weight measurements was the same as in the 1992 experiment. Table 2 shows numbers of yolk-sac larvae released in the enclosures and age at transfer. Total stocking density in the two experiments was 0.15 larvae per litre. To evaluate possible effects of larval handling (counting and transport to the enclosures), control groups of 100 larvae were treated in a similar way to the released groups, but kept in several 5-litre transport bags at a corresponding temperature and light regime to the rearing units. Survival was determined on termination of transport bags during the first two weeks.

Experiment termination and genetic analyses

After harvesting of the enclosures, the cod fry produced were counted and individual wet weights measured. Samples of white muscles from individuals were frozen and kept at −70°C until analysis. Usually, tissue samples of 144 individuals were collected from each enclosure. In cases with fewer survivors, all individuals (91 at lowest) were collected.

The tissue samples were analysed by horizontal starch gel electrophoresis and stained for glucosephosphate isomerase (Harris and Hopkinson, 1976). The CCGM offspring were identified by the staining of the unique band on the gel, corresponding to the *GPI-1*30* allele, easily distinguished from the other genotypes (Jørstad *et*

Table 3. Mean values and standard deviations for size of broodstock fish, egg diameter, and dry weight of newly hatched cod larvae in the 1993 experiments.

	Size of broodstock fish (kg)		Egg diameter (mm)		Larval dry weight (mg)	
	Males	Females	Exp. I	Exp. II	Exp. I	Exp. II
Northeast Arctic cod	5.36 ± 2.50	7.91 ± 2.10	1.40 ± 0.06	1.37 ± 0.04	0.055 ± 0.007	0.052[a] ± 0.005[a]
Coastal cod	6.34 ± 0.95	6.91 ± 1.47	1.37 ± 0.04	1.35 ± 0.04	0.052 ± 0.005	0.050[a] ± 0.004[a]

[a]Values estimated from a theoretical dry weight distribution (see text for explanation).

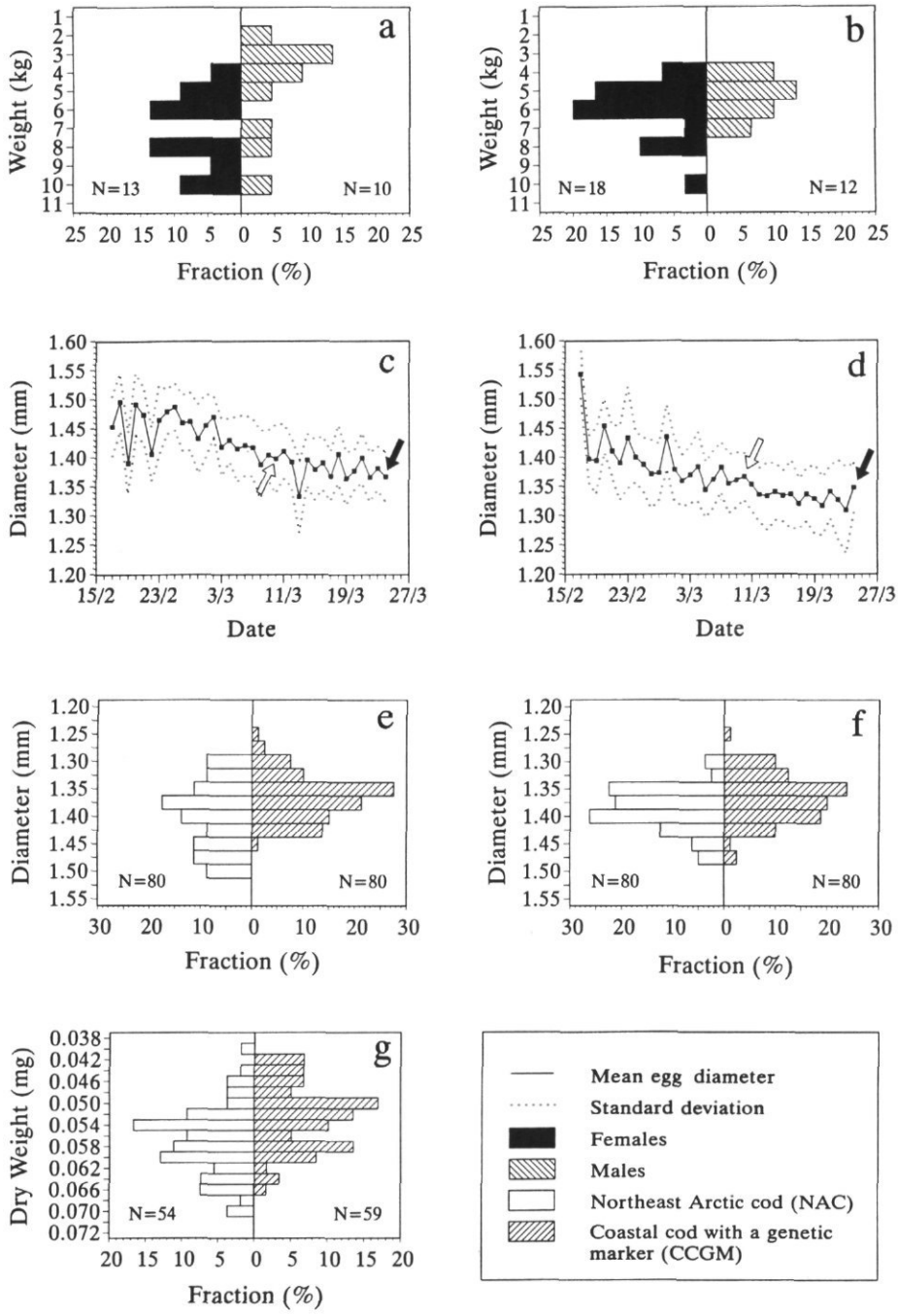


Figure 2. Size of broodstock fish, eggs, and larvae used in the 1993 experiments. a. NAC; b. CCGM; c–d. seasonal variation of egg diameter in NAC (c) and CCGM (d), white and black arrows denote egg groups used in experiments I and II respectively; e–f. distribution of egg diameter used in experiments I (e) and II (f); g. distribution of larval dry weight used in experiment I.

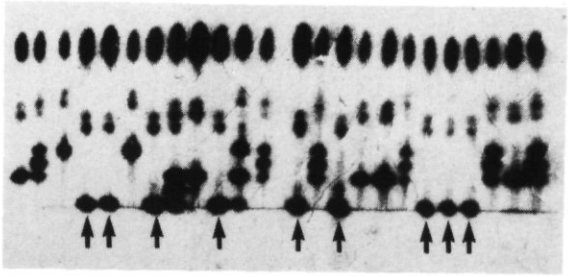


Figure 3. Staining pattern of phosphoglucose isomerase after separation by horizontal starch gel electrophoresis. Muscle tissue samples were taken from individual cod collected from enclosure no. 9 (experiment II, 1993). The genetically tagged individuals possess a single, slow moving band as indicated by arrows in the zymogram.

al., 1991; Svåsand *et al.*, 1991). Figure 3 shows a picture of the banding pattern obtained after electrophoresis. The individuals, being homozygotes for this allele, are indicated in the figure, and are offspring from the genetic-marked coastal cod strain.

Calculations and statistics

To convert the measured wet weights at experiment termination to dry weights, a factor of 0.18 (i.e. 82% water content) was used (N. Finn, Zool. Inst., Univ. of Bergen, pers. comm.). This factor was determined from cod larvae and fry reared parallel to the experiments under similar rearing and food conditions. In 1993, initial dry weights of the larvae stocked in experiment II were misplaced. For use in the calculation of specific growth rates (SGR), they were estimated from a theoretical larval dry weight distribution calculated from regressions between log-transformation of egg radius and larval dry weight obtained from the material used in experiment I (Fig. 2e–g). The resulting equations with regression coefficients for CCGM and NAC are given in Equations (1) and (2), respectively.

$$\text{Dry weight} = 0.23562 \times (\text{egg radius})^{4.04239} \qquad r = 0.9779 \quad (1)$$

$$\text{Dry weight} = 0.14969 \times (\text{egg radius})^{2.78861} \qquad r = 0.9658 \quad (2)$$

Mean dry weights of larval size distribution calculated from Equations (1) and (2) were 0.050 and 0.052 μg for CCGM and NAC, respectively (Table 3).

SGR was calculated as percent daily increments in weight from the exponential model used by Houde and Schekter (1981). In the calculation of SGR values, initial larval dry weights were corrected for mortality, assumed to be size-specific, as shown for turbot (*Scophthalmus maximus* L.) larvae (Rosenberg and Haugen, 1982). The correction was made by computation of a cumulative weight distribution for the initial dry weights of a larval group. A number of larvae, corresponding to the observed mortality, was subtracted from the lower part of the cumulative weight distribution. Mean dry weight was calculated from the remaining larvae of the cumulative weight distribution, and used to determine SGR. This procedure gives conservative SGR estimates, because it leads to the smallest possible difference between the mean larval weights used in the computation of SGR over the time period from the start to the end of an experiment.

Stock differences in wet and dry weights within single enclosures were tested using Student's t-test. Differences in survival were tested using Student's t-test after arcsine transformation (Sokal and Rohlf, 1981). Mean SGR difference between co-reared stocks was tested for significance using the paired comparisons test (Sokal and Rohlf, 1981) This test was only used for experiments of five or more enclosures. Linear regression was used to describe the relation between survival and growth, and deviation of the slope from zero was tested using Student's t-test. The significance level was 0.05 in all tests.

Results

Environmental data

Temperature increased throughout the experiments, both in 1992 and 1993 (Fig. 4). Temperatures in experiment II (1993) corresponded to the temperatures of the 1992 experiment, increasing from a level close to 7°C in the first two weeks and exceeding 12°C after five weeks. In experiment I (1993), temperatures were lower than in the other experiments, increasing from below 5°C initially to 12°C at termination.

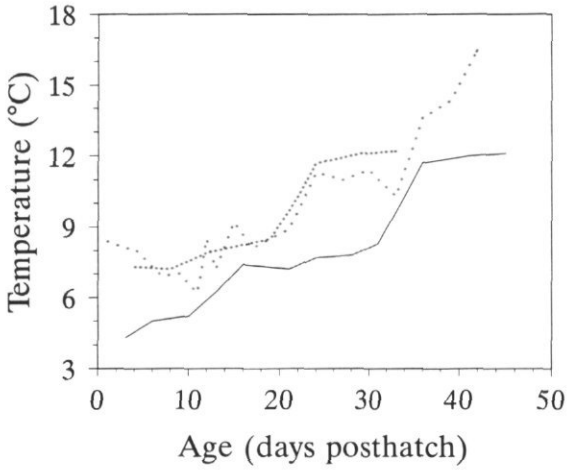


Figure 4. Temperature in the experiments. · · · · 1992; —— experiment I (1993); ····· experiment II (1993).

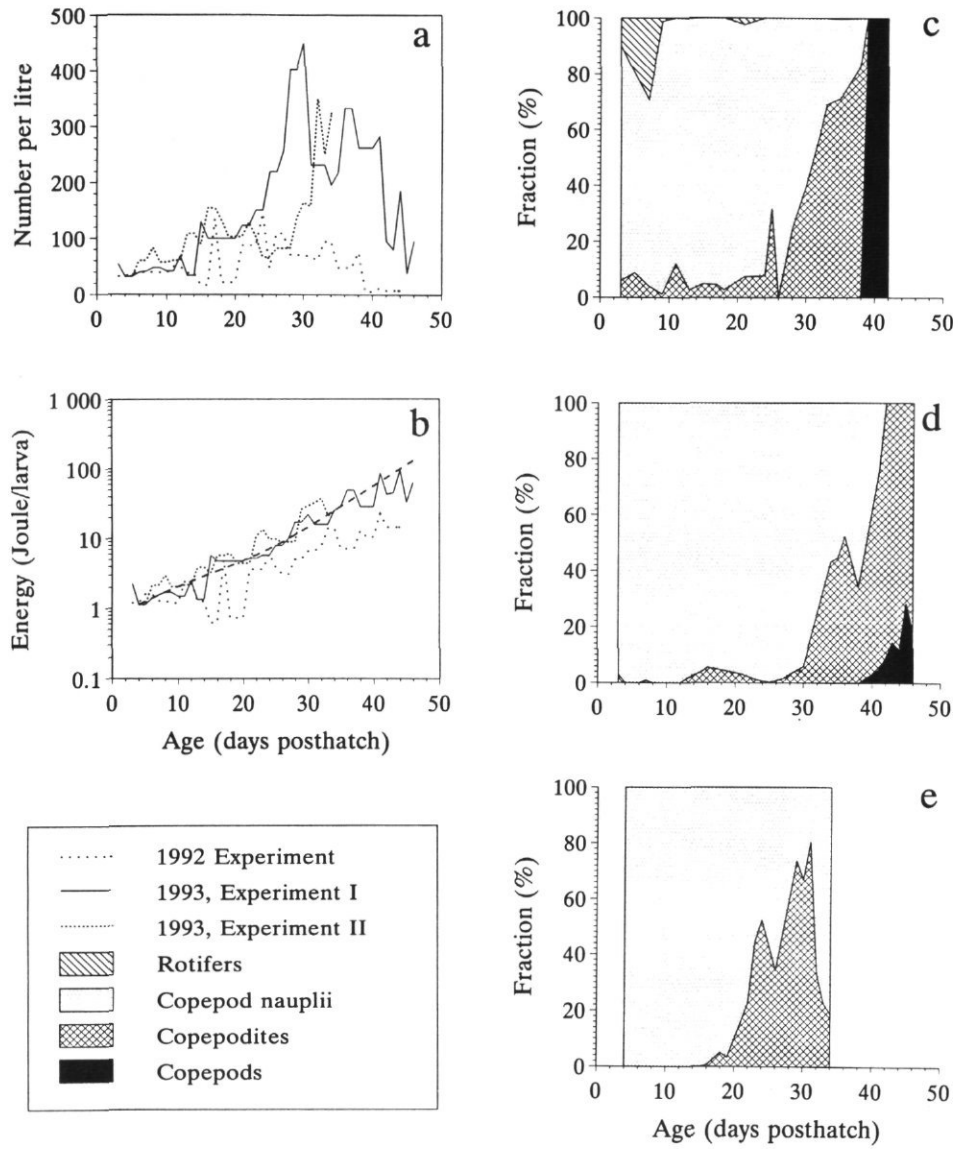


Figure 5. Feeding regime in the enclosures calculated on a daily basis. a. Relative increase in number of zooplankton per litre. b. Energy content of plankton available per larvae calculated from the initial larval numbers (---- denotes energy values corresponding to 15% weight-specific growth rate calculated from a theoretical energy model, see text), note the logarithmic ordinate. c–e. Composition of plankton given as fractions of the different plankton groups in 1992 (c), 1993 experiment I (d), and 1993 experiment II (e).

Oxygen saturation varied between 92 and 108% in 1992, and between 94 and 125% in the 1993 experiments. Salinity was between 31 and 32 in all experiments. The period of daylight increased from 15 to 20 h during the 1992 experiment. Similarly, in 1993 the daylight period increased from 13 to 19 h for experiment I, and from 15 to 19 h for experiment II.

The increase in zooplankton density in the enclosures after the addition of food (Fig. 5a) was variable, both within and between the experiments, but corresponded to the expected increase in energy ration (Fig. 5b). The available energy in relation to initial larval numbers was lower in the 1992 experiment than in the 1993 experiments. Copepod nauplii dominated the offered food early in the experiments, while copepodites became most abundant later (Fig. 5c–e).

Survival

In 1992, total larval survival in the enclosures varied between 7 and 33% at termination on day 46 post-hatch. Survival of the CCGM larvae varied between 10 and 26% (Fig. 6g). The mean survival of CCGM larvae in enclosures 1 to 6 was not significantly different from the mean survival of CCGM larvae in enclosures 7 to 12 ($p = 0.3476$). Survival of the NAC larvae was between 25 and 54%, while survival of CC larvae was from 1 to 9%. In contrast to the other larval groups, most of the CC yolk-sac larvae observed during handling prior to enclosure

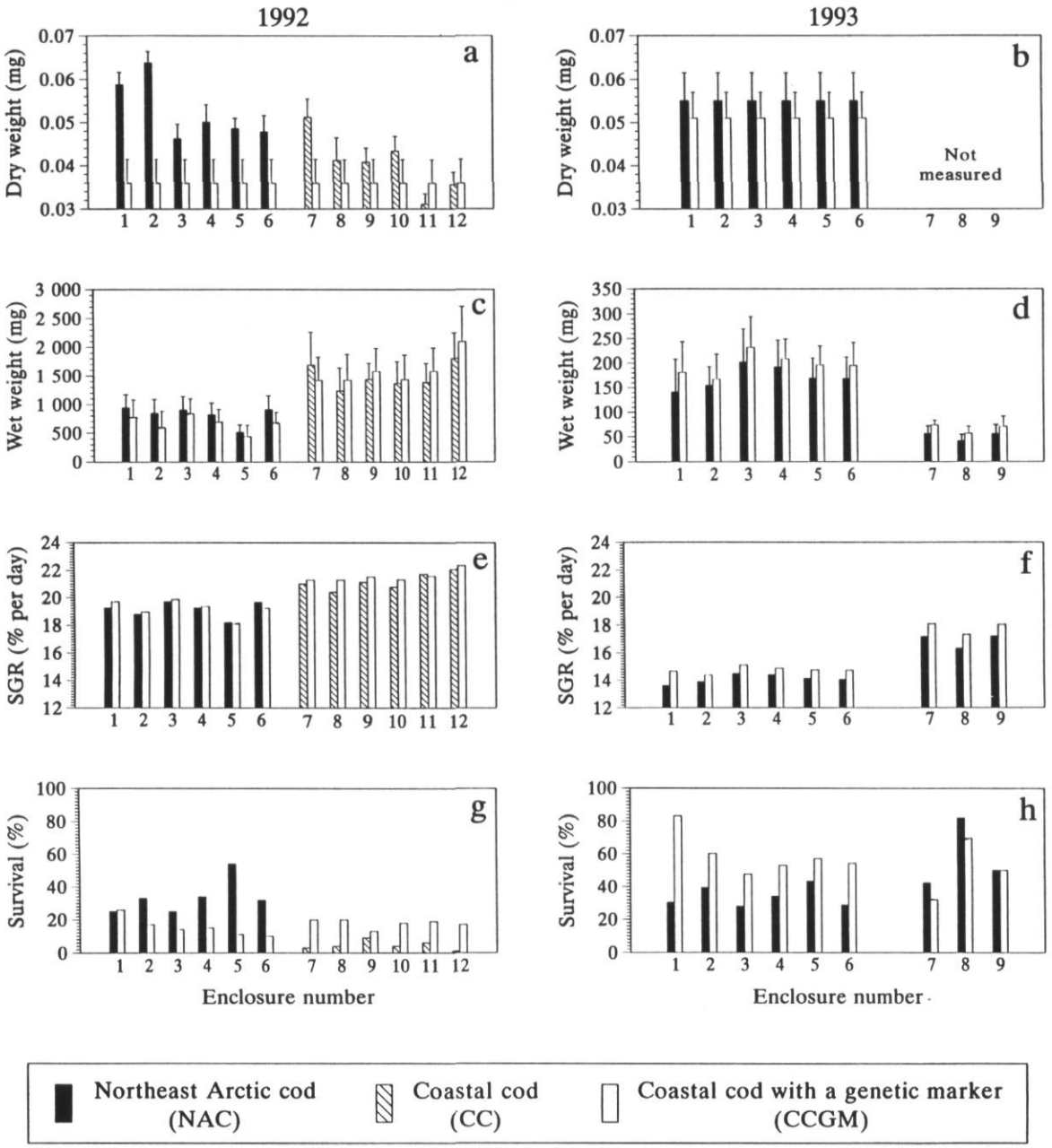


Figure 6. Larval size, growth, and survival. a–b. Initial larval dry weight of the 1992 (a) and 1993 (b) experiments. c–d. Larval wet weight at termination of the 1992 (c) and 1993 (d) experiments. e–f. Specific growth rate (SGR) in the 1992 (e) and 1993 (f) experiments. g–h. Survival in the 1992 (c) and 1993 (d) experiments. Enclosures 1–6 and 7–9 (b–d–f–h) denote experiments I and II, respectively.

stocking were slightly curled. Studies on ovarian samples from the CC and the NAC showed that the vitellogenetic oocytes in the former were 50 to 100 μm smaller than expected in relation to stage of spawning, while the latter showed normal-sized oocytes.

At termination in 1993, total larval survival was in the range of 38 to 57% (experiment I, day 48 post-hatch) and 37 to 76% (experiment II, day 36 post-hatch). Between 28 and 43% of the NAC larvae survived in experiment I, while 42 to 82% of these larvae survived in experiment II (Fig. 6h). Similarly, survival of CCGM larvae was 47 to 83% and 32 to 69% in experiments I and II, respectively. No immediate increase in mortality occurred in the control groups set up for determination of handling effect. Survival here was more than 92% at day 10 post-hatch for both experimental series in 1993.

Considering all the experiments, no trend in stock-specific survival was found (Fig. 6g–h). NAC larvae survived significantly better than the co-reared CCGM larvae in 1992 ($p = 0.0043$), while the opposite was observed in experiment I in 1993 ($p = 0.0019$). In contrast, the survival trend in experiment II (1993) was similar to that observed in 1992.

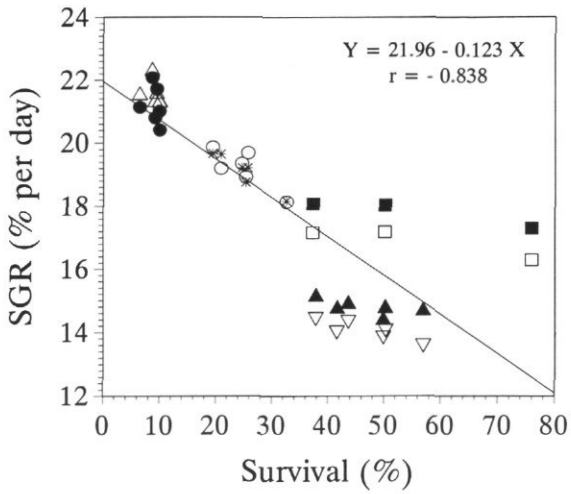


Figure 7. Relation between specific growth rate (SGR) and total survival in the enclosures. ✳ NAC 1992; ● CC 1992; ○ CCGM in enclosures 1–6, 1992; △ CCGM in enclosures 7–12, 1992; ▽ NAC in experiment I, 1993; □ NAC in experiment II, 1993; ▲ CCGM in experiment I, 1993; ■ CCGM in experiment II, 1993.

Growth

In 1992, the size of the larvae from the two different stocks in each enclosure was initially significantly different ($p < 0.000\,02$) except in enclosure number 12 (Fig. 6a). Without exception, the NAC larvae were larger than the CCGM larvae stocked in the same enclosure. At termination of the experiment (Fig. 6c) these differences were reduced, but the NAC larvae were still significantly larger ($p < 0.0027$) than the co-reared CCGM larvae in four of the six enclosures. Specific growth rates (SGR) of the different larval groups varied between 18.1 and 22.3% (Fig. 6e).

In 1993, the difference in initial larval size between NAC and CCGM was less than in the 1992 experiment (Fig. 6b), but still significant ($p = 0.000\,58$). The NAC larvae were largest, but by the end of the experiment the CCGM larvae were significantly larger ($p < 0.0103$) than the NAC larvae in seven of the nine enclosures (Fig. 6d). SGR of the different larval groups varied between 13.6 and 18.0% (Fig. 6f).

A distinct trend in stock-specific growth was found. This can be seen from SGR, which was higher among the CCGM larvae than for the co-reared NAC larvae in all enclosures both years, except for two enclosures in the 1992 experiment (Fig. 6e–f). The mean difference in SGR between NAC and co-reared CCGM larvae was significant in experiment I in 1993 ($p = 0.0005$), but not in 1992 ($p = 0.54$). Considering the experiments in both 1992 and 1993, SGR of all the larval groups negatively correlated with total larval survival in the enclosures (Fig. 7).

Discussion

Although stock-specific differences in larval survival seemed consistent within experimental series (Fig. 6g–h), no trend was observed when all the experiments were considered. However, a distinct trend in growth rate between cod larvae of different stock origin was observed. In general, SGR was better in larvae of CCGM than in NAC. This difference in SGR was consistent in most of the experiments (Fig. 6e–f). However, the lack of significance for the 1992 experiment needs some further comments: correcting the estimates of growth rate for a size-specific mortality that takes place only amongst the smallest larvae will give lower SGR values than would be the case if correction is not done. Thus, size-specific correction diminishes the differences in SGR between the NAC and CCGM, particularly because mortality was highest in the NAC groups. Assuming mortality to be completely independent of size (e.g. no correction) actually produces a significant mean difference ($p = 0.0128$) in SGR between the two cod stocks in the 1992 experiment. The real pattern of mortality most likely lies between the two extremes of being completely size-specific and size-independent.

A wide range of larval survival and growth rates in cod has been found (Laurence *et al.*, 1981; Øiestad, 1985; Pedersen *et al.*, 1989; Otterå, 1993; van der Meeren and

Næss, 1993). Some of the survival and growth rates in the present work are among the highest ever reported for cod. However, the extent to which environmental or stock-specific genetic components affect the spectrum of growth rates is not clear. In rearing trials with cod, differences in growth rates of larvae from separate stocks have been noted by Gamble and Houde (1984). Godø and Moksness (1987) concluded that differences in growth and maturation of NAC and some coastal cod stocks in nature are probably environmentally determined, and not of genetic origin. This contrasts with the results of Svåsand *et al.* (1994), who observed significantly better growth in juveniles of CCGM compared to NAC juveniles, both fish groups being left over from the 1992 experiment in the present paper. Northern anchovy (*Engraulis mordax* Girard) and herring (*Clupea harengus* L.) show regional variations in growth (Parrish *et al.*, 1985; Munk and Christensen, 1990), with the former exhibiting a substantial genetic variation among populations of the California central stock (Hedgecock *et al.*, 1989).

In a review on growth and reproduction, Gjerde (1986) summarizes the knowledge of quantitative genetic variation in commercially important salmonid species, focusing on the potential for selection based on differences in growth rate. The large variation in life history characters described for salmonid species under natural conditions (Ricker, 1972; Saunders, 1981) suggests that this could also be present for other species. So far, possible genetic influence on growth in Atlantic cod has not been investigated under controlled experimental conditions. Thus, the present experiments, where larval growth and survival of different stocks are compared in an identical environment within a single rearing unit, provide a new and more precise method of determining possible genetic components of larval population dynamics.

In the 1992 experiment, survival and growth were compared between full sib groups of the CC and NAC stocks. This approach was chosen mainly because of the large variation reported among Atlantic salmonid stocks (Nævdal *et al.*, 1978), as well as for sib groups within stocks (Gunnes and Gjedrem, 1978). In our design of the 1992 comparative study we attempted to consider the importance of variation within each stock, and therefore based the egg material on single matings. Unfortunately, the actual number of sib groups from each stock was low because of a limited number of available experimental units. The results clearly demonstrated substantial variation in growth and survival between the sib groups (Fig. 6e and g). However, the origin of this variation needs further examination.

First, the use of CCGM larvae in all the enclosures as an internal control for the rearing conditions turned out to be successful. The homogeneity of survival in CCGM larvae released in all the enclosures indicates that rearing conditions did not induce substantial variation among the enclosures. Thus, as confirmed by hydrographical data and a standardized feeding regime, possible environmental differences were minimal, and survival and growth may be compared both within and between experimental series.

Second, survival of the CC larvae was very low compared to the co-reared CCGM larvae. This may be linked to the previously mentioned abnormalities in oocyte growth found in the CC parents, as well as lack of functionality among CC larvae, indicated by their curled appearance. Although not evident, it is questionable whether the improper oocyte growth negatively affected the quality of CC eggs and larvae. Comparisons between CC and NAC sib groups may therefore not be valid and are excluded in the present work.

Finally, a clear negative correlation between growth rate and survival was found (Fig. 7). This relationship indicates density-dependent growth mechanisms. Differences in survival, together with a constant amount of food added daily, led to unequal rations being available to the larvae in different enclosures. Such dissimilarities in food access will inevitably have great impact on growth, particularly if mortality is high during the early larval stages. Also for this reason, direct comparison of growth between CC and NAC larvae is therefore not valid. Since survival was impossible to monitor during the experiments, corrections to obtain equality in larval feeding levels could not be carried out. Thus, growth between stocks may only be compared within each enclosure. However, stock differences in SGR within single enclosures are independent of survival and may therefore be compared between enclosures. In summary, density-dependent factors, which mask a possible genetic component as source of variation, probably caused a considerable part of the variation in growth between the sib groups.

As mentioned above, the egg quality based on stripping and artificial fertilization seemed to vary both within and between the two main cod stocks compared. Screening of potential spawners which were as similar as possible regarding size, age at first maturation, spawning time, and spawning state proved to be an enormous task in practical work. In addition, the quality of larvae hatched from eggs produced by natural spawning was often judged to be better than those obtained from stripping. The effect of timing between stripping and ovulation cycle on egg quality is well documented for batch spawners (McEvoy, 1984; Kjørsvik *et al.*, 1990). For the above reasons, the experimental design was changed in the 1993 study. The parental fish from the two stocks were both kept under farming conditions and had their spawning period and peak at the same time. Further, size of eggs and hence yolk-sac larvae, were

chosen as alike as possible. Thus, in 1993 the larval groups stocked in different enclosures for a given spawning time were replicates, and not different sib groups as in the 1992 experiment.

The consistencies in the superior growth rate of the CCGM larvae in the 1993 experiments, together with a similar trend in the 1992 experiment, led to the conclusion that larvae of the coastal cod stock show better growth capabilities under the biological and physical environment provided in the experiments at Austevoll. Food availability affects growth rates in fish larvae to a much greater extent than the SGR differences found in the present experiments (van der Meeren and Næss, 1993). Within single enclosures, larvae of each cod stock should have equal access to the food. Thus, the superior growth capacity of CCGM compared to NAC may reflect stock-specific differentiation in abilities to convert the given food resource of free-swimming planktonic animals to somatic tissue deposition under the given environmental conditions and feeding regimes. This includes all behavioural and biochemical steps from food detection, selection, ingestion, and digestion, to the share of the absorbed energy between metabolism and growth. The observed difference in growth capacity probably has its explanation in genetic adaptations to specific biological and physical environments, which may differ considerably between the natural habitat of the two cod stocks in question.

One of the most pronounced differentiating factors is light, which is a 24-h daylight/twilight cycle for NAC larvae in the Lofoten area (Suthers and Sundby, 1993), while cod larvae at the west coast of Norway experience much shorter periods of light. Feeding in cod larvae is strongly connected with light (Ellertsen *et al.*, 1980), and in the North Sea they show a diurnal feeding pattern, with distinct day and night cycles (Last, 1978). In contrast, at the latitude of Lofoten, cod larvae feed during a much longer period of the day (Pedersen *et al.*, 1989). Latitudinal dissimilarities in other environmental parameters truly exist. In the Lofoten area, cod larvae experience the lowest temperature of the two stocks in question, although this is partly compensated for by a shift in time of spawning. Differences in predator and feeding regimes most likely occur. The extent to which some or all of these dissimilarities may have selected specific behavioural or physiological patterns in the two cod stocks is unknown. The present results indicate that such stock-specific patterns exist, and are manifested through differences in growth capabilities.

The potentials for using genetic tagging have previously been discussed (Allendorf and Utter, 1979; Shaklee, 1983; Garrett and Seeb, 1990; Utter and Seeb, 1990). In the case of Atlantic cod, the development of a genetically tagged broodstock (Jørstad *et al.*, 1991) has permitted experimental studies, especially on early life stages (Svåsand *et al.*, 1991; Blom *et al.*, 1993), where alternative taggings are difficult or impossible. The original proposal of Blom (1991) to use genetically tagged cod as an internal control in comparative studies permits comparison of different groups of cod larvae under identical conditions. These ideas have successfully been implemented in this work, and should be extended further in the future. However, the comparison between larvae from the two stocks was carried out under "coastal cod conditions", and the superior growth of CCGM may represent a better adaptation to these conditions. Future experiments should incorporate different environmental conditions, such as those found in the natural habitat of NAC larvae, as well as investigations on several other cod stocks.

Acknowledgments

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Impact of physical environment on the behaviour of cod larvae

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Skiftesvik, A. B. 1994. Impact of physical environment on the behaviour of cod larvae. – ICES mar. Sci. Symp., 198: 646–653.

The behavioural development of unfed cod larvae from hatching until death due to starvation and the behaviour of fed cod larvae beyond metamorphosis were studied by means of a PC-aided video system. The development of activity, mean swimming speed, and swimming speed in active periods were found to be closely related to the different stages of morphological development. Cod larvae kept in a natural light regime showed a diel rhythm in activity. Experiments with cod larvae kept at different levels of light intensity from hatching to death by starvation showed that light level strongly influenced both the spatial distribution and the longevity of larvae.

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Introduction

Morphological and behavioural development of larvae are, to a large extent, adaptations to the habitat they occupy. The habitat preference of fish larvae is a compromise between risk of starvation and risk of predation (Aksnes and Giske, 1990). Vertical migration can be understood as a diel habitat shift resulting from changes in both the costs (predation risk) and benefits (food availability) (Dill, 1987).

In Lofoten waters, the majority of first-feeding cod larvae are distributed in the upper 30 m (Ellertsen *et al.*, 1990), and their maximum concentration has been found between 10 and 25 m depth (Gjøseter and Tilseth, 1982). Ellertsen *et al.* (1984) found that cod larvae carry out diel vertical migration during calm weather conditions.

In order to respond to changes in the risk of predation, an animal needs to collect information regarding the risk. If, however, such information is prohibitively costly to obtain (e.g., entails a high probability of being preyed on), evolution will favour fixed behaviours (Sih, 1987). Given the sighting distance of a half to one body length (Solberg and Tilseth, 1984), we can assume that fish larvae in early stages will not obtain information about the predator density. They will thus react in a fixed manner towards factors that can change the relations between themselves and their predators. Light is the physical factor generally believed to be of greatest importance in the determination of behaviour and spatial distribution of fish larvae with respect to prey and predators (Woodhead, 1966; Blaxter, 1975; Batty, 1987).

The objectives of this study are to describe the behavioural development of starved and fed cod larvae, and to show how the diel change in light intensity influences the activity of the larvae. The results are discussed with a view to observations from the natural environment.

Materials and methods

For all experiments naturally spawned eggs from the cod broodstock at Austevoll Aquaculture Research Station were collected (according to Huse and Jensen, 1983) and incubated in 250-l incubators at temperatures between 3 and 5°C. Day 0 was defined as the point at which 50% hatching had occurred.

Experiment 1: Behavioural development

The eggs were transferred to 70-l observation chambers one day prior to estimated hatching. One group of 1500 larvae was starved and died out by day 15. The other group of 1500 fed larvae was studied to day 68. At that time, cannibalism had made an impact on mortality, but 98 larvae were still alive when the experiment was terminated.

The fed group of larvae was given cultivated rotifers (*Brachionus plicatilis*) and *Tisbe* sp. nauplii during days 4–35 and zooplankton collected from the sea thereafter. The temperature was maintained at 5°C and at salinity 34. Approximately 15% of the water was renewed daily. The light intensity was 300 lux at the surface.

Two categories of behaviour were defined: swimming and resting. Activity was defined as the percentage of

time spent swimming during the total observation time. Swimming speed during activity periods was defined as the average speed from commencement of activity to its cessation and was measured in millimetres per second. Measurements were obtained from 10 randomly chosen larvae during each observation period.

Behavioural studies were conducted using a computer-aided video system, allowing three-dimensional measurement of the position of the larvae in 70-l observation chambers (for a more detailed description, see Huse and Skiftesvik, 1985, 1990). Each of 10 randomly chosen larvae was tracked for 5 min and their position and behaviour logged each second.

Experiment 2: Mortality and distribution in relation to light intensity

In experiment 2, 400 larvae were transferred to each of the two parallels kept at the following levels of light intensity: 1250 lux, 250 lux, 2.5 lux, and darkness. The larvae were transferred to the 10-l experimental units at day 1 after hatching. Dead larvae were siphoned out and counted every day throughout the experiment. The larvae were not fed. The temperature was between 4.5 and 5°C, and the salinity was 34.

Experiment 3: Growth in relation to light intensity

In experiment 3, 400 larvae were transferred to each of the five parallels kept at the following levels of light intensity: 1000 lux, 100 lux, 10 lux, and darkness. The larvae were transferred to the 10-l experimental units at day 1 after hatching. The temperature was about 5°C, and the salinity was 34. The larvae were not fed. At days 3, 6, 9, 11, 13, 16, 18, and 20, or to the time when the group died, 24 randomly chosen larvae from each group were sampled for morphometric measurements. Notochord length and myotomal height were measured on live larvae, and thereafter the larvae were washed in distilled water and frozen. After being freeze-dried, the total larval dry weight was measured on a Metler M 3 electrobalance.

Experiment 4: Measuring the larval activity through day and night

In this experiment, 25 larvae were transferred at day 1 to a 100 ml unit with seawater of salinity 34 for activity registration by use of linear array ultrasonographic equipment. The equipment presents the echoes reflected from larvae at a 1 mm wide cross-section. Activity was defined as the number of larvae penetrating the cross-section per unit time. The 100 ml unit was held in a water bath with running water of 8.5°C (Fig. 1). The water bath was placed outdoors in the shade, and the weather was cloudy during the experiment. The light intensity did not exceed 2000 lux. Registration of larval activity lasted 5 days and started at day 2. The larvae were not fed, and no larvae died during the experimental period. The experiment was carried out at the Austevoll Aquaculture Research Station, which is situated at 60°6′N 5°14′E, during the period 10–14 April 1992.

Results

Behavioural development

Activity was below 10% in the first three days after hatching, but rose to above 30% on day 4 in the fed group when the prey was introduced (Fig. 2A, B). The unfed group rose to about 30% on days 6–7. Thereafter, the activity decreased gradually to approximately 2% on day 14, the day before mass mortality (Fig. 2B). The fed group showed an increase in activity to a level of about

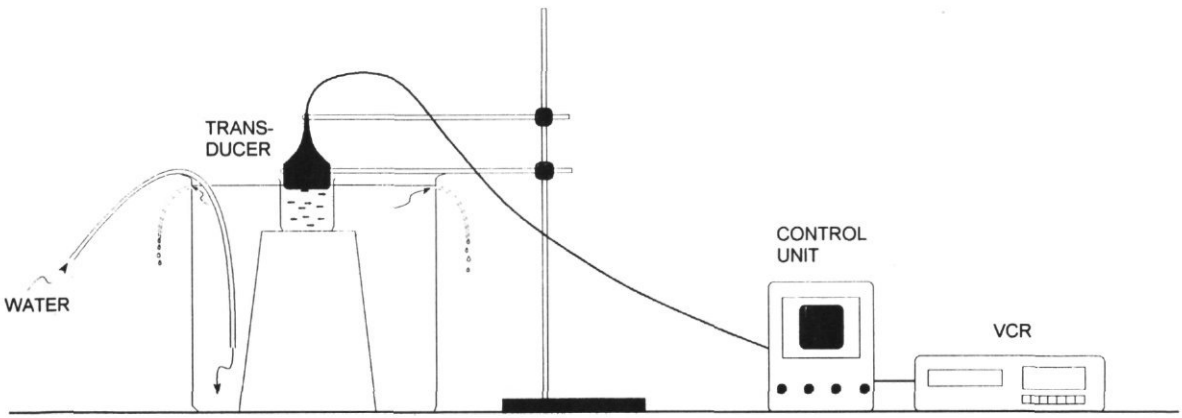


Figure 1. Layout of the experiment system used in Experiment 4 for ultrasonographic registration of larval activity.

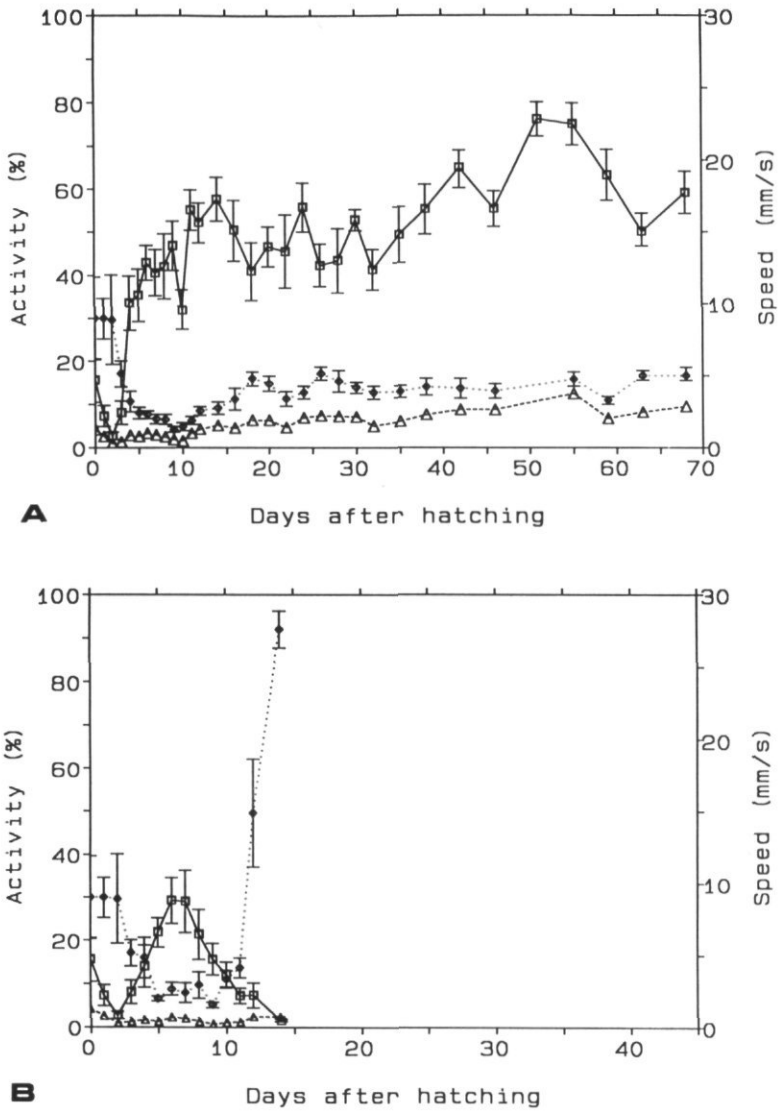


Figure 2. A. Development of activity measured as the percentage of time the larvae were swimming (solid line), swimming speed in active periods (dotted line), and mean swimming speed (dashed line) of fed cod larvae. Each point is the mean and standard error of 10 larvae. B. Development of activity measured as the percentage of time the larvae were swimming (solid line), swimming speed in active periods (dotted line), and mean swimming speed (dashed line) of starved cod larvae. Each point is the mean and standard error of 10 larvae.

40%, and remained at this level until day 35, with a slight increase thereafter (Fig. 2A).

Swimming speed during the active periods decreased from about 9 mm s^{-1} during the first few days to about 5 mm s^{-1} on day 4 (Fig. 2A, B). In the fed group, swimming speed during the active periods decreased further, and was steady at around 2 mm s^{-1} until day 11. After day 11, swimming speed during active periods increased gradually to just below 5 mm s^{-1}, and remained there for the rest of the experimental period. In the unfed group, swimming speed during the active period increased to more than 25 mm s^{-1} at day 14. The mean swimming speed (swimming distance $\times$ time^{-1}) showed a gradual increase throughout the experimental period (Fig. 2A, B).

Based on the observations made, there was no indication that actively swimming cod reacted to prey. They reacted to prey items when they had a stop in their active swimming, sometimes even while occasionally still moving. When a prey item was located, and the prey was in the right position, the cod larvae could suck it into the mouth. If the prey was in an unfavourable position, the cod larva could manoeuvre itself to another position in relation to the prey.

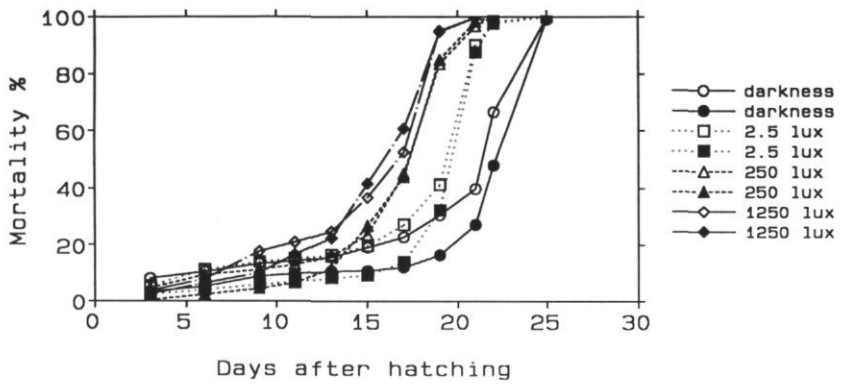


Figure 3. Mortality (%) of cod larvae in relation to light intensity during incubation.

Effect of light intensity on longevity of starving cod

Mortality rate of cod at different levels of light intensity

Mortality was low throughout the first two weeks, but increased thereafter (Fig. 3). It rose first in the groups exposed to the highest level of light, followed by the 250 lux groups, the 2.5 lux groups, and, finally, the darkness groups.

Larval distribution in different levels of light intensity

Larvae from different light intensity groups did not show similar vertical distribution. An increase in light intensity caused the larvae to move down in the water column, as they were observed at the bottom (Fig. 4). The number of larvae in the water column and the length of time they were spread in the water were dependent on the light intensity.

Growth at different levels of light intensity

Length varied significantly in accordance with treatment, with the exception of day 6 (ANOVA one-way, $p < 0.05$). The larvae kept in darkness were longer than the others. Development of larval length of unfed larvae kept at different levels of light intensity is shown in Figure 5A. At day 3, the larvae from the darkness group were significantly longer than those kept at 10 and 1000 lux, and the larvae of the 100 lux group were significantly longer than those at 1000 lux. There were no differences between the groups at day 6. At day 9, larvae in the 100 lux group were shorter than those kept at 10 lux and darkness. At day 11 there was only one significant difference, between 100 lux and darkness. At day 13, larvae from the darkness group were significantly longer than the groups kept at 10 and 100 lux. Three days later, the larvae of the darkness group were significantly longer than those of all other groups, and the 100 lux

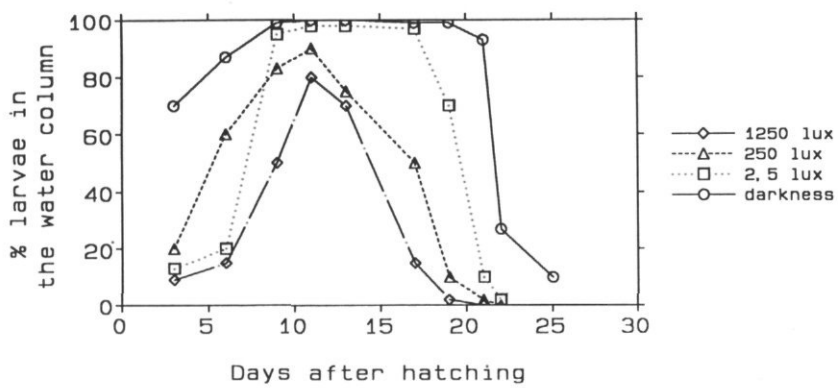


Figure 4. Percentage of cod larvae in the water column in relation to light intensity during incubation.

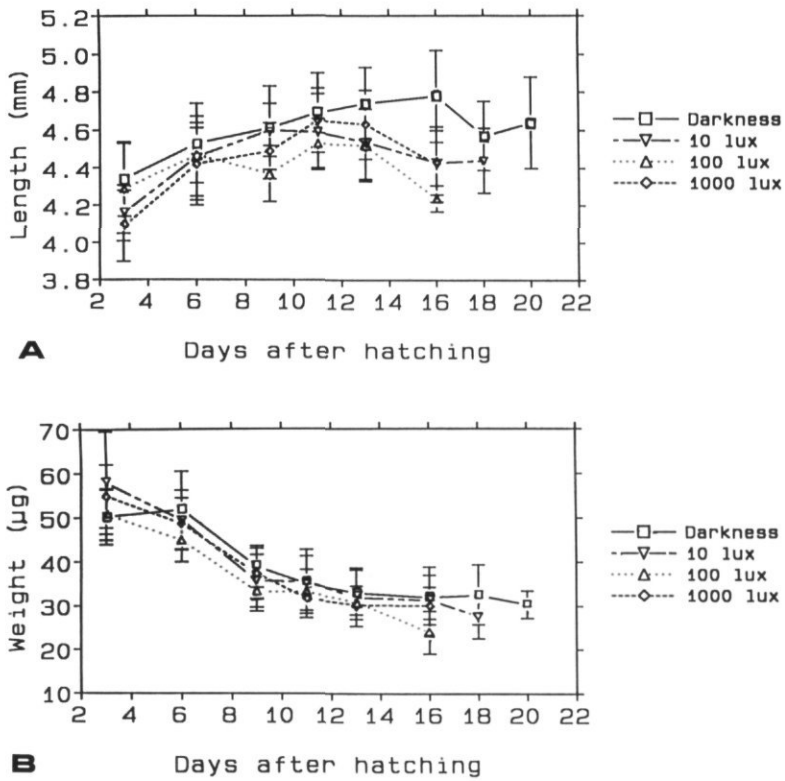


Figure 5. A. Body length of unfed cod larvae in relation to light intensity during incubation. B. Dry weight of unfed cod larvae in relation to light intensity during incubation.

group was significantly shorter than the others. The 100 and 1000 lux groups died before the next measure. At day 18, the darkness group was still longer than the 10 lux group. At day 20, only the darkness group was alive.

Myotomal height varied significantly in accordance with treatment, with the exception of day 9 (ANOVA one-way, $p < 0.05$). At day 3, the larvae of the darkness group were significantly higher than those of the group 1000 lux, and also higher than the 100 lux group at day 6. No differences between groups were found at day 9. Larvae from the darkness group were significantly higher than those from the 100 lux group at days 11 and 13. At day 16, the larvae of the darkness group were significantly higher than those of all the other groups.

Dry weight of the larvae varied significantly in accordance with treatment, with the exception of days 11 and 13 (ANOVA one-way, $p < 0.05$). The larval dry weight is shown in Figure 5B. At day 3, larvae from the 10 lux group had a significantly higher weight than those kept in darkness. The larvae in the darkness group were significantly heavier than those in the 100 lux group at days 6 and 9. No differences were found between the groups at days 11 and 13. At day 16, the larvae from the 100 lux group had a significantly lower weight than larvae from the other groups.

Diel activity of cod larvae

The larvae did not respond to changes in light intensity in the first few days after hatching. From day 3, they had more activity at day than at night (Fig. 6).

Discussion

The development of larval activity, swimming speed, and thereby swimming distance are determined in nature through a selection process and reflect the demand of the larva for food and the requirement of protection against predators. Starvation and predation are the main agents of larval mortality in nature (Hunter, 1976). A laboratory situation may be different in many respects from the natural environment. However, behavioural studies indicate that behaviour in early larval stages is a set of fixed responses triggered by given factors. In addition, to survey the environment for predators would be difficult for a larva with a visual distance of only about 5 mm.

Changes in the behaviour of the larvae may also indicate a change in their demands. The change of swimming mode found at time of start-feeding (Skiftesvik, 1992), as can also be seen in Figure 2, reflects the

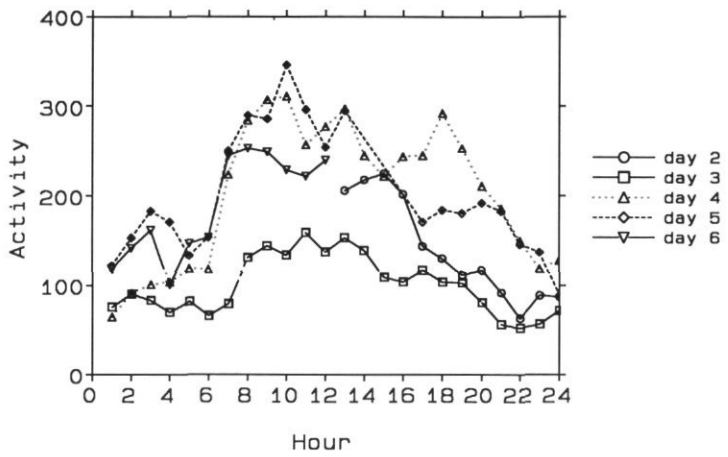


Figure 6. Diurnal activity of cod larvae on days 2–6 after hatching. Activity is measured as the number of times larvae were swimming through an ultrasonic plane.

need for exogenous food. When the larvae start to look for prey, they decrease swimming speed and increase activity. An increase in activity presumably renders the larvae more visible to predators. Moving prey can be detected more easily than motionless prey (Kislalioglu and Gibson, 1976). In studies cited by Sih (1987), reduced activity was a typical antipredator response. Therefore, when the larvae start to search for food, they expose themselves to greater risk of predation.

When cod larvae are ready to start-feed, they increase activity and decrease swimming speed. If they do not find any prey, they reduce their activity. Reduced swimming activity of unfed cod larvae was also found by Ellertsen *et al.* (1980). Low activity implies reduced consumption of energy; thus, reduced activity may delay the point-of-no-return. The change in neutral buoyancy of cod larvae was registered by Ellertsen *et al.* (1980), and the period when the cod larvae were heaviest corresponds with the time the unfed cod larvae reduce their activity. It may be that starving larvae will separate from the fed ones in their natural environment.

Like most marine fish larvae, cod larvae are visual feeders (Ellertsen *et al.*, 1980) and active feeding occurs only above a certain light intensity (Blaxter, 1966). The visual abilities of fishes varies interspecifically (Nicol, 1989) and during development (Blaxter, 1986). Ellertsen *et al.* (1976, 1980) found that cod larvae were able to capture *Artemia salina* nauplii at 0.4 lux, but not at 0.1 lux. So the cod larvae in experiments 2 and 3 would be able to feed in all the light intensities used except darkness. Registration of light intensity from the surface to 40 m depth during 24 h in May in Lofoten was carried out by Gjøsæter and Tilseth (1982). Light intensities below 0.4 lux were observed only at night and only in the deepest part of the registration area. However, a reduced feeding intensity at night is reported by Tilseth and Ellertsen (1984).

The level of light intensity influences larval activity, and can also influence their distribution in the water. In Lofoten, Ellertsen *et al.* (1984) found that cod larvae show diel migration only during calm conditions. When they migrated vertically, they were in the lower part of their distribution field during the day and in the upper part at night, as is the case with many other vertically migrating aquatic organisms (Clark and Levy, 1988). The larvae kept in darkness in experiment 2 were, for most of the experimental period, distributed throughout the water column. In the other groups, the larvae within the water column were fewer, and they were there for a shorter period of the experiment. The number of freely swimming larvae in the water column decreased with increasing light level. As reported by Ellertsen *et al.* (1980), this observation indicates a negative phototaxis.

Larvae kept at different levels of light intensity had different body shapes. Those kept in darkness were significantly longer than those of the other groups and they were also among the highest. Dry weight, however, was not different from the others after day 11, except from the 100 lux group at day 16. It can be assumed that increased swimming activity will give the larvae more muscles and thereby a broader body shape. Zeutzius and Rahmann (1984) found that dark-reared larvae of Tilapia had a different body shape from the control fish; they had an increased body depth.

The shortening of lifetime of the larvae with increased light intensities in experiments 2 and 3 indicates a higher energy consumption when light intensity increases. On the basis of the results from experiment 4, diel activity of the larvae, the shorter lifetime of the larvae in light conditions is probably a result of increased activity. This

concurs with the higher oxygen consumption shown for larvae kept in light compared with those kept in darkness (Solberg and Tilseth, 1984).

Zooplanktivorous fish larvae are either "ambush" (sit-and-wait) or "cruise" (active) searchers; sometimes they use a saltatory search (SS) strategy (Browman and O'Brien, 1992). Cod larvae seem to have a saltatory search style. Their swimming mode was the same as described for white crappie, *Pomoxis annularis* (Browman and O'Brien, 1992). When swimming, cod larvae do not show any response towards zooplankton. They only react towards prey between swimming periods.

An active or passive movement of zooplankton will be of great importance for the larva's contact with prey, and thereby its food supply. In nature, zooplankton and cod larvae will move with small-scale turbulence (Sundby and Fossum, 1990), independent of their vertical migrations and other active swimming. In turbulent conditions, the evolved predator defence of the zooplankton and the cod larvae may be reduced. It is possible that the zooplankton move passively within the field of perception of the cod larva, and are detected by the cod as a moving prey. Feeding experiments carried out in laboratories with cod larvae, without the effect of small-scale turbulence, may have overestimated the prey concentration needed for cod larvae in nature.

An obvious change in swimming speed between fed and unfed larvae came after day 10, a period near the point-of-no-return (Ellertsen *et al.*, 1980). After this point the unfed larvae would die, even if they were offered food. Thus, no selection has worked on the larval behaviour after the point-of-no-return.

In conclusion, the behaviour of cod larvae is related to stage of morphological development. The larvae respond in a fixed manner to changes in light.

Acknowledgments

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ICES mar. Sci. Symp., 198: 654–665. 1994

Stage-dependent density of cod eggs and larvae (*Gadus morhua* L.) in Newfoundland waters

John T. Anderson and Brad deYoung

Anderson, J. T., and deYoung, B. 1994. Stage-dependent density of cod eggs and larvae (*Gadus morhua* L.) in Newfoundland waters. – ICES mar. Sci. Symp., 198: 654–665.

Density of cod eggs and larvae was determined in the laboratory using a density gradient column. Fertilized eggs were obtained from captive cod as well as artificially fertilized eggs from cod captured on the Grand Banks. Egg density was observed: (1) to decrease with increasing age; (2) to increase as a function of poor egg condition; (3) to depend on the environment in which the cod spawned. Eggs in good condition decreased in density at a rate of -0.19 to -0.23 kg m^{-3} d^{-1} from fertilization through to hatch. This rate of change was not significantly different from that estimated for cod eggs and larvae sampled in the field, for which the decrease in density was -0.18 kg m^{-3} d^{-1} for early stage eggs through to small larvae. Cod eggs that were in poor condition increased in density at a rate of $+0.07$ kg m^{-3} d^{-1} from fertilization to 9 days of age, at which point all eggs died. The density of dead eggs was $\gg 1033.9$ kg m^{-3}. The initial density of eggs for captive cod raised in tanks in relatively low salinity surface water was significantly lower than for cod eggs obtained from Grand Banks cod captured in relatively high salinity water at 380 m depth. Initial density measured in the laboratory from Grand Banks cod was not significantly different from that measured for eggs sampled in the field. Increasing egg density resulting from poor water conditions is expected to have a significant effect on cod egg buoyancy.

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Introduction

Cod on the Newfoundland Shelf are reported to spawn primarily along the slope at depths >250 m in waters ≥3°C (Templeman, 1981; Lear and Wells, 1984). Once spawned these eggs are thought to rise rapidly to surface waters, where they develop slowly at cold water temperatures (<0°C) and, therefore, are carried considerable distances by the strong Labrador Current (Templeman, 1981; Lear and Green, 1984). Recent modelling of the drift of cod eggs spawned on the Labrador and Newfoundland shelves assumed eggs occur instantaneously in surface waters and are then carried downstream (Helbig *et al.*, 1992). The modelled distribution of these eggs was a simple function of where the eggs were spawned on the shelf and the advective flow of the Labrador Current.

Studies considering the drift of fish eggs and larvae must incorporate their vertical distribution in relation to currents (Sundby, 1991). Previous modelling studies demonstrated that the vertical distributions of cod eggs is dependent primarily on egg buoyancy ($\Delta\rho = \rho_w - \rho_e$) and vertical eddy diffusivity (Sundby, 1983, 1991; Westgård, 1989). A deeper distribution in the water column is expected to have a significant effect on the drift of fish eggs (Page *et al.*, 1989).

Previous measurements indicated that density of cod eggs increased during development for both Norwegian coastal cod (Sundnes *et al.*, 1965; Mangor-Jensen, 1987) and Baltic cod (Nissling and Westin, 1987). Norwegian cod eggs were initially positively buoyant (Solemdal and Sundby, 1981) and are assumed to remain so during their development (Sundby, 1991). Kjesbu *et al.* (1992) reported a wider range of cod egg densities, such that heavy eggs were deep in the water column while lighter eggs were distributed near the surface.

The purpose of this study was to measure the density of cod eggs and larvae for the Newfoundland region and to compare these measurements with observations from the field. Parameterizing changes in density of cod eggs as they develop is a necessary step towards the development of models describing vertical distributions during

egg and larval development and eventual incorporation into circulation models that will describe the drift of cod eggs spawned over the Newfoundland Shelf.

Materials and methods

Different batches of cod eggs were obtained from captive cod held in tanks at the Marine Sciences Center, Memorial University. These cod averaged 47.2 cm in length for males and 45.2 cm for females. Eggs were obtained at the start of their spawning period each spring 1991 and 1992. The adult cod were held in natural sea water pumped from the surface layer. Fertilized eggs were removed from these holding tanks to incubation tanks at the Northwest Atlantic Fisheries Center, where they were kept at 3°C throughout development to the yolk-sac larval stage. Fertilized cod eggs were also obtained from cod captured at approximately 380 m depth on the Grand Banks in 1992 (Fig. 1). Eggs from one female (51 cm length, 6 years) were stripped and fertilized with sperm from one male (65 cm length, 7 years). These eggs were held at approximately 3°C and returned to the laboratory where they were incubated under the same conditions as the eggs obtained from the captive cod. In 1992, water in the incubation tank initially was allowed to stagnate until there was total mortality of the eggs. Otherwise, a minimum of 50% of the water in the incubation tank was exchanged daily with fresh sea water to maintain favourable water conditions during development.

Measurements of cod egg densities were made in a density gradient column (Martin Instruments Ltd.) as described by Coombs (1981). Throughout this article our reference to egg density refers to mass per unit volume (kg m^{-3}). The column is a 5 × 80 cm graduated cylinder which sits inside a temperature bath. The densities of the two stock solutions used to create the density gradient were 1014.3 and 1033.9 kg m^{-3} each year, made

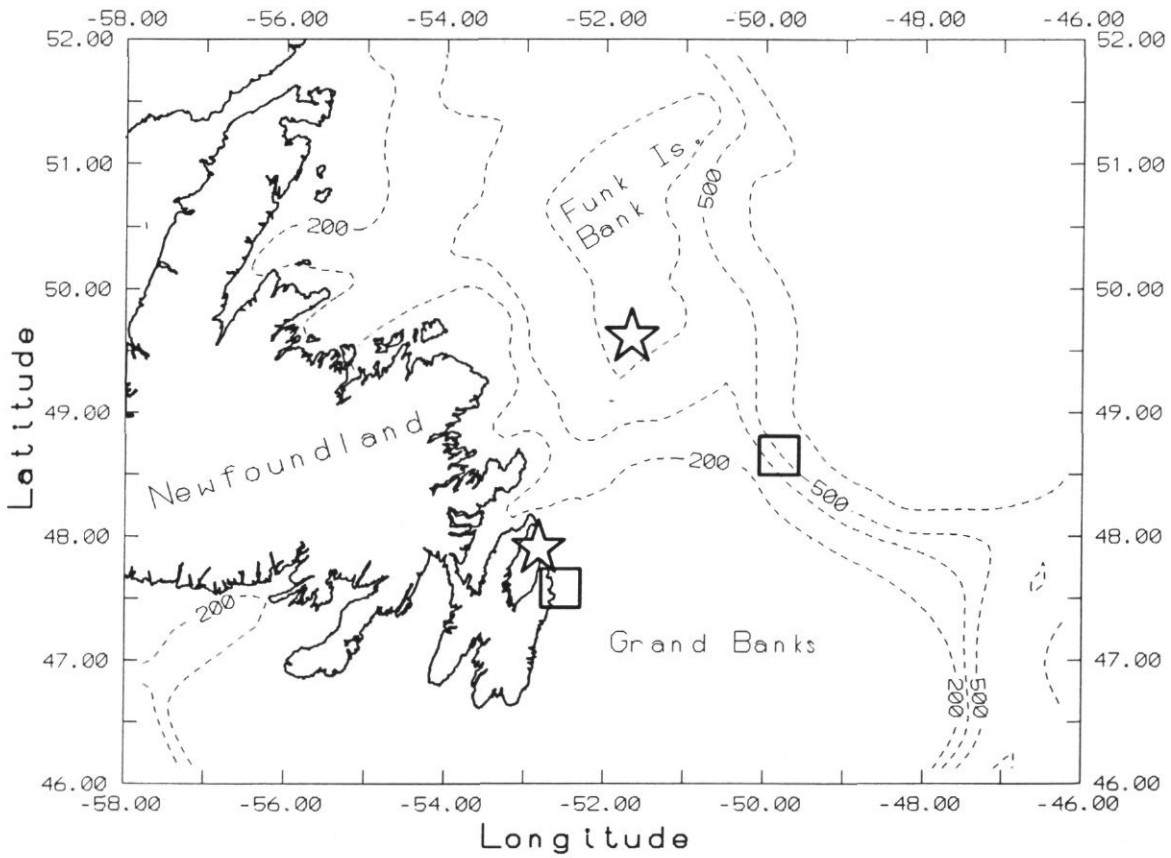


Figure 1. Newfoundland Shelf and Grand Banks indicating areas in which samples were collected. The stars indicate the field sampling locations on the inner and outer shelf, while the squares indicate the areas in which cod eggs were obtained for laboratory measurements from inshore and offshore areas.

from NaCl. In 1991 the temperature bath of the column was 8–9°C. In this case, eggs were placed in a small beaker of water at room temperature and allowed to acclimate slowly to 8°C, at which point they were introduced to the density gradient column. In 1992 the temperature bath in the column was held at 3°C, and eggs were introduced directly into the column. Measurements were made periodically, beginning at days 0–4 after fertilization through to late development just prior to hatch.

Individual eggs were pipetted from the holding tank, staged under a microscope, and then gently introduced into the column at the top. The eggs were measured frequently (at 1-min and then at 2-min intervals) during their initial descent and then less frequently as they decelerated towards a zero change in position (5–20-min periods). Each egg was monitored for a minimum of 1 h, or until it dropped from the column. The density of each egg was read at the point where it decelerated to zero, or to a minimal change in position. Some eggs and larvae dropped through the column without decelerating, in which case it was not possible to measure density. No larvae were measured in the density gradient column during these experiments.

In 1991 cod eggs were maintained in good condition throughout their development until the late stage of development just before hatch (batch A). In 1992 the cod eggs were initially allowed to develop in an incubation tank in which the water was allowed to stagnate through to total mortality of the cod eggs (batch B). This tank was then re-stocked from the original egg source and water quality was maintained through to hatch (batch C). Cod eggs fertilized at sea from adults were maintained in favourable water conditions through their development (batch D).

Questions have been raised regarding the ability of fish eggs to adjust their density quickly in relation to the ambient conditions (Coombs *et al.*, 1985). Therefore, the validity of measuring density for an egg descending through a density gradient has been questioned. To test the validity of our measurements of egg density, the point at which the egg velocity decreased to zero, we compared egg velocity profiles with that predicted for an inert sphere of equal diameter. To validate the theoretical predictions, we measured the descent profiles of small diameter (6.0–6.9 mm) glass beads of known density. The beads were washed in a mild solution of HCl, rinsed in deionized water and then carefully placed just below the surface of the column, using forceps. The descent profiles of both cod eggs and the glass beads were fit to theoretical models of descent versus time for an inert sphere.

Sampling to determine the vertical distributions of cod eggs and larvae on the northeast Newfoundland Shelf was carried out during late June and early July 1991 (Fig. 1). At each site, repeated tows were made every 3 h using a multiple opening and closing sampling system. On the inner shelf, sampling was conducted over a 48-h period and on the outer shelf over a 24-h period. This sampler is similar in design and operation to the BIONESS (Sameoto *et al.*, 1977). The sampler consists of nine 0.333 mm mesh nets 0.25 m^2, which were controlled in real time from the ship. The sampler was fitted with a variety of sensors which allowed precise sampling close to the bottom as well as throughout the water column in relation to the physical structure and plankton biomass. Samples collected at sea were initially examined for cod eggs and attempts made to measure their density in the density gradient column. This proved to be unsuccessful due to the low numbers of cod eggs encountered and the fact that most eggs put in the column passed through and did not settle. Plankton samples were preserved in 5% buffered formalin and processed in the laboratory. Eggs were classified following the four stage criteria outlined by Markle and Frost (1985) while yolk-sac larvae were designated as stage V. Early cod eggs cannot be distinguished from haddock (*Melanogrammus aeglefinus*) or witch flounder (*Glyptocephalus cynoglossus*) eggs (Fahey, 1983). However, haddock do not occur on the northeast Newfoundland Shelf and witch larvae were not encountered in our samples. Therefore, we assume that all cod–haddock–witch eggs were cod. Centre of mass distributions for each stage as a function of either depth in the water column (m) or water density (kg m^{-3}) were estimated by $D = \Sigma_{i=1}^{n} (p_i d_i)$, where D is the centre of mass, p_i is the proportion of eggs/larvae sampled in the i^{th} stratum and d_i was either the depth of the i^{th} stratum or the water density (σ_t) of the i^{th} stratum.

Regressions summarizing mean changes in density with age/stage were carried out using least-squares regression techniques (SAS, 1988). When comparing regressions, the residual variances were tested for homogeneity (Sokal and Rohlf, 1969). When they were unequal the data were weighted by the reciprocal of the mean square error before analysis of covariance. In this way the mean and slope remain unchanged and the weighted least-squares estimates are the best linear unbiased estimates (SAS, 1988). Regression slopes were tested for differences in the rate of change in density with age/stage (H_0:$b_1 = b_2$) and if H_0 was accepted then the intercepts were tested for differences in density (H_0:$a_1 = a_2$) using analysis of covariance.

Results

Descent profiles

Cod eggs followed five different trajectories in the density gradient column. In the first instance cod eggs

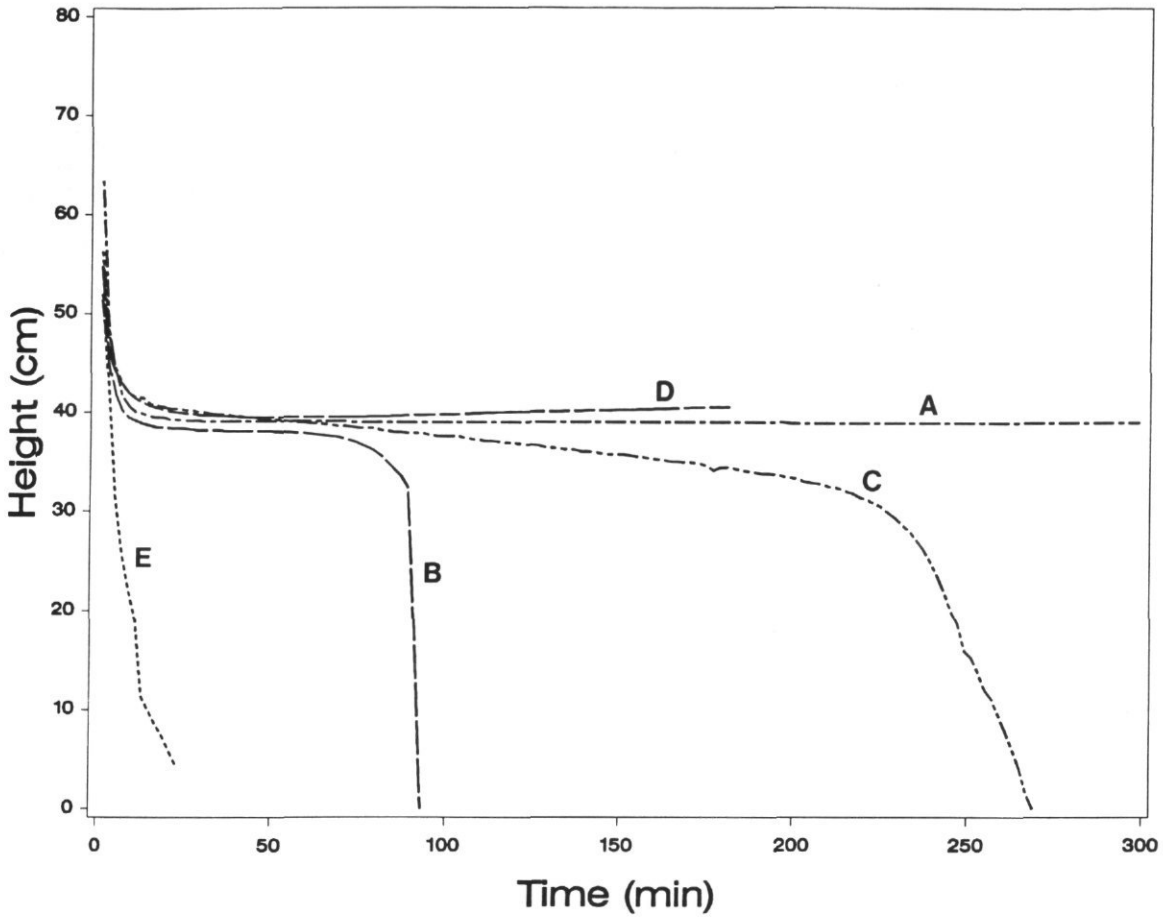


Figure 2. Cod egg descent profiles representative of five (A–E) characteristic profiles observed in this study.

descended as predicted by theory to a stable level in the column, where they remained for up to 5 h, and longer (Fig. 2, A). The second type of profile was similar to the first except that the eggs dropped from the column after a variable amount of time at its original level (Fig. 2, B). In the third instance the eggs descended to near stability in the column but did not decelerate to zero, such that the eggs gradually descended in the column for a variable period of time, after which they would descend to the bottom of the column (Fig. 2, C). In the fourth instance the eggs descended to a specific level in the column but after some period of time began to rise (Fig. 2, D). In the last instance an egg introduced into the column never exhibited a defined deceleration, but continued to sink through the column (Fig. 2, E).

The initial descent rate of the glass beads in the column is roughly 0.01 m s^{-1} (Fig. 3). The solid line in Figure 3 is obtained by fitting a cubic spline to the observed height data and then differencing to obtain the speed. We attempted to fit a descent velocity model to these data to see if the bead trajectories fall consistent with our expectations. There are several possible equations that can be used to describe the descent of a falling body. Most of these rely on Reynolds' number scaling. Reynolds' number (Re = Ul/v, where U is the speed, l is the length of the object, and ν is the kinematic viscosity) is a dimensionless number based on the ratio between the inertial and viscous forces. For the descending beads the Reynolds' number ranges from about 50 down to 1. Thus we would not expect Stokes' law (Kundu, 1990) to apply, nor does it (Fig. 3, dashed line). Several other empirical equations have been developed to parameterize this problem. The primary role of the parameterization is to determine the drag coefficient, which depends upon Re and body shape. We follow Sundby (1983) and apply an equation first developed by

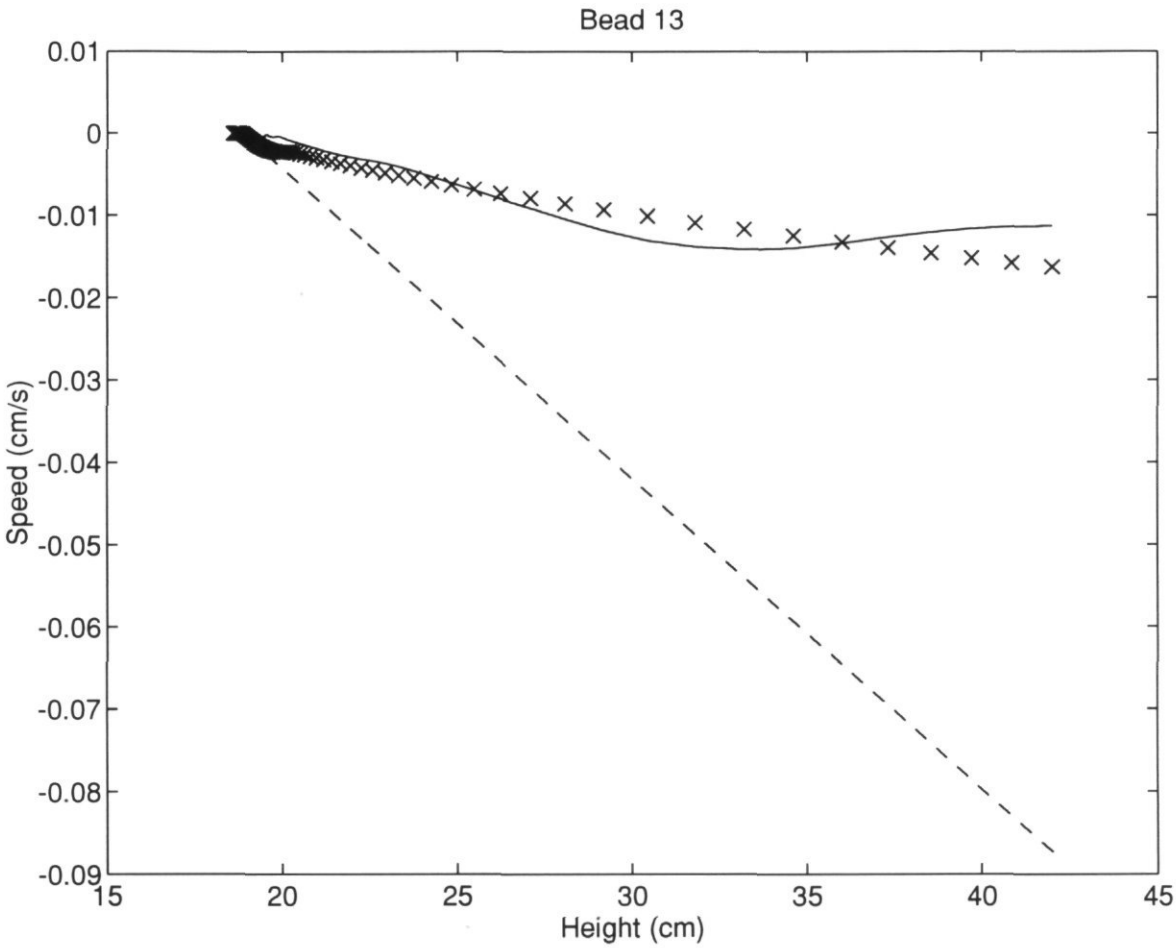


Figure 3. Descent velocity versus height in the column for a single bead. The solid line is computed by differentiating a spline curve of the observed height versus time data. Velocities are calculated from the bead density using two different velocity formulae. The Stokes velocity is shown as a dashed line and Dallavalle's velocity (see text) is plotted as crosses.

Allen (1900) but referred to by Sundby as Dallavalle's formulation (Dallavalle, 1948). The velocity is determined from

$$W = \frac{K_i d_0 (\rho_w - \rho_e)^{2/3}}{\nu^{1/3}}$$

In this equation ν is the molecular viscosity of sea water (1.6×10^{-3} kg m^{-1} s^{-1} at 3°C and 35 ppt), ρ_w is the density of the water, ρ_e is the density of the eggs, g is the gravitational constant (9.81 m s^{-2}), K_i is a constant that has a value of 0.0882 m$^{5/3}$ kg$^{-1/3}$ s$^{-4/3}$, d_0 is an artificial egg diameter given by $d_0 = d - 0.4D$, and d is the true egg diameter. In Dallavalle's formulation the egg diameter is replaced by an effective egg diameter, obtained using the above formula, in which D is calculated from

$$D = \sqrt[3]{\frac{36\nu^2}{g|\rho_w - \rho_e|\rho_w}}.$$

Because the eggs are much smaller than the beads they fall at a slower speed, roughly 10^{-4} m s^{-1}. For the descending eggs the Reynolds' number ranges from 1 to zero, thus we expect Stokes' law to apply. Dallavalle's formula provides a much better fit to the observed egg data than does Stokes' formula. However, a reasonable fit only occurred at velocities $<0.5 \times 10^{-4}$ m s^{-1}. For our purposes, we can see that the empirical relation developed by Allen applies well for the beads and provides a reasonable estimate of the egg descent data. A more detailed discussion of this problem, focusing on the other approaches that have been taken to fitting egg

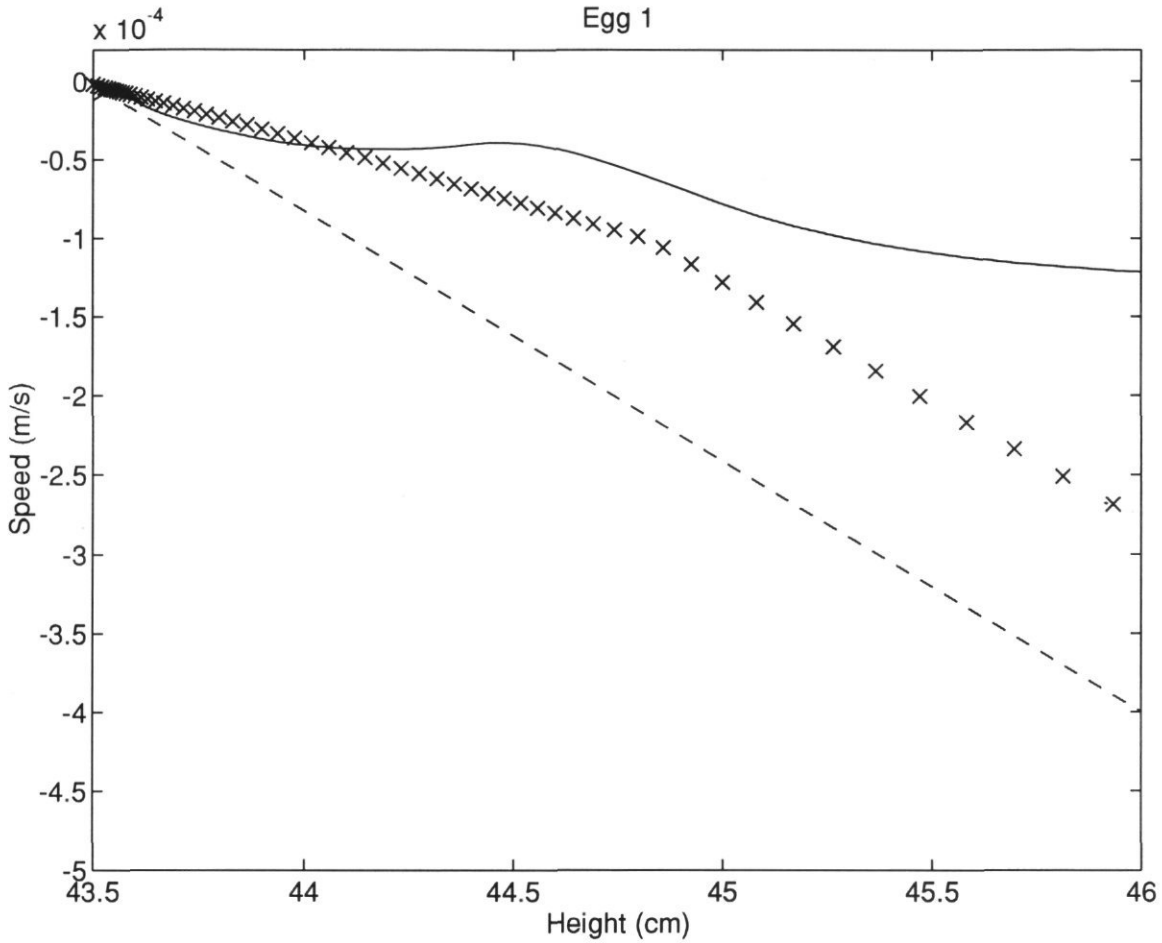


Figure 4. Descent velocity versus height in the column for a single egg. The solid line is computed by differentiating a spline curve of the observed height versus time data. Velocities are calculated from the egg density using two different velocity formulae. The Stokes velocity is shown as a dashed line and Dallavalle's velocity (see text) is plotted as crosses.

data, not discussed here, can be found in Anderson and deYoung (1994).

Laboratory measurements of density

The density of cod eggs measured in 1991 from captive cod was observed to decrease throughout their development until the late stage just prior to hatch (Fig. 5). The mean rate of change in density from 2 to 13 days of age was -0.23 kg m^{-3} d^{-1} (Table 1). In 1992 cod eggs initially measured in poor water conditions were observed to increase their density during the first 9 days of development at a rate of $+0.07$ kg m^{-3} d^{-1} (Fig. 6, Table 1). When the incubation chamber was re-stocked from the original batch of cod eggs that had been raised in favourable water conditions the density was initially lower (at age 10 days) and subsequently was observed to decrease during the final 9 days of development (ages 10–18) at -0.19 kg m^{-3} d^{-1} (Fig. 6, Table 1). Eggs fertilized from cod captured on the Grand Banks in 1992 and held in favourable water conditions decreased in density at an average of -0.21 kg m^{-3} d^{-1} throughout their development from 4 days of age until 15 days of age (Fig. 5, Table 1).

Comparison of slopes among the different batches of eggs indicated that there were no statistical differences between the three batches of eggs measured in the density gradient column, when eggs were raised under favourable water conditions (batches A, C, D; Table 2). The only statistical differences between slopes were for the set of eggs raised initially in poor water conditions in 1992 (batch B) compared to the other experiments (batches A, C, D; Table 2).

Comparison of intercepts, when slopes were not different, indicated that significant differences did exist in some cases. Notably, the initial density of both 1991

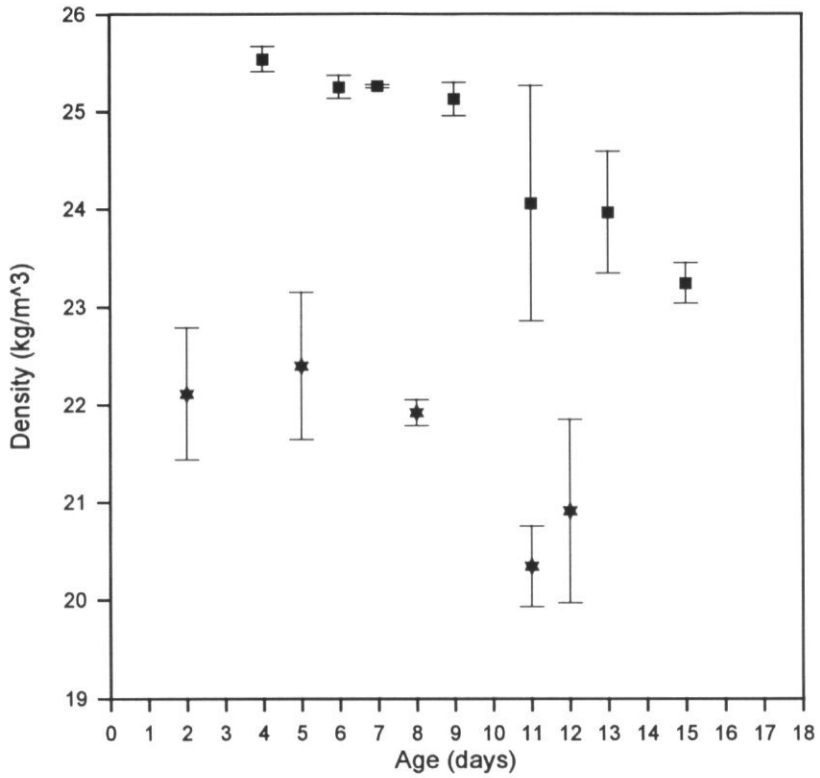


Figure 5. Density (±1 s.e.) measured for eggs from cod which spawned in tanks incubated by inshore surface waters (stars) in 1991 and eggs artificially fertilized at sea from cod captured at 380 m depth offshore (squares) in 1992.

Table 1. Simple regressions relating density (kg m^{-3}) of cod eggs reared in the laboratory with age (days). Batches refer to different experiments: A – 1991 eggs spawned by laboratory cod; B – 1992 eggs that were in deteriorating condition spawned by laboratory cod; C – same eggs as Batch B that were in good condition; D – 1992 eggs spawned by Grand Banks cod. (F-value refers to the Fisher test statistic. p-level refers to the probability of statistical difference.)

Batch	Regression	Ages	df	F-value	p-level	r^2 (%)
A	SG = 1023.0 − 0.23 · AGE	2–13	34	26.2	0.0001	44.2
B	SG = 1023.3 + 0.07 · AGE	0–9	25	11.7	0.0022	32.8
C	SG = 1024.9 − 0.19 · AGE	10–18	22	4.3	0.0502	17.1
D	SG = 1026.5 − 0.21 · AGE	4–15	25	33.9	0.0001	63.1

Table 2. Summary of statistical comparison among slopes and intercepts for the least squares regressions derived from the individual experiments summarized in Table 1. df = degrees of freedom; batches A–D as described in Table 1. NA refers to Not Applicable. (F-value refers to the Fisher test statistic. p-level refers to the probabiliy of statistical difference.)

		Slopes		Intercepts	
Batches	df	F-value	p-level	F-value	p-level
A vs B	60	27.33	0.0001	NA	NA
A vs C	57	0.01	0.9509	24.55	0.0001
A vs D	60	0.14	0.7131	286.8	0.0000
B vs C	48	10.41	0.0023	NA	NA
B vs D	51	42.07	0.0001	NA	NA
C vs D	48	0.02	0.7131	286.8	0.0000

and 1992 eggs from captive cod raised inshore were statistically lower than the initial density of eggs from cod captured on the Grand Banks (Table 2).

Field measurements

Cod egg and larval concentration profiles demonstrated that egg stages I–III were often bimodal in distribution, with eggs occurring abundantly both above and below 100 m depth (Anderson and deYoung, 1994). Calculations here to estimate centre of mass are based only on eggs which occurred at <100 m depth, as eggs found deep in the water column may be sinking (Anderson and deYoung, 1994). The depth of the centre of mass for

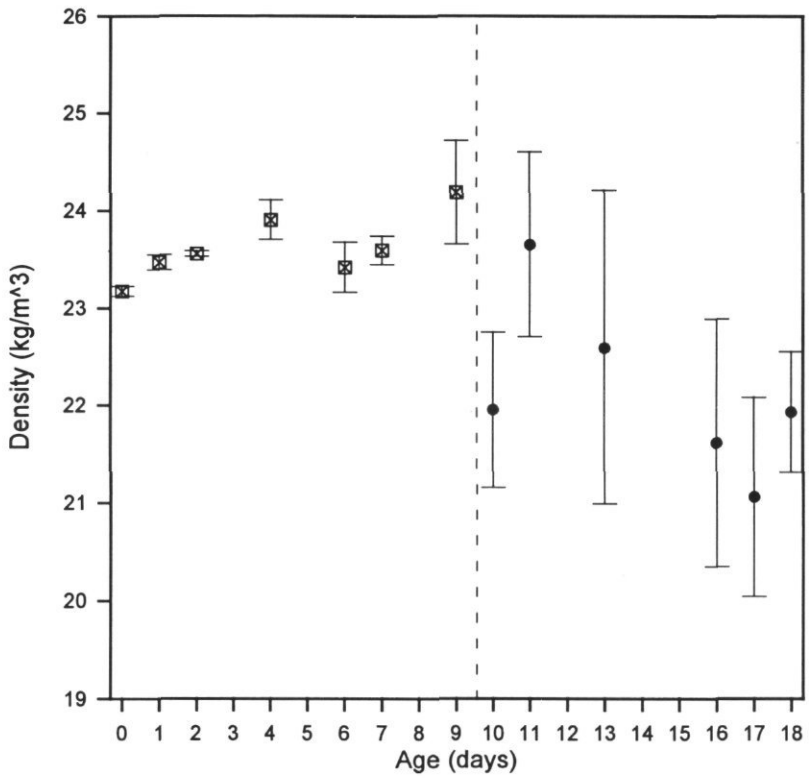


Figure 6. Density (±1 s.e.) measured for eggs from cod which spawned in tanks incubated by inshore surface waters in 1992. The crossed squares are for eggs which initially developed in poor water conditions, and the closed circles are the same batch of eggs which were raised in favourable water conditions. The vertical dashed line represents the point at which eggs were re-stocked from the original holding tank.

each stage (I–V) indicated a progression from deeper to shallower depths as the eggs developed and hatched into larvae. For the inner shelf area most eggs captured were stage I and these eggs were centred around 52.6 m depth. Only 3 eggs were sampled for stages II–IV and these were found between 25 and 40 m depth. Larvae (mean length 5.8 mm, range 5–7 mm), were centred around 16.2 m depth. On the outer shelf, stage I eggs were centred at 35.3 m depth with stages II–IV centred at 16.5, 21.4, and 21.3 m depths, respectively. However, abundances of egg stages II and IV were very low (<10 per stage) and estimates of their mean depth distributions must be treated with caution. Cod larvae (mean length 5.2 mm, range 3–8 mm) were centred around 11.7 m depth.

The mean rate of change in density estimated for cod eggs and larvae on the inner shelf was -0.21 kg m^{-3} d^{-1}; on the outer shelf it averaged -0.17 kg m^{-3} d^{-1} (Table 3). Comparisons between the inner and outer shelf areas indicated there was no statistical difference between slopes or intercepts (batch E vs. F; Table 4). Therefore the results for the inner and outer shelves were combined for subsequent comparisons between laboratory and field estimates of the stage/age-dependent estimates

Table 3. Simple regressions relating density (kg m^{-3}) of cod eggs and larvae captured at sea for different life history stages (I–IV egg stages, V larvae). Batches refer to different experiments: E – 1991 cod eggs and larvae from the inner Newfoundland Shelf; F – 1991 cod eggs and larvae from the outer Newfoundland Shelf; G – 1991 cod eggs and larvae combined for the inner and outer Newfoundland Shelf. (F-value refers to the Fisher test statistic. p-level refers to the probability of statistical difference.)

Batch	Regression	Stages	df	F-value	p-level	r^2 (%)
E	SG = 1026.1 − 0.21 · STAGE	I–V	17	6.7	0.0197	30.0
F	SG = 1026.2 − 0.17 · STAGE	I–V	60	22.9	0.0001	27.9
G	SG = 1026.1 − 0.18 · STAGE	I–V	78	28.3	0.0001	26.9

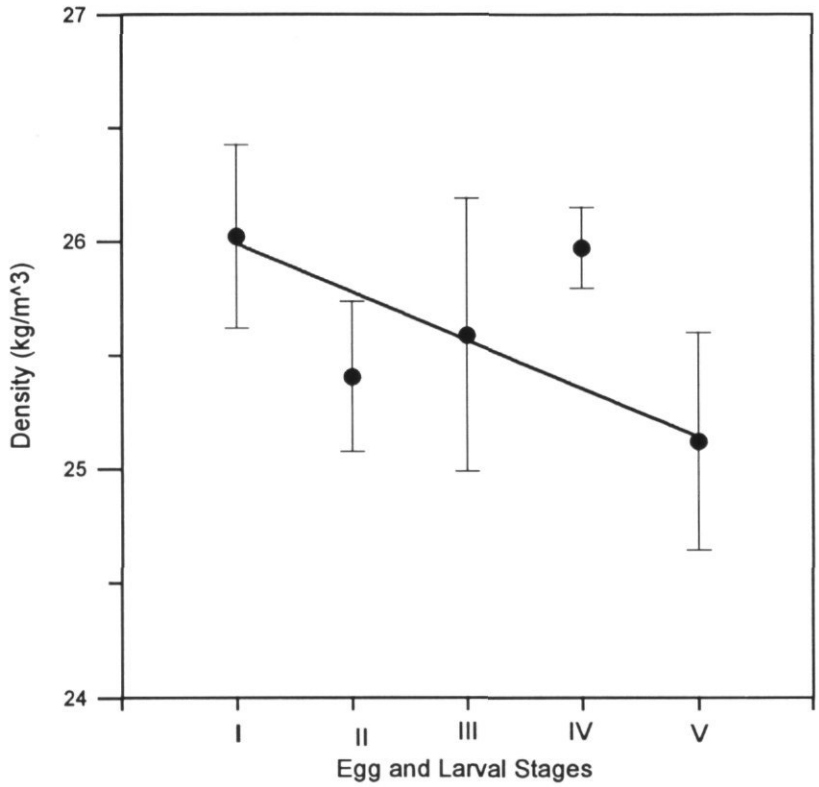


Figure 7. The mean density (±1 s.e.) estimated for field captured cod eggs and larvae, combined for the inner and outer shelf areas. Stages I–IV are cod eggs, stage V is cod larvae.

of density (Table 3). The mean centre of distribution with respect to density of stage I eggs was 1026.0 kg m^{-3}, which decreased to 1025.1 for cod larvae (Fig. 7).

There were no statistical differences between the rate of change in density for eggs and larvae captured in the field compared with eggs raised under favourable water conditions in the laboratory (batch G vs. A, C, D; Table 4). However, there was a difference when compared with eggs raised under poor conditions (batch G vs. B; Table 4). While the laboratory measurements were made for different ages (days) and the field measurements for different stages (I–V), both measurements span the period immediately following fertilization through to hatch and, therefore, are comparable.

Table 4. Summary of statistical comparisons among the least squares regressions relating density (kg m^{-3} d^{-1}) to age (days) for the laboratory experiments and stage (I–V) for field captured specimens. df – degrees of freedom; batches A–D as described in Table 1; batches E–G as described in Table 3. NA refers to Not Applicable. (F-value refers to the Fisher test statistic. p-level refers to the probabiliy of statistical difference.)

		Slopes		Intercepts	
Batches	df	F-value	p-level	F-value	p-level
E vs F	100	0.9	0.356 8	2.63	0.107 9
G vs A	135	0.4	0.697 0	190.6	0.000 1
G vs B	126	15.2	0.000 1	NA	NA
G vs C	123	0.3	0.773 6	5.5	0.005 3
G vs D	121	0.4	0.646 6	1.5	0.220 3

The initial densities (intercepts) were not different when comparing eggs caught in the field with eggs artificially fertilized from Grand Banks cod (batch G vs. D; Table 4). In contrast, there was a statistical difference in the initial densities when compared with eggs from inshore cod (batch G vs. A; Table 4). The initial densities estimated for eggs from cod which were raised inshore (1023.0 to 1024.9) were lower compared to those estimated for eggs which originated from cod which lived offshore (1026.5) and for field captured eggs (from 1026.2 to 1026.3). Qualitatively, the initial densities were similar to the ambient conditions in which the adult cod were living at the time of spawning. Density for inshore waters at the surface during the time of spawning in 1991 and 1992 was approximately 1025.8, whereas

offshore at 380 m depth on the Grand Banks it was approximately 1027.5 in 1992.

Discussion

Cod egg buoyancy is achieved primarily from a high water content of low osmolarity which is maintained through active osmoregulation, pumping salts out of the egg across the chorion (Davenport *et al.*, 1981; Riis-Vestergaard, 1984; Craik and Harvey, 1987). The five classes of cod egg descent profiles in the density gradient column observed in this study appear to indicate varying degrees of egg condition. In the case where eggs descended to a constant position in the column (class A), or rose slowly with time (class D), the eggs appear to be in good condition and capable of maintaining a constant, or decreasing, density through osmoregulation. At the other extreme, some eggs fell directly through the density gradient column without decelerating. These eggs were not dead (non-opaque) when introduced to the column. Their inability to osmoregulate is demonstrated by their descent through water densities up to 1033.9 kg m^{-3}. Such eggs in a natural environment would quickly be lost from the water column. Finally, we observed classes of eggs which descended to a constant depth for varying periods of time before falling to the bottom of the column (class B), or eggs which never decelerated to zero but descended slowly for varying periods of time before falling to the bottom of the column (class C). Both classes of descent profiles indicate a reduced capacity to osmoregulate. Together, these observations indicate that the characteristics of the egg descent profiles may be a direct measure of egg condition varying from eggs in good condition to eggs that were essentially dead.

The descent velocities measured for glass beads closely fit the theoretical values predicted by Dallavalle's formula. The small deviations from the theoretical profiles are ascribed to measurement error. Stokes' law did not apply to the glass beads, as expected, given the large values of the Reynolds' number. The eggs did not exhibit Stokes' law behaviour either, but their velocity was well described by Dallavalle's formula. These results demonstrated that descent profiles defined by Dallavalle's formula closely predict the settling velocity of an inert sphere in the density gradient column. Comparing the theoretical descent velocities for cod eggs (i.e. an inert sphere of known density) to measured values demonstrated that cod eggs initially descended more slowly than predicted. Only at low velocities (approximately $\leq -0.5 \times 10^{-4}$ m s^{-1}) did cod eggs match that predicted by theory. A lower than expected descent velocity higher up in the density gradient column indicates that the cod eggs were more buoyant than expected, based on their final position in the column where we measured egg density. This indicates that the cod eggs may be actively osmoregulating during their initial descent, decreasing in density and, therefore, increasing buoyancy. However, as velocities slowed towards zero the descent of cod eggs closely matched that predicted by theory. This occurred lower in the column, where water densities approached that of the egg. These results suggest two conclusions. First, when water density surrounding the egg is much less than that of the egg, then the egg immediately begins to compensate by decreasing its density through active osmoregulation. Second, our measurements of egg density may systematically underestimate the true egg density if an initial compensation by the egg higher up in the density gradient column results in a reduction in egg density.

We are interested in the vertical distribution of cod eggs and larvae as this will affect modelled distributions of their drift following spawning, and ultimately as it may affect survival. In estimating the density of cod eggs and larvae we are primarily interested in its effect on egg buoyancy ($\Delta\rho = \rho_w - \rho_e$) and how this affects vertical distributions in the water column. These distributions will be a function of vertical eddy diffusivity and egg buoyancy (Westgård, 1989; Sundby, 1991). In the absence of wind and when deeper in the water column, the vertical distribution of cod eggs will be a function of their buoyancy, which depends primarily on the egg density and diameter (Westgård, 1989; Sundby, 1991). Because of the considerable depths in which northern cod spawn (>300 m) we expect that egg buoyancy is an important variable affecting cod egg dispersion and ultimately survival.

Our measurements demonstrated that the density of cod eggs scaled with the water density in which the cod spawned. Eggs spawned by cod which were captive in tanks supplied with low salinity water from the inshore surface layer produced eggs whose density was significantly lower than eggs which originated from cod spawning offshore at 380 m depth in much higher salinities. When compared to the initial egg density estimated from the field samples, the inshore eggs were significantly lower in density, whereas eggs spawned offshore were not statistically different. This result is consistent with experiments carried out on flounder which demonstrated that density of fish eggs is directly dependent on the ambient salinity (density) in which spawning adults occur (Solemdal, 1967, 1973).

The initial densities estimated for cod eggs from the different sources were always lower than the ambient water in which the spawning adults occurred. Comparing laboratory and field-based estimates in 1992, the difference ranged between 0.9 and 1.2 kg m^{-3}. For the 1991 laboratory data the difference was 2.4 kg m^{-3}. In

the first instance, these differences equate to initial terminal velocities from 0.7 to 0.9 mm s^{-1}, which fall mid-way between upper and lower estimates given by Sundby (1983) for cod eggs 1.5 mm in diameter. The 1991 estimate is 1.8 mm s^{-1}, which is near the upper limit estimated by Sundby (1983). By comparison, if the initial density estimated for cod eggs spawned inshore is compared with water densities offshore, the initial terminal velocity would be approximately 3.4 mm s^{-1} for 1.5 mm diameter eggs, which is much greater than that estimated for fish eggs Sundby (1983).

Sundby (1983) stated that dead eggs sink and reported descent velocities greater than 10 times the ascending velocities of live eggs. We could not measure the density of dead eggs, but know that it was greater than 1033.9 kg m^{-3}. Using this value, we estimate that minimum descent velocities for dead cod eggs on the Newfoundland Shelf might range from 4.9 to 6.2 mm s^{-1} for different parts of the water column. These results indicate that dead eggs will be lost quickly from the water column.

The density of cod eggs measured in the density gradient column decreased with age and development when eggs were maintained in favourable water conditions. A decrease in density would be necessary for cod eggs spawned offshore on the Newfoundland Shelf to rise into surface waters; given an initial density of 1026.5 kg m^{-3}, then these eggs would be neutrally buoyant at approximately 100 m depth. This is far below the surface layer, where cod eggs are expected to hatch in waters favourable for larval feeding. By decreasing density as the eggs develop the final density at hatch would be approximately 1022.1 (based on Equation (D) in Table 1 and a hatching age of 21 days at 3°C). This compares with a density in surface waters of approximately 1025.7. Therefore, we expect that cod eggs would always be positively buoyant when they decrease in density during development.

Our result contrasts with that reported for cod from coastal Norway (Sundnes, *et al.*, 1965; Mangor-Jensen, 1987) and for Baltic cod (Nissling and Westin, 1991), where the density increased during development. These eggs are reported to be positively buoyant until the time approaching hatch, when they become neutrally buoyant. By inference, cod eggs off Norway and the Baltic Sea must have initial buoyancies which are much greater than Newfoundland cod, and relatively high initial terminal velocities.

An important result of this study is that the density of cod eggs will increase during development when raised in poor water conditions. An increase in density for cod eggs spawned on the Newfoundland Shelf has serious implications for their survival, as it indicates that the eggs will not rise to the surface waters but will actually sink (Anderson and deYoung, 1994). Sundnes *et al.* (1965) noted that "eggs of lesser quality had a higher density than the perfect ones".

We assume that poor water conditions in the treatment tank resulted in reduced oxygen concentrations. When cod eggs encounter low oxygen concentrations in their natural environment, then we expect that density will be greater, resulting in eggs which may sink. Nissling and Westin (1991) reported that cod eggs which sink towards the bottom, under different salinity regimes, are exposed to low oxygen concentrations. Recent work on the Newfoundland Shelf has demonstrated that water ranged from 65 to 80% oxygen saturation (E. Colbourne, Northwest Atlantic Fisheries Center, St John's, Newfoundland, Canada A1C 5X1, unpubl. data). These low concentrations were observed between June and September and occurred from ~100 m depth to the bottom (350–400 m). Therefore, there is a potential for cod eggs to be exposed to low oxygen concentrations on the Newfoundland Shelf. The implications of low oxygen concentrations on cod egg buoyancy and probable survival is the subject of current investigations.

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New variants of the haemoglobins of Atlantic cod: a tool for discriminating between coastal and Arctic cod populations

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Fyhn, U. E. H.,† Brix, O., Nævdal, G., and Johansen, T. 1994. New variants of the haemoglobins of Atlantic cod: a tool for discriminating between coastal and Arctic cod populations. – ICES mar. Sci. Symp., 198: 666–670.

Coastal and oceanic populations of Atlantic cod (*Gadus morhua* L.) were sampled along the Norwegian coast, in the Barents Sea, and on the Faroe Bank. A new HbI haemoglobin polymorphism of cod was documented using isoelectric focusing electrophoresis, and frequencies of the new phenotypes in the different samples are described. The new phenotypes were strongly associated with the coastal populations and were not found in Arctic cod or cod from the Faroe Bank. It is hypothesized that the new phenotypes might be used as a marker for coastal vs. Arctic cod populations.

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Introduction

The cod (*Gadus morhua* L.) of the North Atlantic comprise several more or less reproductively isolated populations. Identification of the different populations of a species is essential in biological and ecological studies of the species, and several methods have been developed. Thus, to discriminate the Northeast Arctic cod population from the Norwegian coastal populations, differences in patterns of annuli of the otoliths and in frequencies of haemoglobin genotypes have been used (Rollefsen, 1933; Møller, 1968; Dahle and Jøstad, 1993).

The HbI-polymorphism of the Atlantic cod haemoglobins with the genotypes *HbI-1-1, HbI-1-2*, and *HbI-2-2* was first described more than 30 years ago (Sick, 1965; Frydenberg *et al.*, 1965). The frequency of the two alleles *HbI-1* and *HbI-2* shows a north–south cline along the Norwegian coast, with a frequency of the *Hb-1* allele of about 0.1 in the Barents Sea (Northeast Arctic cod), 0.2–0.5 along the coast of northern and western Norway, and 0.7 in the Kattegat (Frydenberg *et al.*, 1965; Møller, 1968). A similar cline, although not so clear, can be seen along the North American east coast (Sick, 1965).

Although it is possible to discriminate between cod populations by the use of haemoglobin frequencies, this method has been questioned because indications of strong selective forces acting upon haemoglobin alleles have been found (Mork *et al.*, 1984). In addition, preferably more than one method should be applied to increase accuracy in population studies of cod.

Polymorphism at several enzyme loci has been described in cod, but their frequencies differ only to a small degree throughout the range of the Atlantic cod species (Mork *et al.*, 1982, 1985; Moth-Poulsen, 1982; Jørstad and Nævdal, 1989; Gjøsæter *et al.*, 1992). In the present article a new haemoglobin polymorphism is described, and tentative results concerning its use as a marker for coastal as well as Arctic cod populations are presented.

Materials and methods

Arctic and coastal cod were sampled along the Norwegian coast, in the Barents Sea, and at the Faroe Bank (Fig. 1 and Table 1). Coastal cod were sampled from three areas in the Bergen district (Puddefjord, Øygard and Masfjord) and off the island of Karmøy and the city of Grimstad. Arctic cod, possibly mixed up with small numbers of coastal cod (see below), were sampled on the spawning grounds at Møre and Lofoten, and outside the spawning season at the Faroe Bank and in the Barents Sea.

†Dr Unni E. H. Fyhn died in November 1992 after a distinguished career of research in fish genetics and physiology. This article is a posthumous tribute to her achievements.

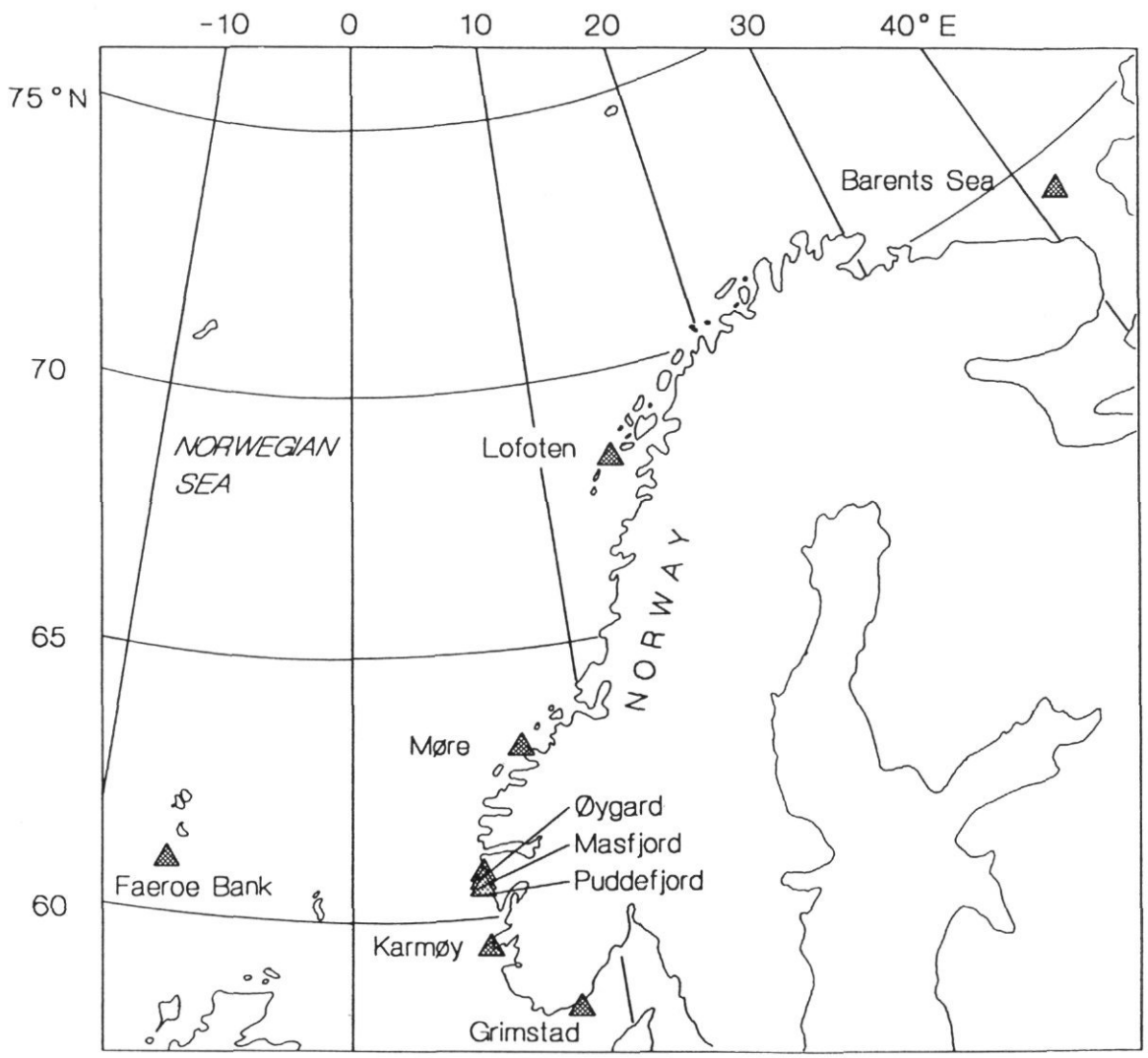


Figure 1. The Northeast Atlantic with sampling sites of cod for analysis of Hb phenotypes.

Table 1. Position, characteristics, and size of samples of cod analysed for haemoglobin polymorphism.

Sample no.	Sample characteristics	Locality	Time period	Sample size
1	Immature coastal cod	Puddefjord	May 1992–Apr 1993	170
2	Immature coastal cod	Masfjord	Apr 1992–Apr 1993	129
3	Immature coastal cod	Øygard	Apr 1992–Apr 1993	187
4	Spawning coastal cod	Karmøy	Jan 1993–Mar 1993	121
5	Coastal cod	Grimstad	Jun 1993	98
6	Spawning Arctic cod	Møre	Apr 1992	69
7	Faroe cod	Faroe Bank	Jan 1992	99
8	Spawning Arctic cod	Lofoten	Mar 1992–Apr 1992	136
9	Immature Arctic cod	Barents Sea	Jan 1993	95

Standard body length was measured to the nearest 0.5 cm below and, for some samples, also individual weight, sex, and maturity stage were recorded. Blood samples were usually taken by cardiac puncture into ice-cold heparinized syringes. Three to five volumes of ice-cold saline solution (1.2% NaCl) were added to each volume of blood and precipitated by centrifugation at 700 × *g* for 3 min at 4°C. The erythrocytes were washed once in 5–10 volumes of saline. Further washing did not change the results. The erythrocytes were hemolysed in 3–4 volumes of ice-cold distilled water. The cell debris was pelleted by centrifugation at 14 000 × *g* for 20 min at 4°C. The hemolysates were stored at 4°C and used for erythrocytes in buffer (HEPES/1.2% NaCl pH 8.0) for 9 days at 0°C before electrophoretic analysis.

Horizontal agar gel electrophoresis was conducted on all samples according to Sick (1965), modified by Jørstad (1984), with 2% gels and Smithies' buffer [45 mM Tris, 25 mM boric acid, 1 mM EDTA, pH 8.6, Smithies (1959)]. Smithies' buffer diluted 1:1 with distilled water was used as gel buffer. Electrophoresis was carried out at 20 mA for 1 h at 3–5°C. The gels were stained with Brilliant Blue G Quick stain in perchloric acid (McFarland, 1977), destained by diffusion, photographed by transmitted light, and stored at 4°C for later phenotype readings and scanning. Stained gels displayed identical haemoglobin patterns to unstained gels.

Part of the material was analysed by polyacrylamide slab and disc gels, starch gel electrophoresis, and cellulose acetate electrophoresis according to standard procedures. Isoelectric focusing was carried out in accordance with the instruction manuals using the Phast-gel system (Pharmacia) with precasted gels with pharmalytes of a range of pH 5–9 and the Multiphor II system (LKB) with precasted slab gels (Ampholine PAGplates, Pharmacia, pH 5.5–8.5). The Multiphor II system gave best resolution of the Hb bands, and all samples were analysed in this system.

The distribution of haemoglobin among the various components was determined, from tracings of the Brilliant Blue G Quick stained gels with transmitted light of 570 nm, by means of a densitometer. The planimetry was done manually. The correspondence between repeated scans of the same gel or scans of the same haemolysate on different gels was within 5%, except for bands containing less that 5–8% of the Hb, when variation in background absorption interfered with the results.

To analyse the globin composition of the individual haemoglobin components were isolated (about 10 specimens) by cutting out gel pieces which contained the respective haemoglobin components from agar gels run for 3 h and from isoelectric focusing gels. The haemoglobins were allowed to diffuse overnight into a minimum of gel buffer and then concentrated by Amicon filtration. The isolated haemoglobin components were analysed by horizontal, low-pH, 8M urea gel electrophoresis according to Tsuyuki and Ronald (1971), with the gel buffer at pH 2.9 and electrode buffer at pH 2.0 and 3.1. Dithiothreitol was omitted, but β-mercaptoethanol (0.25%) was added to all buffers.

Results and discussion

On agar gel the haemolysate of both Arctic and coastal cod showed the HbI-polymorphism with the two homozygotes *HbI-1-1* and *HbI-2-2* and the heterozygot *HbI-1-2* (Fig. 2). The HbI-(1) and HbI-(2) bands appeared as single bands in all gels. These results were in accordance with earlier descriptions (Sick, 1965; Møller, 1968).

On isoelectric focusing gels (IEF) haemolysate of the genotype *HbI-1-2* and *HbI-2-2* of cod from southwestern Norway (coastal cod) showed either a single or a double band in the zones of band HbI-(1) and HbI-(2). Thus, these two main genotypes, determined by agar gel electrophoresis, could be subgrouped by IEF in accordance with the presence or absence of double bands. Such double-banded phenotypes were indexed with a "b", i.e., HbI-1-2b and HbI-2-2b, while those displaying single bands were indexed with an "a", i.e., HbI-1-2a and HbI-2-2a. The different phenotypes are outlined in Figure 2.

The appearance of double bands was consistent in repeated IEF runs of fresh, stored, or frozen haemolysates, in runs of haemolysates made from whole blood stored for 5 days at 4°C, and from erythrocytes which were washed and resuspended in 0.5 M HEPES/1.2% NaOH, pH 8.0, and stored at 4°C for up to 10 days. The double bands were also found in haemolysates with the haemoglobin in the carbon-monoxy as well as the cyanomet form. Haemolysates not showing double bands when run as fresh samples never showed double bands regardless of subsequent treatment.

The globin analyses showed that each of the main components had one globin in common and at least one globin that was not shared by the other component. The heterozygotes appeared to possess all three globin components. No difference in globin components between the subgroups was detected. The extra bands of the subgroups had a higher isoelectric point than the main bands. The densiometer measurements showed that the double bands in phenotypes HbI-1-2b and HbI-2-2b contained about the same amount of haemoglobin as the corresponding single bands in phenotypes HbI-1-2a and HbI-2-2a, respectively. Thus, although the biochemical compositions of the double bands are still unknown, they most probably represent real phenotypic variation in the cod populations.

Table 2 gives the distribution of the five HbI phenotypes among cod from each distribution of genotypes,

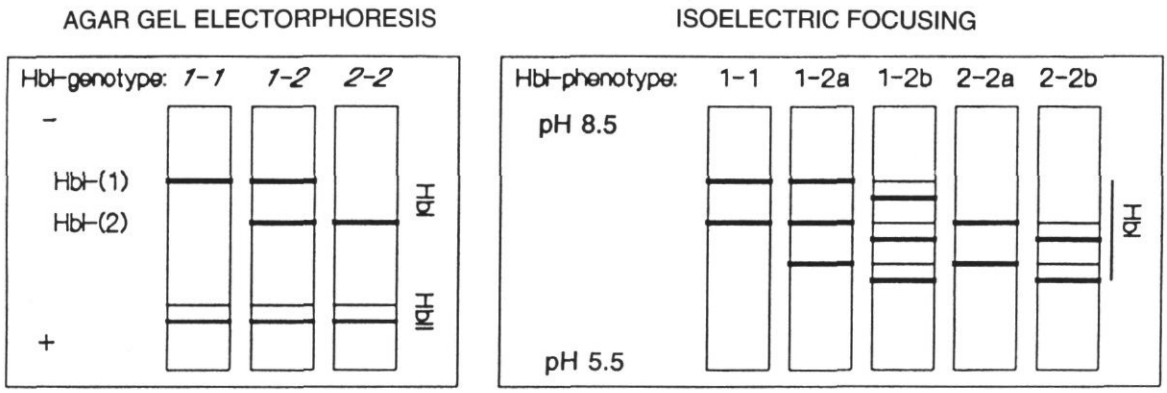


Figure 2. Schematic representation of the patterns of components from agar-gel electrophoresis and isoelectric focusing of haemoglobins of the coastal cod.

referring to the main groups, were in accordance with earlier reports (Møller, 1968; Frydenberg *et al.*, 1965) with low frequencies of the genotype *HbI-1-1* in the Lofoten area, the Barents Sea and the Faroe Bank, intermediate in the Møre sample, and highest in the samples from southern Norway. The intermediate frequency in the Møre sample indicates that this sample consisted of a mixture of Arctic and coastal cod.

Among coastal cod, 8–33% of the *HbI-2-2* homozygotes were of the phenotype HbI-2-2b and 3–19% of the *HbI-1-2* heterozygotes were of the phenotype HbI-1-2b (Table 2). None of the *HbI-1-2* heterozygotes showed double bands in one zone only, nor did any of the *HbI-1-1* homozygotes show double bands. The double bands of coastal cod were found in both females and males, in both large and small fish, and in fish of all maturity stages.

In the Møre samples, double bands were only found in one cod (phenotype HbI-2-2b). In the samples from Lofoten, the Barents Sea, and the Faroe Bank none of the haemolysates showed double bands (Table 2). It thus seems that the samples of Arctic cod can be distinguished from coastal cod by the absence of double bands. More extensive sampling, now under way, will show whether this system can be used to discriminate among coastal cod populations. The samples from the Faroe Bank were more in accordance with the Arctic cod than with the Norwegian coastal cod as regards both main groups and subgroups. To reveal the genetic background of the subgroup variation, controlled crossing experiments are being undertaken as part of a series of experiments on the performance of cod of different origin under rearing conditions.

Table 2. Distribution of numbers of Hb-I phenotypes of cod. For sampling locality see Table 1.

Sample no.	1-1	1-2a	1-2b	2-2a	2-2b
1	53	58	14	30	15
2	46	45	9	22	7
3	66	86	9	24	2
4	33	63	2	19	4
5	35	41	5	14	3
6	5	20	0	43	1
7	1	14	0	84	0
8	1	31	0	104	0
9	2	20	0	73	0

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Studies on associations between genotypes and growth rate in juvenile cod

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Jørstad, K. E., and Nævdal, G. 1994. Studies on association between genotypes and growth rate in juvenile cod. – ICES mar. Sci. Symp., 198: 671–675.

In the present article, studies on the genotype-dependent growth rate of cod are reported. The main part of the material consisted of 0-group cod produced artificially in ponds in western and northern Norway, but also wild caught young cod from the Barents Sea. The material has been analysed for haemoglobin and two tissue enzymes providing genotypic information at three polymorphic loci. The mean growth rate (measured as size at sampling) of cod of the different genotypes was compared by analysis of variance. Out of a total of 12 samples, association between growth rate and genotypes of haemoglobin was found in only one sample, and likewise in the enzyme lactate dehydrogenase, also in one sample. No significant differences were found in the rest of the material studied (consisting of 30 comparisons).

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Introduction

Studies on blood types and blood proteins of cod (*Gadus morhua*) were conducted in Norway in the years 1962–1972 (Frydenberg *et al.*, 1965; Møller, 1968) for identification of self-sustaining populations. Since 1978, tissue enzymes have been studied using starch gel electrophoresis (Mork *et al.*, 1982, 1985; Jørstad, 1984; Jørstad and Nævdal, 1989; Gjøsæter *et al.*, 1992). The more recent studies have mainly been conducted as baseline studies in connection with artificial propagation and sea-ranching of cod.

Both the old and the more recent studies on cod are based on the assumption that the biochemical genetic traits are neutral or at least sufficiently neutral not to be influenced by directional selection over several fish generations. This assumption has been questioned in later years; first by Karpov and Novikov (1980) and Karpov *et al.* (1984), who found that the functional properties of the haemoglobin genotypes of cod were differentially influenced by environmental temperature. Likewise, Mork *et al.* (1984a, b) indicated that the three haemoglobin genotypes possessed different growth rate capacities, and Mork and Sundnes (1985) found different survival of different *LDH-3** and *PGI-1** genotypes of wild 0-group cod which were caught and kept in captivity. Gjøsæter *et al.* (1992) found indications, although not consistently, of genotype-dependent growth rate in juvenile cod from the southeast coast of Norway, and Nævdal *et al.* (1992) found consistently higher mean growth rate of 0-group of the haemoglobin type *HbI-2/2* under experimental conditions. Jørstad (1986) however, found no genotype-dependent growth rate in an extensive sampling programme of cod produced in a marine pond, and Dahle and Jørstad (1993) found no changes in haemoglobin gene frequencies among Arctic cod during nearly 30 years of study.

The aim of the present study was to investigate further the potential genotype-dependent growth rate in young cod by utilizing material of 0-group cod raised in semi-natural ponds and used for sea-ranching. Likewise, young cod sampled in the Barents Sea were analysed. The results were expected to extend the information needed for understanding the significance of biochemical genetic variation, and thus for application of gene frequencies and/or genotype distributions in studies of population structure in cod.

Materials and methods

Sampling of blood and tissue has been described by Møller (1968) and Jørstad (1984). For analysis of haemoglobin, the method described by Sick (1965) was

Table 1. Allele frequencies in samples of juvenile cod produced in marine ponds (0-group) or sampled in the Barents Sea (3-1; 1-group and 3-2; 2-group). 2-3a and 2-4a represent samples of genetically tagged cod, i.e., offspring of broodstock homozygous for the gene PGI*30.

Sample no.	Locality	Year	n	*Hb-I*		*Ldh-3**			*Pgi-1**			
				**1*	**2*	**70*	**100*	**150*	**30*	**70*	**100*	**150*
1-1	Tromsoø	1987	140	0.31	0.69	0.39	0.60	0.01	0.02	0.01	0.63	0.34
1-2	(marine pond)	1988	191	0.24	0.76	0.41	0.56	0.03	0.03	—	0.63	0.34
1-3		1989	172	0.24	0.76	0.36	0.61	0.03	0.01	—	0.61	0.38
2-1	Parisvatnet	1988	286	0.58	0.42	0.38	0.62	—	0.01	0.02	0.76	0.21
2-2	(marine pond)	1989	252	0.47	0.53	0.26	0.74	—	0.01	0.02	0.84	0.13
2-3a		1990	145	0.57	0.43	0.25	0.75	—	1.00	—	—	—
2-3b		1990	160	0.62	0.38	0.32	0.68	—	0.13	0.01	0.71	0.15
2-4a		1991	243	0.58	0.42	0.32	0.68	—	1.00	—	—	—
2-4b		1991	162	0.55	0.45	0.43	0.57	—	0.02	—	0.70	0.28
2-5		1993	188	0.64	0.36	0.40	0.59	0.01	0.07	0.01	0.68	0.24
3-1	Eastern Barents	1993	263	0.09	0.91	0.45	0.55	—	0.02	0.01	0.69	0.28
3-2	Sea	1993	340	0.07	0.93	0.40	0.59	0.01	0.02	—	0.69	0.29

applied with some modifications (Jørstad, 1984). Horizontal starch gel electrophoresis was used for analysis of tissue enzymes. Genetic systems with a reasonably high number of specimens of two or more genotypes within samples were studied. This included the three polymorphic loci; *HbI, LDH-3** and *PGI-1**.

A summary of the 12 samples analysed is given in Table 1. All except two were collected of 0-group cod reared in marine ponds for use in sea-ranching experiments. The samples were taken when the fish were 4–6 months old and close to the time of release into the natural environment. Samples 1-1 to 1-3 were collected from cod produced in a pond near Tromsø, northern Norway, while the rest of the 0-group samples were drawn from cod produced in Parisvatnet, a marine pond located on an island west of Bergen. In 1990 and 1991 two groups of fish were produced in the pond; offspring of non-selected broodfish, and offspring of genetically tagged broodfish. The production of broodfish homozygous for the rare allele *PGI-1*30* is described by Skaala *et al.* (1990) and Jørstad *et al.* (1991). Offspring of the genetically tagged broodfish are treated as two groups (called 2-3a and 2-4a in Table 1) when analysing the *PGI-1** genotypes, but elsewhere lumped with the rest of the year class.

Sample 3-1 and 3-2 represent young cod from the eastern part of the Barents Sea. Both samples were collected in January 1993, one being of the 1992 the other of the 1991 year class, respectively.

Individual lengths were recorded for all fish sampled. Length at time of sampling is regarded as a measurement of realized growth rate from hatching to sampling. Mean lengths of genotypes were compared using one-way ANOVA statistics.

Results

Allele frequencies calculated from observed distributions of genotypes are given in Table 1. Considerable variation between samples was observed. The frequencies of the allele *HbI-1* were below 0.1 for Barents Sea cod, in the range 0.25–0.40 for coastal cod in northern Norway and 0.5–0.6 in western Norway. The frequencies of the most frequent *LDH-3** and *PGI-1** alleles were found to be high in some of the present samples compared to earlier findings (Jørstad, 1984; Jørstad and Nævdal, 1989). Likewise, rare alleles seemed to be absent or extremely rare in some samples. As expected in samples 2-3a and 2-4a, only one PGI genotype, namely *PGI-1*30/30*, was found, while the other genetic systems were unaffected (lumped with 2-3 and 2-4, respectively).

Mean lengths of fish of different genotype within each sample are given in Tables 2–4. These values were tested using one-way ANOVA for each sample and each locus. Concerning haemoglobin, significant differences were found in sample 2-1 (Table 2); fish of genotype *HbI-2/2* showing the highest mean length. No trend or tendencies were seen among the non-significant differences in the nine remaining samples.

Likewise, only sample 2-3 of the 10 samples analysed showed significant differences in mean length concerning *LDH-3** genotypes (Table 3). No significant differences were found concerning *PGI-1** genotypes (Table 4). The genetically tagged cod (*PGI-1*30/30*) were on average smaller in 1990 and larger in 1991 than the rest of the fish raised in the same pond. This, however, was due to differences in age at the start of the pond experiment and not associated with genotype (Blom *et*

Table 2. Mean length (in mm) of cod different haemoglobin genotypes (s = standard error, n = numbers). One sample showing significant genotype-dependent length variation is underlined.

	Hb-1 1/1*			*Hb-1* 1/2*			*Hb-1* 2/2*			
Sample no.	l	s	n	l	s	n	l	s	n	p
1-1	150.9	3.6	14	147.2	1.6	56	145.1	1.9	64	0.32
1-2	131.7	8.7	9	146.3	3.0	72	147.5	2.4	106	0.20
1-3	143.3	5.4	12	147.5	2.3	57	148.2	1.7	97	0.64
2-1	143.2	1.5	94	142.4	1.3	139	150.8	2.3	48	<0.05
2-2	162.5	2.8	54	164.2	1.5	127	161.6	2.3	70	0.61
2-3	156.3	2.2	107	156.6	2.1	135	157.5	3.0	53	0.95
2-4	102.8	3	110	102.9	1.7	167	100.6	2.6	66	0.74
2-5	174.3	1.9	75	173.2	2.3	69	178.1	3.8	21	0.52
3-1	90.0	—	1	109.0	1.7	47	109.2	0.9	214	0.96
3-2	201.7	19.2	3	213.8	4.7	44	209.2	1.5	292	0.48

Table 3. Mean length (in mm) of cod different lactate dehydrogenase (Ldh) genotypes (s = standard error, n = numbers). One sample showing significant genotype-dependent length variation is underlined.

	Ldh-3 70/70*			*Ldh-3* 70/100*			*Ldh-3* 100/100*			
Sample no.	l	s	n	l	s	n	l	s	n	p
1-1	142.1	3.6	19	146.8	1.5	76	146.7	2.1	48	0.74
1-2	141.4	4.5	33	149.1	3	82	146.0	3.1	63	0.35
1-3	147.4	4.1	23	147.6	1.7	77	147.7	2.4	62	1.00
2-1	144.0	2.2	46	142.1	1.3	132	145.9	1.7	107	0.18
2-2	168.5	4.4	23	162.6	1.9	89	162.7	1.6	140	0.40
2-3	172.8	4.6	27	156.8	2.2	120	156.7	1.8	156	<0.05
2-4	99.8	3.4	53	101.1	1.6	188	96.0	1.6	165	0.09
2-5	173.8	3.1	23	173.8	1.9	89	173.6	2.6	54	0.99
3-1	106.5	1.1	47	109.3	1.1	140	110.4	1.7	75	0.24
3-2	212.2	3.9	53	208.8	2.1	167	209.5	2.4	114	0.71

Table 4. Mean length (in mm) of cod of different phosphoglucose isomenase (Pgi) genotypes (s = standard error, n = numbers).

	Pgi-1 30/30*			*Pgi-1* 100/100*			*Pgi-1* 100/150*			*Pgi-1* 150/150*			
Sample no.	l	s	n	l	s	n	l	s	n	l	s	n	p
1-1		—		146.6	1.9	53	145	1.8	73	150.60	2.6	12	0.43
1-2		—		144.5	2.7	77	149.1	3.2	77	141.50	5.3	23	0.35
1-3		—		147.4	2.3	61	147.7	1.8	82	144.10	3.8	23	0.66
2-1		—		143	1.2	161	144.6	1.7	96	140.80	7.4	9	0.75
2-2		—		162.5	1.2	175	165.6	2.8	53	151.40	4.4	5	0.21
2-3a	155.9	1.8	146		—			—			—		
2-3b		—		163.6	2.7	83	158.3	4.3	36	122.00	4	2	
2-4a	102.8	1.5	243		—			—			—		
2-4b		—		98.3	2.5	76	88.4	2.1	71	93.40	3.2	9	
2-5				172.5	2	89	172.7	3.1	42	179.90	3.3	16	0.33
3-1		—		108.4	0.9	127	109.9	1.5	97	110.80	3.7	24	0.57
3-2		—		208.7	2.1	157	210.7	2.4	137	210.60	3.2	27	0.80

al., 1990 and pers. comm.). No trend was found among the non-significant differences in either of the systems investigated.

Discussion

The variation observed between samples was expected, and the allele frequencies were in reasonably good accord with earlier findings in samples of wild caught cod in the area from which the broodfish were drawn (Frydenberg *et al.*, 1965; Møller, 1968; Jørstad and Nævdal, 1989). However, it is uncertain whether the allele frequencies in pond-produced fish are representative of the broodfish populations, because these frequencies are probably influenced by genetic drift. Although the numbers of spawners in the spawning ponds were high (Blom *et al.*, 1990) the actual numbers participating in the spawning in the few days the eggs were collected were unknown and probably fairly low. Thus genetic drift is likely to take place (Jørstad, 1986), and not too much weight should be put on the variation between samples. Genetic drift could also explain the apparent absence of rare alleles in some of the present samples.

The present study has shown indication of genotype-dependent growth rate in only two cases of a total of 32 comparisons, which is no more than could have happened by chance. This is in accordance with earlier findings on wild caught cod (Gjøsæter *et al.*, 1992). Indication of a higher growth rate for fish of the genotype *HbI-2/2* is in accordance with the results of Mork *et al.* (1984a, b) and Nævdal *et al.* (1992).

The allele *PGI-1*30* is rare in natural cod populations (Jørstad and Nævdal, 1989; Gjøsæter *et al.*, 1992), and thus the genotype *PGI-1*30/30* is extremely rare. The present study has not revealed any disadvantages of the allele or of its homozygous genotype that could indicate any reason for the rareness of the allele. Homozygous individuals for this allele survived and grew as well as individuals of other PGI genotypes under the present seminatural environmental conditions.

In conclusion, it seems that genotype-dependent growth rate is not pronounced in young cod under rearing conditions in a semi-natural environment like a marine pond. Neither in the natural environment were there found any tendencies of such dependence, but it should be added that in the present case only two samples were analysed. Thus the present investigation has given no new indication of different functional properties, and thus no further evidence for different fitness, between protein genotypes.

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Antifreeze proteins: their role in cod survival and distribution from egg to adult

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"Northern" Atlantic cod (*Gadus morhua* L.) inhabiting the ocean adjacent to Newfoundland/Labrador (NAFO Divisions 2J and 3KL) face one of the harshest thermal regimes of the cod's distributional range. Winter water temperatures between −1.0°C and −1.8°C (the freezing point of sea water) are frequently observed. The equilibrium freezing point of the unprotected plasma of most marine teleosts (cod included) is approximately −0.7°C. Since plasma freezing points (p.f.p.) approximate to the freezing point of the whole fish, ice inoculation at temperatures below the p.f.p. results in mortality. Thus, at times, the waters of 2J + 3KL are potentially lethal. Investigations have shown that cod eggs and early larvae can survive such conditions because of the ice impermeability of their outer coverings (chorion and epithelial tissue), and the developmental state of certain vulnerable tissues (e.g. gills). In common with many teleost species living at high latitudes, juvenile and adult Atlantic cod are able to occupy potentially lethal habitats by producing antifreeze proteins in response to low temperatures. These lower the animal's freezing point and possibly also protect against cold-damage at the cellular level. We report on how data on the physiology of northern cod antifreeze production can be used to (a) interpret distribution patterns of wild cod within the temperature field; (b) infer the recent thermal history of wild adult cod and hence, distribution within the available temperature field; (c) monitor (in the laboratory) any changes in antifreeze capacity within a geographical area as a possible indicator of stock composition or distributional changes.

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Introduction

Atlantic cod (*Gadus morhua* L.) of the northern cod stock are found in NAFO Divisions 2J, 3K, and 3L (Fig. 1). This area approaches the most northerly extent of cod distribution in the western Atlantic, and its inhabitants face harsh environmental conditions. Extreme low temperatures (down to −1.8°C) and ice are a regular occurrence, both in the coastal waters (Fig. 2) and over the banks of Newfoundland and Labrador (Scobie, 1975; Symonds, 1986; Narayanan *et al.*, 1992). In addition, a permanent oceanographic feature of the area is the cold intermediate layer (C.I.L.), a core of sub-zero water with a characteristic thickness of 100–200 m extending 200–300 km offshore (Petrie *et al.*, 1988; Drinkwater *et al.*, 1992).

Seawater temperatures generally fall to −1.8°C before freezing occurs, because of the concentration of dissolved salts present. However, although supercooling is possible in the absence of ice, the equilibrium freezing point of the blood of most marine teleost fish is between −0.5 and −0.8°C, the concentration of solutes in the plasma being only one-third (approximately) that of sea water (Holmes and Donaldson, 1969; Davies *et al.*, 1988).

The blood plasma of the Atlantic cod is no exception, generally freezing at approximately −0.7°C (Hew *et al.*, 1981; Fletcher *et al.*, 1982). Thus, northern cod living in the sea off Newfoundland are at risk of exposure to temperatures a full degree centigrade lower than the freezing temperature of their unprotected plasma. In order to avoid or survive the lethal effects of such an



Figure 1. Chart showing the location of NAFO Divisions 2J, 3K, and 3L, home of the "northern" cod. N = Newfoundland, L = Labrador, G = Greenland, I = Iceland.

environment, cod have evolved a combination of behavioural (patterns of migration) and physiological (production of antifreeze) mechanisms (Templeman, 1979; Lear and Green, 1984; Fletcher *et al.*, 1987; Kao and Fletcher, 1988).

Our laboratory studies have focused on the pattern of antifreeze production in cod and its importance in survival at different stages in the life cycle.

General properties of antifreeze proteins

Protection against freezing

The ability of certain teleost species to survive in polar waters was first described by Scholander *et al.* in 1957, and has since been the subject of considerable study. Some fish spend their entire lives in a supercooled state, surviving exposure to temperatures as low as −1.8°C, provided they can avoid contact with ice (Scholander *et al.*, 1957). Others, however, are able to produce antifreeze protein or glycoprotein molecules which are found in the blood plasma and extracellular fluids (Scott *et al.*, 1986; Davies *et al.*, 1988). Although variable in structure, the antifreezes all act in a similar fashion, inhibiting ice propagation by binding to the prism faces of embryonic ice crystals and preventing water molecules from being added to the ice lattice (Davies and Hew, 1990). They lower the freezing point of solutions in which they are found by more than 200–300 times that which would be expected on the basis of colligative properties alone, while showing the expected (small) colligative effect on the melting point of the solid phase (ice) (DeVries, 1988). As their action is primarily to inhibit ice crystal growth at the expected freezing point, and their presence has little detectable effect on the melting point of the plasma and extracellular fluids, antifreeze activity within a solution can be measured as the difference (termed thermal hysteresis °C) between the observed freezing and melting points. The more antifreeze a fish has in its plasma, the greater the thermal hysteresis, and the lower the temperature that such a fish can survive in the presence of ice (Fletcher *et al.*, 1986).

However, in addition to the above ability, recent experiments have revealed that the antifreezes possess a second property, of possibly equal significance to their ability to increase absolute freeze resistance.

Increased tolerance to low environmental temperatures

In mammalian tissues, a major cause of cell damage or death during the exposure to low temperatures is the decoupling between metabolic activities and membrane function. Low temperatures reduce the metabolic rate to the point where there is insufficient energy available to keep cell membrane ion pumps (Na^+/K^+) operating

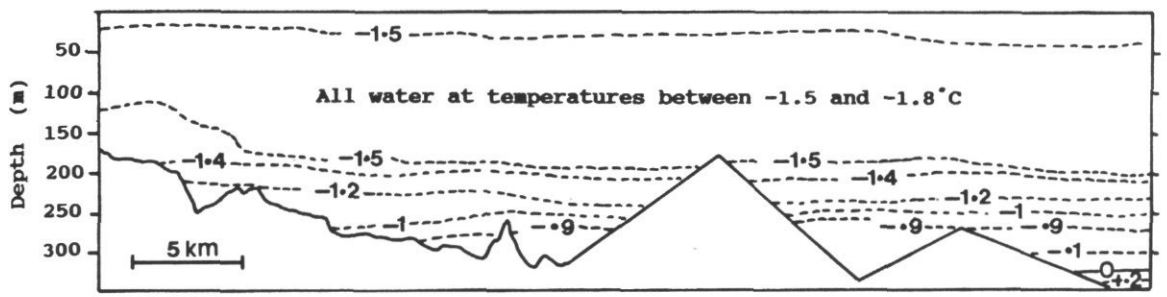


Figure 2. Generalized temperature section of a Newfoundland inshore (bay) area constructed for late March. Modified from sections taken over several years in the Random Island area of Trinity Bay, Newfoundland by Wroblewski *et al.* (1993). The section runs from the coast (left) out to sea (right). ----- = Isotherms (°C).

effectively. However, ion flow through passive cell membrane channels is largely unaffected by temperature. At low temperatures, this leads to an imbalance between ion flow through passive channels and that taking place via ion pumps. This results in a loss of the ionic gradient necessary for normal cell function, and ultimately, cell depolarization and death (Hochachka, 1986). In a recent series of experiments, Rubinsky and colleagues showed that physiological concentrations of all the known types of fish antifreezes can render cold-sensitive mammalian cells cold-tolerant. Further research demonstrated that these antifreeze proteins can inhibit or suppress calcium and potassium currents across the cell membrane (Rubinsky *et al.*, 1990, 1991, 1992). Taken together, these two findings suggest a mechanism whereby antifreeze proteins could reduce ion leakage across cell membranes, possibly protecting cells from depolarization at low temperatures. If this is the case in teleost fish, then the presence of antifreeze in the extracellular fluids may play a vital role in allowing fish to function normally at extreme low temperatures.

Antifreeze production in northern cod at different stages in the life cycle

The pattern of antifreeze production in Atlantic cod changes during the life cycle and appears to reflect the requirement for freeze protection at different life history stages (Fletcher *et al.*, 1987; Kao and Fletcher, 1988; Goddard *et al.*, 1992; Valerio *et al.*, 1992).

Egg stage

There is general agreement that cod spawning takes place off the coast of Newfoundland during the spring, and that conditions of surface ice and low water temperatures can be encountered at the time when eggs are present in the water column (Serebryakov, 1965, 1967). Although this would suggest that cod eggs risk mortality due to freezing, studies have shown that they are remarkably freeze-resistant, remaining unfrozen at temperatures down to −4.0°C (Valerio *et al.*, 1992). Since the minimum seawater temperature is approximately −1.8°C, cod eggs seem to be in no danger of freezing in the ocean (Table 1). However, this is not due to the presence of antifreeze within the egg, but rather to the fact that the chorion surrounding the egg is impervious to ice crystal penetration (Valerio *et al.*, 1992). Cod eggs have been reported to develop and hatch at temperatures <0°C (Hardy, 1978), thus cod appear to be well protected up to the point of emergence from the egg.

Larvae

On hatching, the protection of the chorion is gone, and the seemingly fragile cod larvae are exposed to the elements. However, somewhat like the eggs, the larvae are remarkably freeze-resistant and can survive exposure to temperatures down to approximately −1.3°C in the presence of ice (Table 1). Again, they do not appear to possess any measurable levels of antifreeze in their body fluids but, like the eggs, the key to their freeze resistance seems to lie in the relative impermeability to ice of their external epithelial tissues, coupled with the lack of secondary gill structures (Valerio *et al.*, 1992). It is thought that the gill filaments and secondary lamellae could be a major route of ice penetration and inoculation of the extracellular fluids, and that the vulnerability of the larvae to freezing increases as these structures develop (Valerio *et al.*, 1992). Since the rate of development of such structures is temperature-dependent, low environmental temperatures may result in the larvae having time to drift into ice-free waters before their more ice-permeable tissues develop.

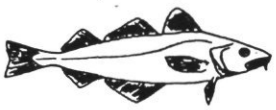
Post-metamorphic cod

In the eggs and larvae, considerable freeze resistance is conferred by the external epithelial tissues. Thus, the question arises, does measurement of the freezing points of plasma samples taken from postmetamorphic cod give an accurate representation of their lower limit of temperature tolerance in the presence of ice in the wild? To answer this question, cod, ranging in size from 29 to 54 cm, were individually subjected to gradual cooling and lethal freezing (ice inoculation) conditions. Details of the method used can be found in Fletcher *et al.* (1986, 1988). Prior to actual fish freezing experiments, the internal temperature of large and small cod was measured by inserting a thermistor probe through the mouth into the stomach. The surrounding water temperatures were measured simultaneously, and it was found that at temperatures near the expected fish freezing point (i.e., below the mean unprotected plasma freezing point of −0.7°C), fish were very slightly (by less than 0.1°C) warmer than the surrounding water. This was taken into account when using water temperature as fish freezing temperature during the following experiments.

In ice-free water, cod could be cooled to temperatures below the plasma freezing point without showing the typical freezing response exhibited when inoculated with ice at such low temperatures. For each fish, the lethal freezing point was determined by gradually lowering the water temperature in steps over a period of hours (allowing time for stabilization between steps) with ice continuously present in the water. In addition, cod were periodically inoculated with ice using a frozen, seawater-soaked wooden splint.

At the point of death, the water temperature was recorded and a small blood sample taken for antifreeze analysis using the method of Kao *et al.* (1986). The

Table 1. Mean lethal freezing temperatures and possible risk of mortality in the wild of cod eggs, larvae, juveniles, and adults during their period of maximum freeze protection.

Life history stage	Mean lowest limit of freeze resistance	Risk of freezing mortality in the wild
Eggs 	−4°C (Valerio *et al.*, 1992)	Nil
Larvae 	−1.3°C (Valerio *et al.*, 1992)	Possible risk if developing in the plankton during a cold, icy year.
Juveniles (<30 cm) 	−1.55 ± 0.06°C (Kao and Fletcher, 1988) −1.41 ± 0.07°C (Goddard *et al.*, 1992) −1.64 ± 0.02°C (Goddard, unpublished data for 1990–1991)	Well protected under most circumstances, but extreme low temperatures and ice mixing in shallow water could cause mortalities.
Adults (>50 cm) 	−1.15 ± 0.05°C (Fletcher *et al.*, 1987) −1.23 ± 0.02°C (Kao and Fletcher, 1988) −1.28 ± 0.03°C (Goddard, unpublished data for 1990–1991)	Possible risk of mortality since sea temperatures in NFLD waters often fall below cod freezing point with ice present in the water column.

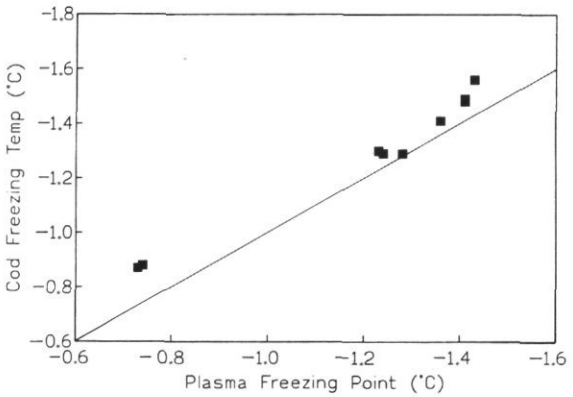


Figure 3. Lethal freezing temperature of Atlantic cod modified by the presence of antifreeze. Results of experiments to determine the relationship between fish freezing point and plasma freezing point. Each point represents an individual fish (n = 9). Water temperature at the time of death is used to represent cod freezing temperature. Solid line represents exact coincidence between plasma freezing point and whole fish freezing point.

results show that taking into account the very slight difference between internal and external temperatures, the freezing point of the plasma sample (plasma freezing point) gives a close approximation to the whole cod freezing point (Fig. 3). In other words, in the presence of ice (where supercooling is not possible) the freezing point of postmetamorphic cod is approximately equal to their plasma freezing point.

Thus, unlike the eggs and larvae, where freeze-protection is conferred mainly by the integrity of the external epithelial tissues, the freeze resistance of post-metamorphic cod appears to depend primarily on their ability to produce antifreeze glycoproteins.

Juvenile cod

From September onwards, pelagic 0-group cod juveniles are found both inshore and over the offshore banks in 2J, 3K, and 3L (Bulatova, 1973; Lear and Wells, 1984;

Anderson *et al.*, 1992). Since migratory behaviour in cod seems to be mainly a feature of late juveniles and adults, it is likely that young juvenile cod will remain for some time in the area where they first settle out of the plankton (Lear and Green, 1984). Young cod are widely distributed, therefore the range of winter habitats they occupy will vary. Those overwintering inshore will most likely be living at sub-zero temperatures for at least part of the winter (Fig. 2). Since juveniles tend to occupy shallower water than the adults (Jean, 1964; refs. in Goddard *et al.*, 1992), even those overwintering offshore may experience sub-zero temperatures (although their thermal regime is harder to predict).

As winter approaches and water temperatures gradually decline, experiments have shown that juvenile cod produce large amounts of antifreeze. The induction temperature for antifreeze production in juveniles appears to be somewhere between 2 and 3°C, and therefore, by the time temperatures fall below 0°C they are well prepared to meet all but the most severe winter conditions (Table 1) (Goddard *et al.*, 1992). This is in contrast to the situation in adult cod where temperatures of 0°C are necessary before the rise in plasma antifreeze levels can be seen (Fletcher *et al.*, 1987). If, as winter approaches, juvenile cod inhabiting water at 2°C and below produce and accumulate high levels of antifreeze, it is difficult to imagine that they would encounter dangerously low winter temperatures for which they were unprepared. Indeed, development of high levels of freeze protection appears to be almost obligate in juvenile northern cod, suggesting that they adopt a "ready-for-anything" approach to winter, whether they are spending it inshore or offshore.

Adults

Antifreeze production in adult northern cod has been the subject of study for some time (Hew *et al.*, 1981; Fletcher *et al.*, 1982; Fletcher *et al.*, 1987; Goddard *et al.*, 1992). While some degree of interannual variation can be observed in cod held in the laboratory, the cycle of production is relatively consistent from year to year (Fletcher *et al.*, 1987). Antifreeze first appears in the plasma as water temperatures fall below 0°C (early January), and, provided temperatures stay low, plasma antifreeze levels build up to a maximum around mid-March. At temperatures of 1°C and above, plasma levels remain low or undetectable (Fletcher *et al.*, 1987).

Recent experiments on adult cod suggest that although low temperatures (0°C and below) are necessary for the accumulation of plasma antifreeze, it is the gradual decline in water temperatures with the onset of winter that provides the stimulus for antifreeze synthesis. In these experiments, two groups of adult cod were maintained in two specific temperature regimes

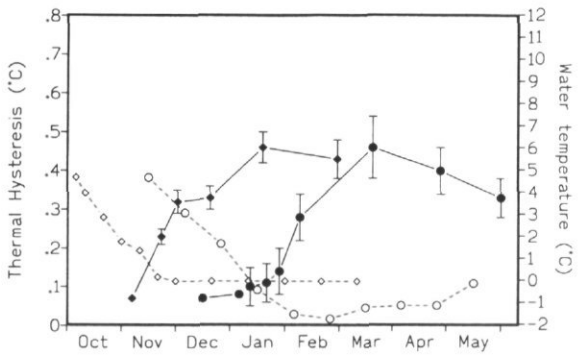


Figure 4. Early induction of antifreeze in adult cod (>50 cm) exposed to an advanced falling temperature regime during the fall–winter of 1990–1991, as compared to antifreeze production in adults (>50 cm) exposed to the ambient (naturally occurring) temperature cycle during the same period. Filled circles = Thermal hysteresis in adults exposed to ambient temperature cycle (open circles). Filled diamonds = Thermal hysteresis in adults exposed to advanced (induction) temperature cycle (open diamonds). All values of thermal hysteresis are means ± 1 s.e.

(Fig. 4) during the winter of 1990–1991, and were monitored for antifreeze production in the usual way (Fletcher *et al.*, 1987; Kao *et al.*, 1986). One group (n = 10) was kept under ambient (natural) conditions of photoperiod and temperature, sea water being pumped directly into the tank from the surface waters of Logy Bay, Newfoundland. This group experienced a gradual decline in water temperatures from 5°C during the first week in November, to 0°C on 7 January. Detectable levels of plasma antifreeze were first recorded on 9 January, rising to a peak in mid-March (Fig. 4). Individuals in the second group (n = 10) were also exposed to natural photoperiod, but in their tank the water temperature was manipulated to mimic ambient conditions shifted forward in time by approximately 6 weeks, i.e., exposure to mid-December temperature on 1 November, etc. (Fig. 4). These cod first experienced 0°C on 20 November and were held at 0°C for the duration of the experiment. Water temperatures in both tanks were recorded daily (Cole Palmer "Quick" electronic thermometer, Model no. 8517-00). The results of this experiment clearly show that antifreeze production in adult cod can be advanced in response to an early progressive fall in water temperatures (Fig. 4). It appears that at some point during exposure to a falling temperature regime (5°C to 1°C) synthesis of antifreeze is initiated. If temperatures continue to fall to 0°C and below, antifreeze levels in the plasma build up to detectable levels. Thus, provided the fall to sub-zero temperature is not abrupt, adult cod in the wild do have the ability to prepare for sub-zero temperatures before such conditions arrive. Such an ability appears to be vital to

survival under certain circumstances, for example, in adult cod overwintering inshore.

Use of laboratory data to interpret data from the field

Laboratory data on the physiology of antifreeze production in adult "northern" cod can be used to interpret data on antifreeze levels found in free-living cod in the field (provided that care and caution are exercised). The build-up of antifreeze in the plasma of adult cod depends on their continued exposure to temperatures at or below 0°C. We have found that antifreeze levels are significantly correlated to the length of exposure to sub-zero temperatures during the rising phase of antifreeze production (approximately 75 days from day 1 at 0°C) (Fig. 5). This relationship can be used to estimate cod residence times in sub-zero waters. Thus, by measuring plasma antifreeze levels, it is possible to make some deductions as to the recent thermal history of the cod, and, when viewed in conjunction with the relevant field temperature data (an essential component), to draw conclusions as to fish distribution within the temperature field. In other words, plasma antifreeze levels can act as biological indicators of exposure to sub-zero temperatures in the wild.

Current and future research

There is little doubt that environments characterized by freezing conditions select for cold-tolerant, freeze-resistant species. Therefore it is reasonable to hypothesize that the level of freezing resistance exhibited by a species or population is a reflection of the freezing conditions they have encountered.

Within one species, there can be considerable population differences in the ability to produce antifreeze. For example, under the same conditions of temperature and photoperiod, ocean pout (*Macrozoarces americanus*) from Newfoundland waters develop considerably more freeze resistance than those from New Brunswick (Passamaquoddy Bay) (Fletcher *et al.*, 1985). The difference between the two populations appears to be a reflection of the number of antifreeze genes they possess. Newfoundland ocean pout have approximately 150 antifreeze genes, whereas those from New Brunswick have less than a quarter of that number (Hew *et al.*, 1988). Similar results have been obtained from winter flounder (*Pleuronectes americanus*, formerly *Pseudopleuronectes*) inhabiting several geographic locations (Hayes *et al.*, 1991). Thus, there is a strong positive correlation between antifreeze gene dosage, antifreeze levels, and the environmental freezing conditions likely to be experienced. This suggests that observed population differences in cold adaptation and freeze resistance are the result of environmental selection. It also seems possible that changes within a population could be the result of a similar selection process, or of changes in population structure due to migration.

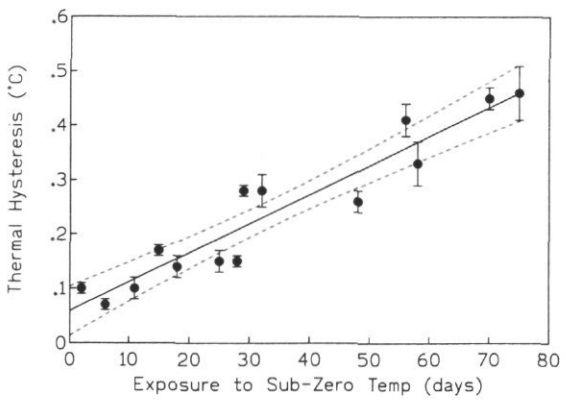


Figure 5. Relationship between thermal hysteresis (plotted as means ± 1 s.e.) and length of exposure to sub-zero temperatures in adult cod. Dotted lines are the 95% confidence limits around the regression.

Bearing this in mind, it is of considerable interest to note that adult cod sampled on 6 January 1993 (Fig. 6) had mean antifreeze levels considerably higher than expected or indeed ever observed on this date in adults exposed to ambient temperature cycles in the past. Indeed, the levels recorded for the adults on this date were closer to those observed in the larger juveniles sampled on 13 January 1993 (Fig. 6) than to our previous findings for adult cod. These preliminary results cannot be explained by any obvious difference in water temperatures between years (Fig. 6, and Fletcher *et al.*, 1987). Thus, it appears that there has been a shift (yet to be explained) in the timing of antifreeze production in these adult cod.

While the phenotypic expression of antifreeze in cod from different geographic locations is currently under investigation, the ability to quantify genetic differences between cod populations in terms of antifreeze gene dosage would be of great value in any discussion on the ability resident within different populations to adapt to changes in the ocean climate. For example, information on population differences in gene dosage could be useful in understanding population or stock distribution over the geographic range occupied by the Atlantic cod. Inter- and intra-population differences in gene dosage could give an indication of the ability to adapt to changing environmental conditions. Finally, examination of cod tissue samples collected in previous years might identify changes in antifreeze gene dosage within a population or geographic area, providing clues as to the impact of extreme low temperatures on different cod stocks, both in terms of selection and migration.

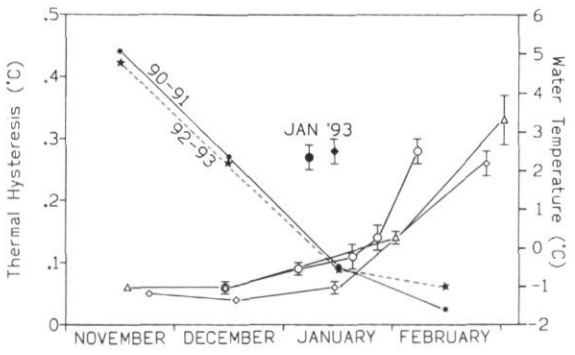


Figure 6. Shift in the onset of antifreeze production in adult northern cod monitored during the winter of 1992–1993 compared with three typical years from the past decade (1983–1984 = open triangles; 1987–1988 = open diamonds; 1990–1991 = open circles). All antifreeze levels are expressed as mean values (± 1 s.e.), and values of n for each data point range from 10 to 18. Monthly mean water temperatures are given for the winters of 1992–1993 and for 1990–1991 (typical of preceding years during the past decade, see Fletcher *et al.*, 1987). Mean thermal hystereses ± 1 s.e. for adults and juveniles sampled in early January 1993 are represented as follows: Adults (mean length 50.1 ± 1.3 cm) = filled circle, n = 20: Late Juveniles (mean length 30 ± 0.5 cm) = filled diamond, n = 48. In all years, cod were obtained from the same geographic location (Conception Bay, Newfoundland) and overwintered during the sampling period in the Logy Bay Laboratory raceway facilities.

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Genetic studies of families of Arcto-Norwegian and Norwegian coastal cod: preliminary random amplified polymorphic deoxyribonucleic acid studies

Geir Dahle

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Information about reproductive success is difficult to obtain, since observation of spawning behaviour may be deceptive. Certain molecular biological methods could make such results easily obtainable. In this study RAPD (Random Amplified Polymorphic DNA) is examined as a way of determining parentage. PCR (Polymerase Chain Reaction) amplifications with short primers produce many fragments that can be exceedingly variable between individuals. Twenty-three of the 60 primers (10-mers) used produced readable profiles, and two produced diagnostic bands which may be used to exclude incorrect relationships.

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Introduction

Accurate measurements of reproductive success are critical to an evolutionary approach to behaviour, and such information is difficult to obtain. Methods of evaluation of relatedness have in the past been based on observations and genetic markers in artificially reared individuals (Jørstad *et al.*, 1987). Observations of spawning behaviour and spawning success may be deceptive because offspring may not be the product of observed matings, and some matings might not be observed.

The availability of different molecular biological methods facilitates such studies. Genetic methods involve sampling the offspring and determining the parents from a large or small pool of individuals using some genetic marker. Diagnostic markers make parental inclusion possible, but, alternatively, identification may be based on exclusion when individuals from a small population (i.e., spawning pen) are eliminated as the parents.

In most cases of allozyme analysis there is too little variation to make an inclusion identification of the parents. Exclusion and likelihood analysis could be used in the identification, but this would require a high level of variation in cod allozymes.

DNA markers have been used for assessing the reproductive success, the best-known technique being DNA fingerprinting with minisatellite sequences as probes (Dahle, 1994). Owing to great variability, minisatellite DNA fingerprinting offers an enormous advantage over allozyme analysis in establishing parentage, and has been used successfully in the study of reproductive strategies in birds (Burke and Bruford, 1987; Burke 1989) and mammals (Reeve *et al.*, 1990; Packer *et al.*, 1991). The dominant method of analysis in most studies determining parentage and relatedness is band-sharing. When there are few potential parent couples for each offspring as in a spawning pen, it is possible to assign parentage with absolute certainty, especially since unrelated cod individuals share only about 15–28% of their minisatellite DNA bands (Dahle, 1994).

RAPD (Random Amplified Polymorphic DNA) might be an excellent option for determining parentage. This technique uses a single short primer (10–20 bp long) to amplify regions of the genome. PCR (Polymerase Chain Reaction) amplifications with these primers produce numerous fragments that can be exceedingly variable between individuals and have proved useful for parentage analysis (Scott and Williams, 1993). The only limit to the amount of variation is the number of primers used. The main objective of this study was to identify short primers that can be used in pedigree studies of cod.

Materials and methods

Arctic and coastal cod (*Gadus morhua* L.) were stripped by hand and fertilization of the egg from one female with milt from one male was carried out in small plastic containers to ensure the parentage of each family group. A biopsy was taken from all parents for DNA isolation. Two or three groups were placed in the same tank and after metamorphosis 15 larvae were collected from each of 15 tanks.

DNA from all samples was isolated by normal phenol/chloroform extraction (Sambrook *et al.*, 1989). Four families, three coastal and one Arctic cod family, consisting of four offspring and both parents each were used in the study. Parentage has been established previously with multilocus analysis of all samples by using a multilocus probe – 33.15 (Jeffreys, *et al.*, 1985) on both parents and possible offspring (Dahle, in prep.).

RAPD was carried out on an MJ RESEARCH PTC-100 cycler for 35 and 45 cycles in 0.2 mM dNTP, 2 mM $MgCl_2$, 50–60 pmol primer and 25–100 ng cod DNA (template). Sixty 10-mer primers (Operon Technologies, CA, USA) and four 15-mer and 20-mer commercial primers (Promega) were tested. The temperature profile used on the cycler in this study was: 1 min at 94°, slow transition (2 min) from 50° to 34°, 2 min at 34°, slow transition (1 min) to 72° and 2 min at 72°. The amplification was started with a denaturating step, 94° for 3 min. The reaction mix was overlaid with two drops of mineral oil. All primers had a GC percentage of between 60 and 70.

All amplifications, including the control PCR samples (without template), were tested on a 1.4% agarose gel. Samples with amplification products were run on a 3% NuSieve agarose gel (5 V/cm, 3 h) (Fig. 1).

Table 1. Oligonucleotide primers (10-mers) and their sequences used in this investigation (data from Operon Technologies, CA, USA). The right-hand column shows maximum number of bands obtained by amplification with the respective primer and NuSieve gel electrophoresis.

Primer	Sequence	Max. no. of bands
OPA-01	CAGGCCCTTC	13
OPA-02	TGCCGAGCTG	10
OPA-04	AATCGGGCTG	3
OPA-06	GGTCCCTGAC	5
OPA-08	GTGACGTAGG	11
OPA-09	GGGTAACGCC	6
OPA-10	GTGATCGCAG	4
OPA-11	CAATCGCCGT	6
OPA-12	TCGGCGATAG	9
OPA-20	GTTGCGATCC	3
OPB-04	GGACTGGAGT	2
OPB-05	TGCGCCCTTC	2
OPB-06	TGCTCTGCCC	4
OPB-07	GGTGACGCAG	5
OPB-08	GTCCACACGG	6
OPB-11	GTAGACCCGT	4
OPB-12	CCTTGACGCA	5
OPB-15	GGAGGGTGTT	7
OPB-17	AGGGAACGAG	5
OPC-02	GTGAGGCGTC	8
OPC-05	GATGACCGCC	6
OPC-09	CTCACCGTCC	2
OPC-20	ACTTCGCCAC	9

Results

With the amplification conditions used in this study, 23 (38.3%) (Table 1) of the tested 60 10-mer primers produced amplified products that could be scored on agarose gels. Four long primers (15-mers and 20-mers) tested at these amplification conditions gave no scorable

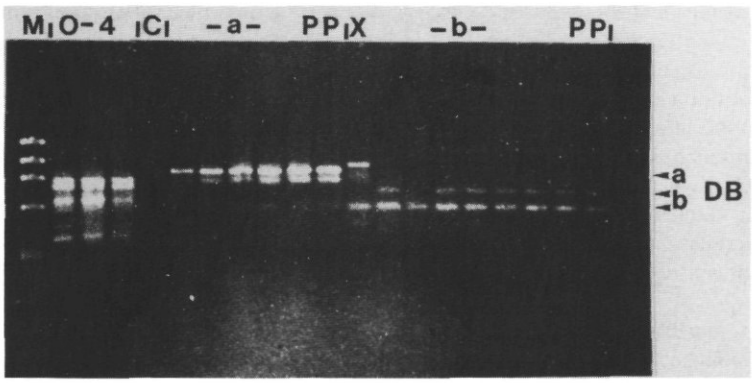


Figure 1. DNA from two of the four families amplified with one of the primers, OPA-08. **M** = marker DNA (fag øX174 digested with *Hae* III), **P** = parent; **a** and **b** = offspring. **NB** = non-parental fragment (family A). **DB** = diagnostic band (family A and B), **C** = control (without template) and **X** = individual with non-parental fragment. **O–4** = DNA from three individuals amplified with primer OPA-04.

product (data not shown). The products varied in length from approximately 0.1 to 2.5 kb, although most products were in the range 0.3–1.4 kb. All bands were scored by absence vs. presence of amplification product and a maximum of 135 bands were generated by the 23 primers. The number of bands per primer varied from 2 to 13 (Table 1), with an average of about 6. Among the 135 bands, 56 (41.5%) were constant among all samples, only two of the primers producing an amplification product (OPB-04 and OPC-09) were monomorphic.

Only one primer produced a non-parental band, and primers OPA-08 (Fig. 1) and OPB-06 produced diagnostic bands to exclude incorrect relationships.

Discussion

The development of DNA fingerprinting from hypervariable sequences (Jeffreys *et al.*, 1985) was a significant advance, and made it possible to determine parentage for the investigation of reproductive success and behaviour of species like birds (Burke, 1989; Burke and Bruford, 1987), mammals (Reeves *et al.*, 1990), and fish (Dahle, in prep.). DNA fingerprinting is time-consuming, however, and requires both technical experience and large amounts of DNA (5–6 μg). The RAPD method is technically easy, fast, and requires very small amounts of DNA (10–100 ng), which makes it suitable for studies of minute animals (i.e. cod larvae prior to metamorphosis). The method has already been used successfully to provide information on parentage in other species (Scott and Williams, 1993).

The PCR is a very sensitive method and the nature of the amplification process might result in contamination of the PCR reaction. This could be a problem in larval studies because DNA is often extracted from the whole organism, and DNA from gut content may be simultaneously extracted. The larval DNA in this study was extracted from either head or tail to reduce the possibility of contamination from the digestive system.

Although only one non-parental band was observed (Fig. 1), non-parental bands have been reported in other species (Scott *et al.*, 1992; Riedy *et al.*, 1992). The appearance of non-parental bands in the offspring using 10-mer primers has raised some concern over the RAPD technique. The number of such bands is probably dependent on the PCR conditions and on the various concentrations of the components (i.e., primer, template DNA, DNA polymerase, dNTP's and $MgCl_2$) in the reaction solution. If diagnostic bands exist in the parents (Fig. 1), these could be used in the analysis, and absence of a parental band in the offspring could be regarded as insignificant in a pedigree study.

RAPD studies in other species have shown that primers should be at least 40% GC and that good amplification patterns were seen with primers of up to 100% GC (Williams *et al.*, 1990). High GC primers result in more amplification products (Caetano-Anolles *et al.*, 1991). However, there was no correlation between GC percentage and number of bands (amplification products) in this study.

The temperature and length of time required for primer annealing is dependent on base composition and length of primer. Primers might be expected to anneal more strongly if they are high in GC, resulting in a high melting temperature, i.e., high annealing temperature. Depending on the application, annealing temperature should be as high as possible (an annealing temperature of around 50°C is desired). A high annealing temperature enhances discrimination against incorrectly annealed primers, which could be a problem working with small primers (10-mers) in RAPD analysis. Using the rule-of-thumb calculation for melting temperature of the DNA strand (Thein and Wallace, 1986) the annealing temperature for the Operon primers (10-mers) used in this study should be 32–34°C, a low annealing temperature.

The reproducibility of PCR experiments is important. The reaction is very sensitive to alterations in PCR conditions, such as template, primer and $MgCl_2$ concentration, but also to small changes in temperature profile (data not shown). Consistent results require accuracy and no change of cycler throughout the experiment. Small changes in template and primer concentration did not alter the PCR products, nor did alteration of the annealing temperature from 34°C to 32°C.

The result of this study indicates strongly that RAPD PCR with short primers (10-mers) can be used in pedigree studies of cod larvae. By using two or three different primers in conjunction, non-parental individuals can be excluded in small populations. This study will be continued with an examination of other primers and combinations of two different primers in the same PCR reaction. Experiments with the latter have shown that two short primers together produce discrete and reproducible profiles that differ from those obtained with each single primer (Micheli *et al.*, 1993), and therefore could give more information.

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General discussion and closing of the symposium

The final session of the Symposium was divided into three parts. The Convener, Jakob Jakobsson, gave a summary of the main features, and this was followed by a general discussion, after which the Symposium was closed. The session was taped and the main points are published here.

ODD NAKKEN (Chairman):
You will have the floor Jakob.

JAKOB JAKOBSSON:
I would like to start this review by dealing with *Session 3*, which was on the physical processes and models of North Atlantic circulation and shelf systems. The presentations and discussions in this session focused on the effects of wind and temperature changes. It was demonstrated that although effects of slow shifts in the large-scale North Atlantic windfield were seen simultaneously throughout the area, the actual effects in the various subareas are different because of varied regional responses. Examples of such responses relevant to cod stocks were given as follows. Decadal to centennial changes in the atmospheric circulation pattern, for example as expressed by the North Atlantic cyclonicity/anticyclonicity index, affect the intensity of the four major cyclonic gyres in the subpolar North Atlantic Ocean, namely in the Labrador, Irminger, Iceland, and Greenland seas. This implies that the intensity of advection of the cyclonic current system changes, and thus also the larval drift pattern, affecting inter-stock exchanges like the one for example between Iceland and Greenland. It also implies changes in the upwelling intensity within the gyres. Through the stratification this affects the intensity of deep and intermediate water formation, resulting in changes in upper layer temperatures and a change in the intensity of the Polar Fronts and the Arctic Fronts related to the gyres. These changes also control the flux of fresh water from the Arctic Ocean within the system of polar currents, leading to pulses of cold and low saline water like the Great Salinity Anomaly. Changes in the windspeed also occur on large time scales. Enhanced turbulence in the near-surface layers increases the contact rates between predator and prey. As regards changes in directional windspeed, important effects are known about the exchange of deep waters in semi-enclosed seas like the Baltic, where direct relations between living conditions for cod and series of intense westerly winds have been shown. The effects of global warming were discussed in relation to large-scale atmospheric temperature changes. Since we cannot yet conclusively distinguish between global warming and natural fluctuations, models with coupled ocean/atmosphere circulation are applied to conditions with increasing CO_2 in the atmosphere and the results derived through these models show maximal warming in high latitudes with several important exceptions, such as at Greenland and Iceland.

Session 4 dealt with models of biophysical processes influencing the dynamics of cod populations. The term biological processes addresses a wide range of topics which can influence recruitment and growth. From a very general point of view the relevant physical parameters in this context are limited to temperature, salinity, light conditions, buoyancy, and motion. All the papers and posters in this session addressed different aspects of motion. We are certainly all aware of the importance of dynamics in the drift and dispersion of eggs and larvae from the spawning areas. However, it is only recently that the importance of the currents in the microscale environment in relation to the feeding of larvae has come to our attention. In recent years we have seen great improvements in the numerical models simulating drift and the dispersion of eggs and larvae. To some extent, this has had to do with the modelling techniques, but it is also because of the input of data on factors such as spawning period, spawning site, buoyancy, and vertical behaviour of the larvae. The modelling from three regions, Georges Bank, the Newfoundland Shelf and the Barents Sea, shows that the mechanisms for transport and dispersion are very different. The vertical distribution of eggs and larvae seems to be very important for the resulting transport of Georges Bank and Labrador cod, while for the Arcto-Norwegian cod the horizontal transport is much less sensitive to variations in the vertical distribution of the larvae. However, all three model results demonstrate the importance of windfield variations on the interannual variations of the distribution of the juveniles. On the level of small-scale dynamics we are now seeing increasing evidence of the Rothschild and Osborn theory.

Session 5 dealt with the biology of cod, stock identity, migration, stock structure, recruitment processes, and population dynamics. During this session we realized that it is of critical importance to correctly identify discrete populations and associated time and

space scales if population processes are to be resolved. Our present predisposition to study biology at the stock or management unit level may result in oversights of wider issues and general patterns. For example, it appears that spawning on the Labrador and Grand Banks takes place over a more extensive period than in the Northeast Atlantic. However, this difference may be an artifact of aggregation across spawning concentrations and years. A comparative approach is an effective means of identifying factors which influence cod production and distribution. The general distribution of cod stocks is well known and can be related to temperature, salinity, oxygen, and depth. It could be an advantage to look for general patterns in cod growth, such as the relationship between size-at-age across stocks and the average annual hydrographic condition. One could also seek relationships between mean recruitment and the magnitude of certain attributes common to cod spawning grounds, such as the volume of water of a critical temperature for the survival or distributional area of the eggs or larval stages. It is generally recognized that the processes which limit distribution and production could be contingent on the geographic location of the stock, and levels of data aggregation need to be considered carefully. Distinguishing between the effects of fishing and environmentally induced changes in stock distribution and production has proved very difficult, but it is a highly important task. Several cod stocks have recently experienced declining recruitment, environmental extremes, and severe exploitation. In addition, the loss of spawning components, low spawning-stock biomass, and change in age composition due to fishing could possibly increase a stock's susceptibility to environmental variation. Many studies have shown that 0-group abundance indices correlate reasonably well with year-class abundance levels, leading to the conclusion that year-class strength is established during the first few months of life, although there was evidence of important periods throughout the first winter of the 0-group. Studies in which correlative and descriptive approaches have been taken have shown that biological and physical factors influence distribution, growth, and survival. Warm years are generally associated with higher cod production among high latitude cod stocks. One potential shortcoming of such studies is that proxies, like temperature, may not adequately represent the assumed processes being modelled. The emphasis on studying factors influencing survival during the early life stages is not balanced by a similar emphasis on studies dealing with survival processes acting on juveniles and adults.

Session 6 dealt with the trophic relations of cod. Trophic interactions of cod were reviewed for the Barents Sea, North Sea, Iceland, Newfoundland, and Baltic ecosystems. Diet composition was similar across ecosystems in that fish were the major prey of adult cod, while crustaceans constituted the most important prey of juvenile cod. However, the particular prey species differed in each of the ecosystems, although capelin is the main prey in at least three of them. Cod is preyed upon by other fishes, marine mammals, marine birds, and several invertebrate species. However, this is mainly true for juvenile cod and the magnitude of these impacts is unknown. Much more information is required before reliable quantitative estimates of predation mortality on cod can be derived. Cannibalism may occur in some regions but not in others. Most cannibalism involves predation on younger age groups and small-sized fish and is most significant in 0-group and 1-group individuals. Again, however, there are only a few reliable estimates of the intensity of cannibalism in any region. Studies of changes in the stock distribution of each stock are essential if we are to better understand and evaluate the intensity of cannibalism and its possible significance in affecting recruitment. Temporal and spatial changes in the abundance and biomass of the prey of cod are generally reflected in the composition of the diet, although there are few data on the suitability of alternative prey species or on the ability of cod to seek out particular prey species. Statistical analysis of cod stomach content data is often hampered by a large proportion of empty stomachs and stomachs that have been bulked or aggregated before the contents have been measured or counted. However, models and procedures have been developed to take account of these factors in deriving statistically reliable estimates of average stomach contents by length group. These models also take account of other independent variables.

Sessions 7 and 8 dealt with experimental studies, physiology and genetics. It was demonstrated how the experimental approach can help in the testing of hypotheses concerning the life history of cod which otherwise would be difficult or impossible in the complex and highly variable marine environment. However, careful design of the experiments is of vital importance and care must be taken when inferences are made about field situations. The study of eggs and larvae seems to be particularly well suited to experimentation, as indicated by the numerous articles presented on these subjects. Interesting relationships between egg size, size of spawning cod, and time of spawning were presented. These studies may shed some light on the quality of the spawning stock in relation to its age/size structure. Further studies may give fisheries' managers information about the optimal age/size structure of the spawning stock of cod.

Relationships for predicting the time of spawning of cod from the size of oocytes and the temperature were also presented. The experimental approach was also used in the study of the difference in growth rate and survival of two different cod stocks. A new method for studying the activity of cod larvae under different light conditions was introduced and the stage-dependent changes in the density of cod eggs were studied in the laboratory in an attempt to understand the observed vertical distributions of cod eggs in the sea. Finally, we learned that new techniques seem to be on the horizon which, together with tagging and migration studies combined with genetic investigations augur well for the future. Such studies could explain genetic variation between populations and subpopulations and thus help managers in identifying management units. I believe this is something to look forward to.

Sessions 1 and 2 dealt with historic reviews and diagnosis of the causes of trends and fluctuations. We learned that archaeological excavations of fish bones indicate that cod of 1–1.5 m were regularly taken in the period from the 12th to the 19th century throughout the North Atlantic. Historical records of the cod fisheries around both Iceland and the Northeast Arctic since the 16th century show that there were considerable fluctuations, and that these appear to have been linked to changes in climate. It was expressed that the climatic fluctuation could also have affected the actual fisheries and not just the fish stocks. In cold periods it is true that the catch per unit effort fell, but showed an increase when environmental conditions became more favourable. This was the case for cod stocks in general until the beginning of the 1950s.

We have seen that landings of the North Atlantic cod stocks reached a maximum of 3.7 million tonnes in the late 1960s but have been declining in recent years. This decline is really the main issue under debate at this Symposium. The data presented in large part cover the period to 1990 and there have been some very interesting occurrences since then. First, there is now a moratorium on the northern cod at Newfoundland. In the Barents Sea, where fishing pressure was temporarily decreased, the Arcto-Norwegian cod has responded very favourably and there the fishing is now increasing. However, heavy fishing is or has been common to all cod stocks. But they have also been affected by environmental conditions, although these are very different from one area to the next. In the Baltic, for example, the Baltic cod, apart from having suffered from very heavy fishing, is also faced with reduction in salinity and oxygen. In the North Sea we have to pose the question: What is the cause of the low level of recruitment in the most recent years? Is it recruitment overfishing or is it because the North Sea is returning to normal after the "gadoid outburst" during the 1960s. I don't think we have had a clear answer to this. At the Faroes, recruitment did not fluctuate very much for several decades until the present recruitment failure. Has this failure been because of the heavy fishing which certainly has taken place, or is it related to a change in the circulation pattern around the Faroes? Similarly, recruitment to the Icelandic cod stock has remained exceptionally steady for the last three decades, with the ratio between the lowest and the highest year class varying only threefold compared to the 20-fold in the Barents Sea. Taking the Iceland–Greenland area as a whole, it is obvious that there has been a contraction of cod distribution in recent years. However, even in Greenland, where the environmental signal is quite clear, we have to admit that just before the environmental conditions deteriorated very heavy fishing was reducing the stock rapidly. As regards the northern cod at Newfoundland, it was suggested that the low temperature and the change in salinity in the northern part of the distribution area are the main reasons for the reduction in the distribution of the stock. Further, the changes in distribution then rendered the stock vulnerable to uncontrolled distant-water fishing. In addition, a stock–recruitment relationship has been observed and, finally, it was suggested that perhaps increased natural mortality had contributed to the collapse of the stock. As in other areas, the Georges Bank cod has been subjected to very heavy fishing. So, it is very difficult to discern between the effects of overfishing and changes in environmental conditions. Nevertheless, I think we have to admit that, with the exception of the Arcto-Norwegian cod, all the North Atlantic cod stocks have been exposed to very heavy and increasing fishing pressure in the past. In 1988 it was decided to act on the ICES proposal to greatly reduce fishing pressure on the Arcto-Norwegian cod for at least two or three years and the stock responded beautifully. But why did it respond so quickly? The answer is of course that this wise decision was taken just when the environmental conditions in the Barents Sea were improving and the cod had plenty to eat. This brings me to the comment made during the Symposium that the cod is by nature a long-lived species and the heavy fishing is changing this. The longevity is possibly an adaptation to varying environmental conditions. Thus, when environmental conditions have deteriorated, for a while longevity and high fecundity help the cod to survive until the conditions return to normal. However, the present exploitation of the species is generally so great that the long-lived cod has become a relatively short-lived species. When exploiting wild animal populations, whether they are marine mammals, codfish, or invertebrates, it has to be taken into account that we can

only control the exploitation rate, we cannot control the changes in the environment. Therefore, exploitation must always be within the limitations of nature and the cod and the environment should not be considered in isolation. Instead, the large ecosystems that we have been harvesting should be studied in all of their complexity. As far as I can judge, the major message from this Symposium is the plea for a reduction in the exploitation rate of cod.

ODD NAKKEN:

This was the Convener's review of the Symposium and it is now open for comments and additions.

KEITH BRANDER:

The review we have just heard is a very useful contribution to the debate which I hope will continue during the ICES Statutory Meeting in Dublin [1993], and my suggestion or question is whether it should be incorporated as an appendix in the report of the Cod and Climate Change Working Group. I would also like to pass on a couple of things about an issue which underlines a lot of the thinking and way in which we are looking for explanations. If we are to confront an issue such as whether the fluctuations we have seen in captures in the North Sea are due to the effects of fishing or to the effects of the environment, the first thing that is fairly obvious is that it doesn't make very much sense to talk about either one or the other in isolation, they are both probably involved to some degree. And going on from that I believe that it is unreasonable to expect that we will ever know why there was a "gadoid outburst". The explanation will perhaps become slightly clearer, but I don't think we can ever expect clear answers to many of these issues. In general, the advance of knowledge helps us to understand things at a different level but it never provides clear or rarely provides clear and unambiguous explanations of events in the past. However, people who suggest that the climate should not be investigated because the effect is going to be difficult to detect against the effects of fishing are missing the point. These are perhaps small but nevertheless extremely important signals that we have to try to tease out in some way and I don't expect that we will be able to do that quickly at all. I think we have to accept that life is a bit of a mess and we just have to try and find particular ways of proceeding as a community and gradually over a long period of time begin to understand these things better.

SVEND-AAGE MALMBERG:

As a physical oceanographer I must admit that with a few exceptions the climate itself was not quite as much discussed as it should have been. We heard a lot about temperature and wind but much less about how these things are structured in the sea. Therefore, I think it might be useful if physical oceanographers or the climatological people were to make a thorough analysis, from west to east, of how the physical conditions have changed.

MIKE HOLDEN:

Like Jakob Jakobsson, I too have been looking at the lessons that we might learn from this Symposium. David Griffith commented in his opening speech that fishery managers would be looking at the results from this Symposium to provide them with guidance on managing fish stocks under variable climatic conditions, and during the course of the Symposium I have been looking at the implications of climatic change for fishery management and trying to tease out some answers. One conclusion that I fear fishery managers might draw is that climatic change makes fishery management totally impossible. That message I think might come from Dickson and Brander's article, in which they state: "we cannot manage these stocks effectively while we remain in ignorance of the many ways by which shifting climate can suddenly impose change, since these delicate and diverse mechanisms will often be the factors which will determine whether a given level of exploitation is sustainable or excessive". Drawing on that, if I have interpreted Dickson and Brander correctly, we cannot therefore determine at what rate each fish stock should be exploited. I think that many fisheries administrators might draw the conclusion from this that if a fish stock appears to be threatened by climatic change it should be exploited as heavily as possible before it disappears as a result of natural causes. I had hoped in fact that fisheries managers might take a different line of guidance from this Symposium and I really come down to the points that you, Jakob, have referred to and the points Niels Daan referred to. The guidance that I see is that, first, cod is a very resilient species, tolerating a wide range of physical factors, particularly temperature. Second, although it cannot be guaranteed that climatic changes within the range which the stock of cod presently inhabits will not reduce that stock to such a low level as to make the fishery which it supports economically unviable, the experience of what has happened at Greenland, Iceland, the Baltic, and even in the North Sea shows that under favourable conditions a stock of cod will expand rapidly and enormously when the climate improves. Small stocks can generate large recruitment; I think that's an important message that should come out of this Symposium: and, third, as Niels has pointed out, cod is a long-lived species, if we allow it to be. So from these three points I hope that fisheries administrators will

draw the conclusion that the best management strategy will be to exploit cod stocks at low to moderate levels in order to maximize the possibility of leaving as many cod as possible in the sea to benefit from climatic changes favourable to recruitment. Compared with the concept of management based on maintaining a minimum biological acceptable level of spawning-stock biomass, this is a compromise strategy which also permits fishermen and the fishing industry to survive. I think that is important; we do not want to wipe out industries by suddenly stopping fisheries when the spawning stock falls to a very low level. Personally I consider that another message from this Symposium is that climatic change makes the concept of management based on the minimum biological level of spawning-stock biomass unacceptable because climatic variability undermines the whole basis on which this level or these levels are determined. They are based on historically observed levels and, if the carrying capacity of the area changes, as it has done for the North Sea for example, the historically observed levels may become totally inappropriate. I think for the same reason that the concepts such as F med and F low are also inappropriate as bases for management. Exploiting cod stocks at low rates of fishing is not a strategy which is relevant to climatic variability alone. This is the strategy which fisheries managers should be pursuing in order to achieve the objectives which all parties pretend to want even when stocks are abundant. These objectives are stability of catches, high catch rates, better utilization of the growth potential of the fish and, what should interest the industry most, high profits. This message is not new, Michael Graham said most of it in 1935.

ODD NAKKEN:

There was a suggestion made by Keith Brander which the Convener perhaps might want to respond to and also to some of the inputs of the other participants.

JAKOB JAKOBSSON:

Keith suggested that this overview should be made available as an appendix to the Cod and Climate Change Working Group report. This is accepted, but in addition I will be giving the Council a report on the Symposium at the opening session of the ICES Statutory Meeting. I agree with most of the things that Mike Holden said, except that I think it would be very remiss if fisheries managers took it that the statements in the article by Dickson and Brander meant that fisheries management was impossible. What I was trying to emphasize in my summary was that fishery management must always be carried out within the framework of nature and that this may be different from one time to another. For instance, I think that everyone would agree that it would be silly to try to get 500 000 t a year out of the Icelandic–Greenland cod stock complex now, although this was quite easy to achieve in the 1950s. I think that managers on both sides of the Atlantic are wise enough to realize that you have to play within the natural framework. We know that it is very difficult to predict climatic changes but we will have to monitor them. It is of course better to be on the safe side, because if environmental changes take place in a favourable direction then, as often stated during the Symposium the cod is a long-lived species, it can only mean that there will be more the next year. I know that small stocks can produce large year classes; however, our recent experience in Iceland has been that small spawning stocks seem to produce large year classes less often than moderate spawning stocks. In addition, we must not forget the interesting work which is going on into the composition of the spawning stocks. Researchers ought not only to be thinking about spawning-stock biomass but also taking into account age distribution within the spawning stock. But then I am absolutely in agreement with Mike Holden that we should be exploiting these living resources at moderate levels.

NIELS DAAN:

My response to Mike Holden would be that managers have to decide how fish stocks should be exploited. If the managers do not make the decision themselves to aim at certain objectives, we can only give the advice containing various options and I think that is the approach the AFCM has taken recently.

ODD NAKKEN:

Mike Holden made some interesting points which I know could be debated at much greater length, but only a few of us would participate in such a discussion and it is therefore now closed. I now invite the participants to comment on other points in the Convener's review or anything else about the Symposium.

SVEIN SUNDBY:

Just one comment on the management of the fish stocks. It is not every day that we find physical oceanographers, recruitment people, and management people all at the same meeting, and so I ask whether we are now at a level of knowledge where we could start to use more of the information the recruitment scientists use in the management of the cod stocks. Some years ago, the Recruitment Processes Working Group took the initiative to establish the so-called cod checklist, where information was gathered on the recruitment parameters of the different cod stocks. This is now available from Lowestoft and I think it would be a good idea if ICES were to take over

and maintain it. It may contain a lot of important information that could be used in the management of the cod stocks.

ODD NAKKEN:

Perhaps you are thinking of the work the Assessment Working Groups are doing and to widen their area. One of the main discussions going on within ICES at present is how to change the ICES working procedures and therefore this should be taken care of within ICES.

FRED SERCHUK:

I see this Symposium as a great success, and not simply for cod and climate. If we evaluate the Symposium with just that merit, that we are getting some linkages between cod and it's climate, between physical factors of the environment and one species, we have really lost the broader message that I think was evident throughout this Symposium. We clearly should be focusing on the linkages and interactions between living marine resources in the case of ICES and their physical environment. So there are great incentives for future research programmes, but I think they must be seen in a wider perspective. It has been stated that Assessment Working Groups within ICES have been narrowly focused. I would point out that this is not a problem that ICES is unaware of, and over the past several years Assessment Working Groups have been restructured away from species-specific working groups to area- or environment-orientated working groups. It is recognized that we are dealing with a larger problem than just a single species, whether it be biology or management. And in this context I think the discussion that we have had here merits an audience wider than the appendix would get in the report of the Working Group on Cod and Climate Change. I think it's certainly appropriate that this Symposium will be introduced at the opening session of the Statutory Meeting but it really should receive a much larger scientific audience, because just as Assessment Working Groups have been changing in order to broaden their vista, so has ICES. One major initiative that ICES will be presenting to the scientific community at the Dublin meeting is some idea on how ICES can better harness its resources. In very much the same fashion as here at this Symposium, we have been trying to take a much wider spectrum of interest into consideration. ICES has recognized this and is trying to re-examine its structure, trying to promote it into a multidisciplinary approach and I would submit to you, Mr. Chairman and Mr. Convener, that the success of this Symposium has proved the enormous value of taking an interdisciplinary approach to the matter of the interaction between marine resources and their environment.

ODD NAKKEN:

I thank the Convener for his review and particularly those who contributed to the discussion we have had here, but first and foremost, on behalf of all of us, I thank ICES for arranging this Symposium and thus for getting us together to learn and to exchange information about the things we love. There are two scientists who have been involved in cod research throughout the North Atlantic for a very very long time. One of them is Albrecht Schumacher, who was unable to be present here, the other is David Garrod, and he will retire from research next year. If those of you who are interested in cod research and cod assessment study ICES publications since the mid 1950s you will see that these two names crop up time and time again.

It is impossible to conduct a Symposium like this without the assistance of a big staff, and someone to orchestrate its smooth running. We are all grateful to Hafrannsóknastofnunin and its Director, Jakob Jakobsson, for making all the arrangements and for the hospitality shown to us during our stay.

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