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Spawning and life history information for North Atlantic cod stocks

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1 Introduction

This synthesis of information on spawning and life history of North Atlantic cod stocks is an update of *ICES Cooperative Research Report, 205 (CRR 205)*, published in 1994, but it has been completely re-written. A comparison between the current publication and its predecessor gives a fairly detailed appreciation of the enormous body of new information which has become available over the intervening decade.

ICES Cooperative Research Report, 205 was initiated by the ICES Larval Ecology Working Group to bring together the existing data on early life stages of cod and haddock in 1987, using a checklist which was circulated to Working Group members and participants at the ICES Symposium on The Early Life History of Fish held in 1988. The ICES Study Group on Cod Stock Fluctuations (which became the ICES/GLOBEC Working Group on Cod and Climate Change) also produced syntheses of information on North Atlantic cod stocks (ICES CM 1990/G:50) and these two sources, plus a large amount of additional material were published, together with nearly 800 references and six summary tables.

The main purpose of this update is unchanged: to provide information for comparative studies of cod biology and population dynamics. The checklist used to elicit specific information was only very slightly extended from the original, to include some additional questions about migration and adult growth. A copy of the checklist is included at the end of this introduction.

The impetus for putting together this revision came from the ICES/GLOBEC Cod and Climate Change Working Group, with the active support and encouragement of the Chair, Dr Ken Drinkwater. *CRR 205* had provided a substantial reference source for many of the studies within the Cod and Climate Change programme and it was clearly valuable to bring it up-to-date.

Many of the updated sections include a substantial amount of descriptive material on the physical and biological environment and the recent changes which have taken place in the cod stocks. This was not the primary purpose of the report, but it provides a useful background for comparative studies. Much of the background information in *CRR 205* has not been repeated here and some sections have not been updated (e.g. White Sea cod).

The checklist was not designed to elicit comprehensive information from stock assessments and only asks for estimates of recruitment and spawning-stock biomass. Stock assessments are regularly updated in ICES, CSAS and other publications. They require careful interpretation, based on more background detail than could easily be included in this *Cooperative Research Report*, which is more concerned with biological information, in particular about early life history.

The checklist tries to elicit information in a systematic and clearly defined way by means of a series of detailed questions, but the difficulty of defining terms and posing questions unambiguously quickly becomes apparent. In many cases there has been an iterative process of formulating questions and defining and obtaining information. In some cases it may be more useful to have an address list of experts who are familiar with the information available for their area and are able to point out further relevant details than to have a necessarily incomplete synthesis.

The reference list for the present *ICES Cooperative Research Report* has been expanded to about 2000 references. Each section has its own separate reference list, but a complete list will also be available via the existing reference database on the ICES/GLOBEC website (www.ices.dk/globec). This database may be particularly useful in finding grey literature, since it is compiled by experts on each stock.

The arrangement of the report into separate sections for each stock is a natural one given that most research on cod is divided up in this way, to correspond with units of assessment and management, but the main purpose of the report is to encourage comparisons between stocks and perhaps to help to overcome the fragmentation which such stock divisions bring about. Underlying this is a belief (which needs to be tested) that the processes, which govern cod population dynamics (growth, reproductive strategy, behaviour patterns), have shared properties at the species level, rather than being different for each stock.

Given the quantity of assessment related and biological research on the cod stocks of the North Atlantic, this species probably has a greater body of population and biological data than any other marine species and any exploited non-farmed species. For this reason it has been recognised as a key species in studying the effects of physical factors on biological production in the sea and in particular for examining the effects of climatic change. This report is a contribution by the ICES/GLOBEC Cod and Climate Change Programme to that study and to co-operative research among the ICES countries.

Checklist for the synthesis of information on spawning and life history of North Atlantic cod stocks

Some sections have adopted the numbering used in this checklist and have included the questions as section headings. When reading the individual stock sections it is worth bearing in mind that the form of the answers depends on the way these questions were posed.

1 Species, stock and area of distribution:

- 1.1 Evidence of stock discreteness, e.g. genetic distance, tagging, meristics.
- 1.2 Units for which assessment of spawning-stock biomass and recruitment are available.
- 1.3 Time-series of spawning-stock biomass and recruitment data e.g. from commercial catch and effort data, fishing surveys or VPA.
- 1.4 What is the geographical location of the stock and does it change seasonally, i.e. is there evidence of migration? Please provide chart showing location of distribution seasonally.
- 1.5 What is the depth range and temperature associated with the stock and does it change seasonally?

2 Time of spawning:

- 2.1 Date of spawning and interannual variability or trend (mean date and standard deviation, if possible).
- 2.2 Time of day when spawning occurs.
- 2.3 Timing of spawning season in relation to planktonic production cycle.
- 2.4 Timing of spawning season in relation to hydrographic events i.e. temperature, salinity and stratification, currents.
- 2.5 Timing of spawning season in relation to other fish species that spawn in the same location.

3 Location of spawning:

- 3.1 Geographic location and extent of spawning area (please provide chart) and evidence of its variability from year to year.
- 3.2 Does spawning regularly begin in one part of the spawning area and then move to other parts?
- 3.3 Can the location be described in relation to hydrographic features, e.g. "at the boundary between two water masses"; "in the upper, mixed layer"?

- 3.4 Can location be described in relation to other species, including food organisms and predators?
- 3.5 Can location be described in relation to water mass circulation, e.g. "in the north flowing coastal current"; "in the Taylor column circulation over a bank"? How might this affect transport of eggs and larvae?

4 Biological details:

- 4.1 Fecundity, i.e. number of eggs produced per female per year (as a function of age). Specific fecundity, i.e. number of eggs produced per unit weight.
- 4.2 Evidence of changes in fecundity with time.
- 4.3 Percentage mature-at-age (including the population not on the spawning grounds). Length and weight at 50% maturity.
- 4.3a. Is there evidence of changes over time in maturity? What hypotheses have been advanced to explain any such changes?
- 4.4 Egg size and evidence of changes with age and with time during the spawning season. Specific gravity of eggs and larvae.
- 4.5 Typical densities, i.e. number per m³ of eggs and larvae.
- 4.6 Incubation rate of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larva.
- 4.7 Larval development rate as a function of temperature.
- 4.8 Condition factor and nutritional status.
- 4.9 Egg and larval mortality rates.
- 4.10 Time of first-feeding of larvae and food at first-feeding.
- 4.11 Food of larvae during development.
- 4.12 Evidence of predation during the egg and larval stage?

5 Recruitment:

- 5.1 Are there several spawning sites (sub-populations) which contribute to the same stock unit e.g. "there are several spawning areas which contribute to the North Sea stock and their relative contribution may vary from year-to-year".
- 5.2 Earliest time in the life history when year class strength can be predicted.
- 5.3 Hypotheses which have been put forward to account for year-to-year variability in year-class strength.
- 5.4 Evidence of long-term trends in recruitment.

- 5.5 Evidence that variability in recruitment is linked to variability of other species in the same area, the same species in other areas or other species in other areas.
- 5.6 Evidence of inter- or intraspecific competition.

Some additional information has been requested on:

Migration:

- 1. Is there evidence of adult migration?
- 2. If so, where and when do they migrate?
- 3. What is the purpose of the migration, i.e. movement to spawning grounds, to feeding grounds, etc.?

Adult growth:

- 4. Is there evidence of density-dependent growth?
- 5. Is there evidence of temperature-dependent growth?

2 Summary tables

The six tables presented in this section provide summaries of stock size and early life history information for eight cod stocks in the NE Atlantic and nine in the NW Atlantic. The equivalent tables for Greenland are extremely detailed and are subdivided into inshore and off-shore components; therefore they have been left in the section on Greenland.

Readers should check the data provided in the Tables against the text in the relevant section for each stock, if they intend to use the material. This is because there will often be a great deal of background information and relevant references. It is also often the case that the information (e.g. on age and length of maturity) is too complex to present in a simple tabular form, therefore a blank in the Tables does not necessarily mean there is no information.

There are a number of difficulties in presenting comparative information in this way. One is that the information rapidly becomes out of date, particularly when it derives from annual stock assessments, which not only add new information each year, but often revise and recalculate figures for earlier years. Readers are advised to consult the most recent assessment reports and to seek advice from those carrying out the assessments on how to interpret them.

A second difficulty is in using standard definitions and estimates. For example the concentrations of larvae can be given per square m or per cubic m and it is not always easy to convert.

The purpose of the Tables is to allow simple comparisons of early life history characteristics across all North Atlantic cod stocks in order to identify common features and patterns (e.g. relationship between temperature and duration of the pelagic stage). These may help in studying the causes of variability in population dynamics for the species.

Tables 2.1 and 2.2 – Stock summaries

These are based on standard stock summaries, as prepared for ICES, CAFSAC, NMFS and NAFO. They give basic information on the size of all stocks and the range in landings, stock biomass and recruitment. The methodology is generally some form of sequential population analysis, based on data from commercial fisheries and fishing surveys.

Table 2.3 – Spawning and egg stage data summary

Individual sections should be consulted for further detail. Most stocks contain more than one spawning area, often with different spawning periods and duration. The mean date of spawning in such cases may be misleading.

Depths are in meters.

Temperature is in degrees C. In many cases the temperature at which spawning occurs is not known precisely, for example where depth of spawning is not known in a vertical thermal structure.

Egg size is in mm.

Density of eggs means specific gravity and is given as $(\text{Specific gravity} - 1) \times 10^3$

Concentration is $\text{number} \times \text{m}^{-3}$, unless otherwise noted in the Table.

Mortality is daily instantaneous rate.

Table 2.4 – Larval stage data summary

Sizes at hatch, metamorphosis and settlement are all lengths in mm.

Growth is in $\text{mm} \times \text{d}^{-1}$.

Mortality is daily instantaneous rate.

Dates at hatch, metamorphosis and settlement are either calendar dates or days from spawning.

Distances from spawning to settlement are in km. They are linear rather than following the actual track. For example in a retention area eggs and larvae may travel a long distance but end up where they started, in which case the distance from spawning to settlement would be nil.

Table 2.5 – Adult stage and biological data summary

A great deal of information on “stock reproductive potential” has been collated for cod and many other species by NAFO and ICES Working Groups. This information can be accessed from Morgan *et al.* (2003) and ICES (2004). It will also be made available via the respective websites.

Age-at-maturity is estimated in different ways for different stocks (e.g. age in catch or age in population) and has varied considerably with time in some stocks, therefore the individual stock sections should be consulted carefully when using these data.

Fecundity is average number of eggs produced by a mature fish or specific fecundity (i.e. $\text{eggs} \times \text{g}^{-1}$).

Table 2.6 – Factors affecting survival

The table gives an overview of the possible causes of variability in survival, which is being investigated in different areas.

References

- ICES. 2004. Report of the Study Group on Growth, Maturity and Condition in Stock Projections. ICES CM 2004/D:02.
- Morgan, M. J., Burnett, J., Tomkiewicz, J., and Saborido-Rey, F. 2003. The availability of data for estimating reproductive potential for selected stocks in the North Atlantic. Scientific Council Studies 37, Dartmouth: Northwest Atlantic Fisheries Organization. 378p.

Table 2.1. Stock summaries for NE Atlantic cod stocks. The data are from summaries produced by ICES Assessment Working Groups.

Stock	ICES Area	Landings ('000t)			SSB ('000t)			Recruits (in millions)			CV of SSB	CV of R	First Year	Last Year
		Min	Max	Mean	Min	Max	Mean	Min	Max	Mean				
Arcto-Norwegian (North-East Arctic)	Subareas I and II	212.0	1 343.1	661.9	102.3	1 165.1	379.6	112.0	1 818.9	608.4	66%	62%	1946	2003
Baltic	Subdiv 25-32	45.2	392.0	168.1	90.5	696.7	287.8	82.6	829.1	301.5	59%	61%	1966	2003
Celtic Sea	Div VIIe-k	2.9	19.8	8.7	6.3	24.0	10.9	0.5	16.6	4.3	33%	76%	1971	2003
Faroe Plateau	Subdiv Vb1	6.1	40.4	25.1	20.6	116.7	64.2	3.7	47.8	17.2	35%	57%	1961	2003
Iceland	Div Va	168.6	545.3	352.3	121.1	932.1	320.5	62.7	350.4	389.4	69%	37%	1955	2003
Irish Sea	Div VIIa	1.8	14.2	8.4	2.0	20.8	10.9	0.6	15.7	5.4	47%	63%	1968	2003
North Sea	Subarea IV, Div VIIId and IIIa	66.7	580.5	244.8	37.5	252.7	139.2	87.6	2517.1	612.1	47%	84%	1963	2003
West of Scotland	Div VIa	1.3	27.8	13.8	3.2	37.7	10.4	13.7	571.0	127.6	103%	95%	1978	2003

Greenland

Stock summaries are given in separate tables in the Greenland section

Table 2.2. Stock summaries for NW Atlantic cod stocks. The sources of the data are given in the final column.

Stock	NAFO Area	Landings ('000t)			SSB ('000t)			Recruits (in millions)			CV of SSB	CV of R	First Year	Last Year	References
		Min	Max	Mean	Min	Max	Mean	Min	Max	Mean					
Flemish Cap	3M	<<1	58.0	21.0	2.0	40.0	21.0	<1	90.0	19.0			1972	2001	NAFO SCR Docs 02/58, 04/53
Georges Bank	5Z+6	8.0	57.0	29.0	17.0	93.0	53.0	2.0	43.0	15.0	51%	74%	1960	2001	NEFSC Ref.Doc.02-16
Gulf of Maine	5Y	16.4	17.8	8.1	10.6	24.2	1.6	0.6	25.2	7.4	27%	70%	1982	2001	NEFSC Ref.Doc.02-16
N. Gulf of St Lawrence	3Pn4Rs	0.1	106.0	59.0	36.0	604.0	270.0	10.0	206.0	84.0			1964	2002	Frechet <i>et al.</i> , 2003
S. Grand Bank	3NO	0.0	226.8	52.5	4.1	125.0	47.8	0.4	253.0	52.0	71%	121%	1953	2002	NAFO SCR Doc. 03/59
S. Gulf of St Lawrence	4TVn	1.0	105.0	43.0	62.0	420.0	190.0	27.0	322.0	98.0			1950	2002	CSAS Res.Doc. 2003/015
S. Newfoundland	3Ps	<1	87.0	42.0	35.0	115.0	74.0	12.0	80.0	38.0			1959	2002	CSAS Res.Doc. 2003/092
S. Labrador and E. Newfoundland	2J3KL	<1	810.0	275.0	66.0	1677.0	596.0	62.0	1 185.0	421.0			1959	2002	CSAS Res.Doc. 2003/0023, NAFO SCR Doc 93/86
W. Scotian Shelf	4X	5.6	35.6	19.9									1956	2003	CSAS Res.Doc. 2004/100

Greenland

Stock summaries are given in separate tables in the Greenland section

Table 2.3. Information on spawning and egg characteristics.

Stock	Area	Date of spawning		Depth	Temperature		Egg characteristics			
		Mean	Duration		Adults	Eggs	Size	Density	Conc'tn	Mortality
Arcto-Norwegian (North-East Arctic)	Subareas I and II	29 March-5 April	Feb-May	60–150	4–6	1.3–3.6	1.2–1.6	23.5–26	300	0.109
Baltic	Subdiv 25–32	June-July	Mar-Sept	60–80		3–7	1.4–2			
Celtic Sea	Div VIIe-k	March	Feb-Apr	70	8–9	8–9		0.002–0.155	1–10 (m ⁻²)	
Faroe Plateau	Subdiv Vb1	March	Feb-May	80–180	6–7					
Iceland	Div Va	April	Mar-May	30–100	5–7	5–7	1.2–1.6	22.6–26.6		
Irish Sea	Div VIIa	Mar-Apr	Jan-May	20–50	6–7	6–7	1–1.8		97(m ⁻²)	0.21–0.36
North Sea	Subarea IV, Div VIId and IIIa	Feb-Mar	Jan-Apr	30	5–7	5–7			up to 300	0.027–0.404
West of Scotland	Div Via	March		<200						
Flemish Cap	3M	March	Feb-Apr	300–400	3–4	3.5–4.5				
Georges Bank	5Z+6	Feb-Mar	Nov-May	60–90	3–5	3–7	1.5	25–26	100–300	0.094–0.195
Gulf of Maine	5Y	see text	Nov-May	100						
N. Gulf of St Law- rence	3Pn4Rs	May	Apr-June	250	4-6		1.37–1.46	25.4	up to 400	
S. Grand Bank	3NO	May	Apr-June		0.6	0–4				
S. Gulf of St Law- rence	4TVn	June	Apr-Sept	35–100	-0.1 to +0.3		1.2–1.8			
S. Newfoundland	3Ps	May	March-Aug	75–400	0–2			23–25 in- shore 26.2 offshore	218.0	
S. Labrador and E. Newfoundland	2J3KL	Apr-June	Mar-July							
W. Scotian Shelf	4X	Feb-Mar Oct-Nov							10–20	0.15–0.3

Greenland Stock summaries are given in separate tables in the Greenland section

Table 2.4. Information on the larval stage and the pelagic phase of the life history.

Stock	Area	Size			Growth	Mortality	Date			Distance spawn to settlement
		at hatch	at meta- morphosis	at settlement			at hatch	at meta- morphosis	at settlement	
Arcto-Norwegian (North-East Arctic)	Subareas I and II	4	12–15	60–100	0.2–0.4	0.1	late April	June	Oct	600–1600
Baltic	Subdiv 25-32									<200
Celtic Sea	Div VIIe-k									
Faroe Plateau	Sub-div Vb1			35-40					July	
Iceland	Div Va									
Irish Sea	Div VIIa									<100
North Sea	Subarea IV, Div VIIId and IIIa									
West of Scotland	Div Via									
Flemish Cap	3M									Retention
Georges Bank	5Z+6	3-5	15.0	40–70	0.13–1.0	0.03–0.09	14	40–55	100–120	10–150
Gulf of Maine	5Y									
N. Gulf of St Law- rence	3Pn4Rs	5.03 (range 3.12–7.4)								100
S. Grand Bank	3NO									Retention?
S. Gulf of St Law- rence	4TVn									0–150
S. Newfoundland	3Ps									Retention?
S. Labrador and E. Newfoundland	2J3KL									
W. Scotian Shelf	4X									

Greenland

Stock summaries are given in separate tables in the Greenland section

Table 2.5. Information on maturity and fecundity. See the notes and references for further sources of information.

Stock	Area	Mean latitude	Maturity		Fecundity
			50% age	50% length	
Arcto-Norwegian (North-East Arctic)	Subareas I and II	73	changing	changing	$0.5-15 \times 10^6$
Baltic	Subdiv 25-32	55			
Celtic Sea	Div VIIe-k	51	2.3	60	
Faroe Plateau	Subdiv Vb1	62	3	50-55	
Iceland	Div Va	65	♀ 6.6 ♂ 5.8	♀ 75.6 ♂ 67.2	$0.23-31.7 \times 10^6$
Irish Sea	Div VIIa	53	2		
North Sea	Subarea IV, Div VIId and IIIa	57	2-3	50-75	
West of Scotland	Div Via	58	2-3	42	
Flemish Cap	3M	47	4-7	40-70	
Georges Bank	5Z+6	42	♀ 2.1 ♂ 2.1	♀ 43.3 ♂ 42.2	$2.7-9.1 \times 10^6$
Gulf of Maine	5Y	45	♀ 2.6 ♂ 2.9	♀ 43.3 ♂ 44	10^6
N. Gulf of St Lawrence	3Pn4Rs	49	5.4	46.8	874×10^3 (56 cm age 8, 2002)
S. Grand Bank	3NO	45	4.8-7.4		
S. Gulf of St Lawrence	4TVn	48	4-4.5	37-39	$415-520 \text{ g}^{-1}$
S. Newfoundland	3Ps	46	5-7	47-65	
S. Labrador and E. Newfoundland	2J3KL	50	5.4-7.5	57-40	
W. Scotian Shelf	4X	43	2.5	45.0	

Table 2.6. Summary of the factors which are thought to affect survival and hypotheses being tested in relation to recruitment.

Stock	Area	Starvation	Predation	Advection	Other
Arcto-Norwegian (North-East Arctic)	Subareas I and II	X	X	X	microturbulence, condition and age of spawning females
Baltic	Subdiv 25-32	X	X	X	oxygen, salinity, large scale environmental forcing
Celtic Sea	Div VIIe-k				Large scale environmental forcing
Faroe Plateau	Subdiv Vb1				phytoplankton production, exchange rate of shelf water
Iceland	Div Va	X		X	population richness, large scale environmental forcing
Irish Sea	Div VIIa				temperature, large scale environmental forcing
North Sea	Subarea IV, Div VIId and IIIa				plankton production, timing and size; temperature; large scale environmental forcing
West of Scotland	Div Via				
Flemish Cap	3M				12 hypotheses proposed. Possible retention, cannibalism.
Georges Bank	5Z+6	X		X	Climate, stratification, general productivity, retention, optimum temperature and growth, eggviability/spawning-stock age structure
Gulf of Maine	5Y				
N. Gulf of St Lawrence	3Pn4Rs		Seals		Low oxygen, shrimp b-catch (before Nordmore grid), temperature, increased M and decreased individual performance due to winter food-deprivation
S. Grand Bank	3NO				Spawning stock characteristics
S. Gulf of St Lawrence	4TVn	X	mackerel and herring	X	Environmental effects (temperature, ice duration, RIVSUM,NAO), maternal effects (age diversity of spawners, mean age and size of spawners, proportion of old fish)
S. Newfoundland	3Ps				Spawning stock characteristics
S. Labrador and E. Newfoundland	2J3KL				temperature, salinity, characteristics of spawning stock
W. Scotian Shelf	4X				

Greenland Stock summaries are given in separate tables in the Greenland section

3 Spawning checklists and stock summaries

3.1 Arcto-Norwegian cod

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Stock and area of distribution

Evidence of stock discreteness

The Arcto-Norwegian (N.E. Arctic) cod is managed as a single stock unit. There is a distinction between the Barents Sea and the Svalbard components, which are geographically separated when immature (Trout, 1956; Maslov, 1972). Although not strictly proven, several studies of migration and general biology indicate a partial separation between spawning individuals from the two components. While the eastern Barents Sea component mainly spawns in coastal areas from Lofoten and northwards, the western component generally spawns more off-shore and also in areas south of Lofoten (Trout, 1956; Hylan *et al.*, 1961; Randa, 1984; Godø, 1986). However, a considerable portion of the Svalbard component mixes with the Barents Sea cod during the post-spawning feeding season in the eastern Barents Sea (Trout, 1956; Garrod, 1967). Tagging experiments confirm that there is a relatively distinct western component confined to the West Spitsbergen region. Still, tagging and genetic studies do not indicate reproductive isolation.

There are definitely several components to the coastal cod all along the coast of Norway. Although, in mid and northern Norway the coastal cod spawn partly at the same spawning grounds as the Arcto-Norwegian cod, differences between the eggs and larvae have not been observed, which implies that they are subjected to the same processes of transport and spreading as the Arcto-Norwegian cod. Nevertheless, trained fishermen and fisheries biologists can see differences in body shape of the adults between the coastal and the Arcto-Norwegian cod.

The Norwegian coastal cod is considered a separate management unit based on its unique biological characteristics and geographically limited distribution (Rollefsen, 1953; Godø, 1986; Jakobsen, 1987). These characteristics seem to be strongly related to environment (Møller, 1968; Randa, 1984; Godø and Moksness, 1987). The genetic separation of the two units has been a question of scientific disagreement (compare Møller, 1968; Mork *et al.*, 1985; Jørstad, 1984; Dale, 1991).

Units for which assessment of spawning-stock biomass and recruitment are available.

Assessments are carried out by the ICES Arctic Fisheries Working Group for the Arcto-Norwegian stock (NE Arctic) and the Norwegian Coastal stocks.

Time-series of spawning-stock biomass and recruitment data

VPA has been carried out for cod 3 years and older on data for the period 1946 to present and spawning-stock biomass estimates are available. However, Hylan (2002) recently compiled data back to 1913 and ran a VPA for the full period 1913–1999. Up to 1980 only data from the commercial fisheries were available for the VPA. Indices of 0-group abundance (and length) are available since 1965 from a systematic pelagic trawl survey carried out annually in August–September (Randa, 1984). New indices, corrected for varying capture efficiency, were introduced by Nakken and Raknes (1987). Indices of early juveniles (2–3 months) are available for the period 1978–1991.

Since the mid-1980s estimates of recruitment and indices of abundance by age from Norwegian and USSR scientific surveys have become increasingly important both for the VPA and for the predictions (Hylan and Nakken 1986). The surveys are carried out from September to March using a combination of bottom trawl survey and acoustic survey techniques (Hylan and Nakken 1986). In addition the spawning-stock is acoustically surveyed in March–April. Year-class strength at recruitment (age 3) varies by a factor of about 20. Assessment and prediction is made more difficult by large interannual variations in growth and age of maturation (Jørgensen, 1989).

What is the geographical location of the stock and does it change seasonally?

Arcto-Norwegian cod are widely distributed along the Norwegian coast and in the oceanic regions of the Barents Sea – Spitsbergen area (see Figure 3.1.1). The southernmost distribution is found during spawning, which normally occurs in Norwegian coastal areas south towards 62°N. Minor spawning has occasionally been recorded even as far south as Bergen. The northernmost and easternmost distribution is found during the summer–autumn feeding season, when cod feed close to the polar front, mainly on capelin and shrimp. One effect of short-term climate variability is the considerable interannual variation in horizontal distribution of fish due to changes in the position of the front. In the Spitsbergen area cod may be found in considerable concentrations as far north as 80°N. The distribution in the east, which reaches to Novaya Zemlya, is more southerly than in the Spitsbergen area. In the winter major concentrations of cod may occur in ice covered areas. The western distribution is

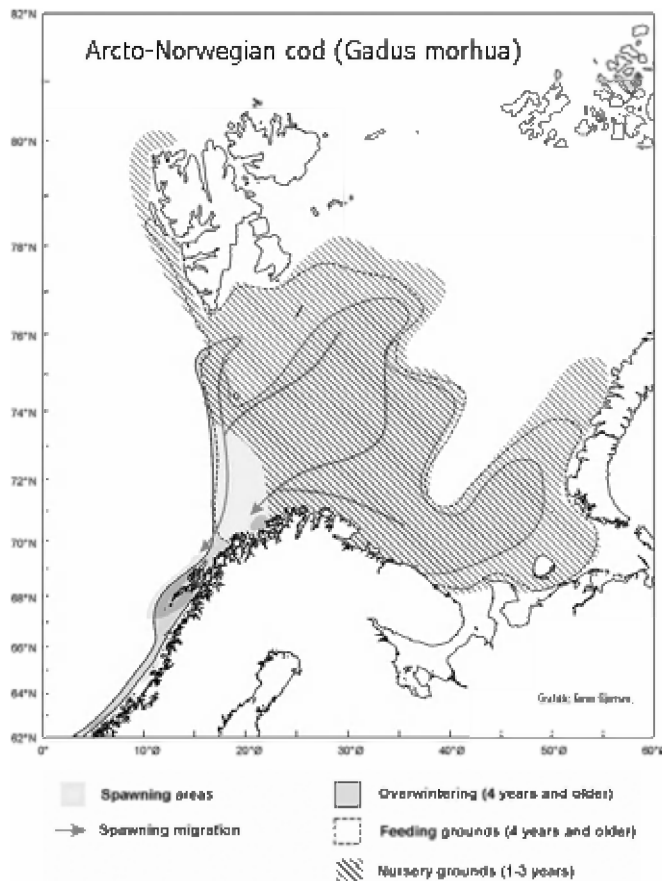


Figure 3.1.1. Seasonal spawning migration patterns, spawning, feeding and nursery areas for Arcto-Norwegian cod.

limited by the continental shelf, although tagged vagrants have been recaptured in very small numbers in Greenland and Iceland fishing areas (Godø, 1986). The feeding habitat of the juvenile and adult cod comprises the ice-free parts of the Barents Sea and the narrow shelf region to the west of Spitsbergen. This is an area of about $0.6\text{--}0.7 \times 10^6 \text{ km}^2$, 40–50% of the entire area of the Barents Sea.

What is the depth range and temperature associated with the stock and does it change seasonally?

Mature cod undertake migrations between relatively warm, deep wintering grounds and shallower, colder, summer feeding grounds (Bergstad *et al.*, 1987; Jørgensen, 1992; Ottersen *et al.*, 1998). Godø and Michalsen (2000) found by means of data storage tags, that the fish generally stayed deeper/closer to the bottom during winter and spring than during the summer and autumn. They also confirmed that cod experience higher temperatures during winter than during summer. The reason for this is mainly that the fish are distributed in the cold, northern and eastern parts of the Barents Sea during summer and autumn, while they migrate to the warmer southwestern part during winter and spring. The temperature in the Barents Sea is relatively stable at depths greater than 100 m, and therefore the seasonal variation has a minor influence on the distribution area of cod, compared to the geographical differences (Ottersen *et al.*, 1998; Godø and Michalsen, 2000).

Time of spawning

Date of spawning and interannual variability or trend

Spawning starts in the middle of February and lasts until end of April/early May. The date of 50% spawning during the period 1976–1986 varied between 29 March and 5 April (Ellertsen *et al.* 1989). Experimental work by Kjesbu *et al.* (1996) shows that larger and older Arcto-Norwegian cod tend to have a longer spawning period than smaller and younger fish. Peak spawning has been delayed by 10–14 days since 1930, due to the effect of fishing, which has caused a reduction in age (Pedersen, 1984) and has changed the genetic composition of the spawning population (Heino *et al.*, 2002; Heino, 2003).

Time of day when spawning occurs

Spawning occurs mainly in the evening and during the night. This has been demonstrated both in field (Sølemdal, pers. comm.) and experimentally (Kjesbu, 1989).

Timing of spawning season in relation to planktonic production cycle

While cod spawning shows small interannual variations with respect to time, the production of the main prey, nauplii of *Calanus finmarchicus*, is very temperature dependent and therefore more variable in time.

In years when temperatures during the egg and early larval stages is near average, the peak of the production curve of copepod nauplii is some days ahead of the peak of first-feeding cod larvae (Ellertsen *et al.*, 1989). By increasing the age of the spawning population a better overlap between peak of nauplii and first-feeding larvae would occur. Interannual variations in temperature in the coastal water have great impact on the degree of overlap between the production cycles of nauplii and first-feeding cod larvae. Taking into account the critical nauplii density of 5–10 per litre for high larval survival, it can be demonstrated that large year classes result in years with above average coastal water temperatures (Ellertsen *et al.*, 1989). However, not all such years have resulted in large year classes, showing that other factors also control recruitment.

Timing of spawning in relation to hydrographic events

Since the time of cod spawning is very constant between years, variations in hydrography are of no significant influence.

Timing of spawning in relation to other fish species that spawn in the same location

Haddock (*Melanogrammus aeglefinus*) spawning peaks in the last days of April, i.e. 3–4 weeks later than the cod (Sølemdal *et al.*, 1989). Haddock spawn to a limited extent at some of the cod spawning grounds. The main

spawning grounds of haddock are located more offshore than those of the cod.

In some years when the capelin spawning is westerly, there may be an overlap in the distribution of first-feeding larvae at the spawning grounds to the north of Lofoten (the banks between Andøya and Sørøya).

Location of spawning

Geographic location and extent of spawning area

The spawning areas of Arcto-Norwegian cod are patchy, located in the Norwegian coastal current off mid and north Norway between Møre and Sørøya, along a 1200 km long coastline. Spawning takes place at the same sites every year, although the magnitude of the spawning may vary between sites. Most of the eggs (2/3–3/4) are spawned along a limited part of the coastline, in Lofoten and Vesterålen, between 67°30'N and 68°30'N. The intensity of spawning at Møre and at the offshore grounds off Vesterålen is rather variable (for further information see Sundby and Bratland, 1987).

Does spawning regularly begin in one part of the spawning area and then move on to other parts?

Peak spawning in Lofoten occurs during the first days of April and shows very little variation between years. Peak spawning is delayed by about 14 days at the northernmost spawning field, Sørøya, (Sundby and Bratland, 1987), while the spawning at the southernmost ground (Møre) occurs at about the same time as in Lofoten (Godø *et al.*, 1985).

Can the location be described in relation to hydrographic features?

Spawning occurs mainly in the transition layer between the upper, cool coastal water (2–4°C; salinity 33–34) and the warmer Atlantic water (6–8°C; salinity 34.8–34.9) below. The preferred spawning temperature is 4–6°C. Spawning may occur pelagically in this transition layer, but most often it occurs near the bottom, where the transition layer intersects the bottom. The depth and position of the layer may vary both between years (due to variations in the fresh water content and convection processes in the coastal water during winter), and between days (due to upwelling, internal waves and other motions generated by atmospheric processes). This means that the positions of spawning within a certain spawning ground may vary due to the motions of the transition layer.

Can location be described in relation to other species, including food organisms and predators?

Production of *Calanus finmarchicus* nauplii takes place at the same locations where the cod are spawning, and Ellertsen *et al.*, (1987) suggested that the highest densities of food organisms occur at the same time as the highest densities of first-feeding cod larvae. However,

this favourable situation does not occur each year (the match-mismatch hypothesis, Cushing, 1990).

Furthermore, zooplankton concentrations are generally higher in the Norwegian Sea than along the Norwegian coast and in the Barents Sea. This implies that variable volume transport onto the northern Norwegian shelf and into the Barents Sea may cause variations in the zooplankton biomass in these regions (Sundby, 2000).

Can location be described in relation to water mass circulation?

About 70–80% of the spawning occurs in near-shore regions where advection is relatively low. At the spawning grounds between Andøya and Sørøya the eggs and larvae are trapped in the clockwise circulation above the banks, and advection out of this region is reduced (but not stopped!). In Lofoten (the Vest Fjord) the eggs and larvae are not trapped by Taylor columns, but advection out of the Vest Fjord is relatively low.

The remaining stock spawns at offshore banks off Vesterålen and close to the shelf edge where there is a rapid transport of eggs and larvae.

For further information see Furnes and Sundby, (1981), Sundby and Bratland (1987), and Ellertsen *et al.* (1989).

Biological details

Fecundity

Mean individual fecundity varies from 0.5×10^6 to 15×10^6 (age 4–15). Fecundity is a function of body weight rather than of age, ($r^2 = 0.93$ and 0.84 , respectively). $F = 6.84 \times 10^3 \times A^{2.83}$ (where A = age) (Kjesbu, 1988).

Evidence of changes in fecundity with time

Relative annual potential fecundity (i.e. number of vitellogenic oocytes per g per prespawning fish) increased by 40% from 1987 to 1991, but the increase may be much more than this. Potential fecundity was positively related to environmental temperature and availability of capelin during vitellogenesis (Kjesbu *et al.*, 1998).

Percentage mature-at-age

Values based on Norwegian data for 2002 (ICES, 2002)

Age	3	4	5	6	7	8	9	10
%	-	1	5	46	71	89	97	100

Is there evidence of changes over time in maturity?

There is a biologically significant downward trend in age-at-maturity over time. In the 1930s cod typically matured at 8–11 years, while now they mature at 6–8 years. Early maturation may generally be explained as a result of compensatory growth, due to the stock being fished down and the remaining fish having less competition for food. However, fishing could also be causing a genetic change in fish stocks as early maturing fish are more likely to survive and pass on this characteristic to the following generation (Heino *et al.*, 2002; Heino, 2003).

Egg size and evidence of changes with age and with time during the spawning season

Egg diameter varies between 1.20 and 1.60 mm with an average of 1.40 mm (Solemdal and Sundby, 1981). A significant reduction in egg size during the spawning period was demonstrated in field material (Solemdal and Sundby, 1981). This is caused by the reduction in egg size with successive egg batches from an individual female (Kjesbu, 1989), and the probably delayed spawning of smaller, first-time spawners spawning smaller eggs (Sundby, 1983).

Specific gravity of eggs and larvae

The specific gravity of the eggs ranges from 1.0235 g cm⁻³ to 1.026 g cm⁻³. This implies that the surplus buoyancy of the eggs in their natural habitat ranges from 0.001 g cm⁻³ to 0.0035 g cm⁻³.

Typical densities, i.e. number per m³ of eggs and larvae

During maximum spawning at the spawning sites in Lofoten up to 13 000 eggs m⁻² have been recorded (Wiborg, 1950; Sundby, 1980). The eggs are confined to the upper 50 m with increasing concentrations towards the surface. The highest concentrations of eggs per unit volume are found at the surface during calm weather conditions when turbulent mixing is at a minimum (Sundby, 1983). Peak concentrations in normal years are about 300 eggs m⁻³ or 7000 eggs m⁻².

The larvae are confined to the upper 40 m. The highest concentrations are normally found between 10 and 20 m depth. The larvae seem to stay out of the upper 5 m. Maximum concentrations recorded are about 2700 larvae m⁻², and about 600 larvae m⁻³ (1992). More typical concentrations are about 100 larvae m⁻² or 10 m⁻³.

Incubation rate of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larva

At the prevailing temperature in the Lofoten the incubation time is about 3 weeks. The larvae hatch at a length of about 4 mm, depending on temperature (Solemdal, 1970). The larvae grow to about 5 mm on their own yolk reserves (Sundby *et al.*, 1994). Incubation rates are given in Strømme (1977).

There is a positive correlation between egg size and larval length at hatching (Solemdal, 1970; Knutsen and Tilleseth, 1985). A special staging system for early cod larvae based on the size of the yolk sac has been developed by Fossum (1986).

Condition factor and nutritional status

Extensive data exist on the condition of spawning females, including seasonal dynamics of organs and gonads (Marshall *et al.*, 1999; Yaragina and Marshall, 2000). The data are suitable for bioenergetic modelling work and may provide answers to questions like: how much energy does a fish need in order to enter spawning modus? Above this threshold value: is fecundity dependent on the nutritional status or is it exclusively an either-or situation? (Andersen *et al.*, 2002)

Larval condition has been measured as feeding incidence, feeding ratio or dry weight in relation to length (Ellertsen *et al.*, 1987). The dry weight/length relationship was significantly higher in the strong year class of 1983 compared to other years.

Egg and larval mortality rates

Egg mortality has been estimated for the years 1983 and 1984 at about 90%. Mortality from hatching (in April) to juveniles (June-July) is 10.9% per day (Sundby *et al.*, 1989). About 2–3% of the larvae that hatched survived to day 20 (Sundby *et al.*, 1989).

Time of first-feeding of larvae and food at first-feeding

At 5°C the cod larvae start feeding on day 5 post-hatching. The prey organisms consist almost exclusively of the nauplii of *Calanus finmarchicus*.

Evidence of predation during the egg and larval stages

In some instances medusae, especially ephyra of *Aurelia aurita*, have been observed with cod eggs in their stomachs, in a few cases also with cod larvae (Melle and Ellertsen, 1984; Melle, 1985). Herring are found with large numbers of cod eggs in their gut (Melle, 1985).

Recruitment*Are there several spawning sites (sub-populations) which contribute to the same stock unit?*

The spawning both in the Vestfjord, off Lofoten, and further north to the Tromsøflaket area contribute to the same stock unit.

Earliest time in the life history when year-class strength can be predicted

This has been examined systematically, first by Sundby *et al.* (1989), more recently by Helle *et al.* (2000) and

Mukhina *et al.* (2003). The year-class strength is mainly determined before the post-larval (juvenile) state, and, therefore, reliable assessments of juveniles (2–3 months) might have a prognostic value (Sundby *et al.*, 1989). A cohort's relative abundance as early juveniles is the best early indicator of its abundance as 2- and 3-year-olds (Helle *et al.*, 2000). Mukhina *et al.* (2003) found that either the transition from potential to realised egg abundance is a critical stage and/or SSB is a poor index of potential total egg production. However, contrary to the expectation that the signal in year-class strength should become stronger as the penultimate recruitment stage is approached, the significance of the correlations with recruitment decreased for the larval and juvenile stages relative to the egg stage, which suggests that the measurement error for these latter stages is high (Mukhina *et al.*, 2003). Temperatures during the post-settlement period explained a significant portion of the residual variation in stage abundance/recruitment relationships for the larval, pelagic juvenile and demersal juvenile stages (Mukhina *et al.*, 2003).

Hypotheses which have been put forward to account for year-to-year variability in year-class strength

Investigations have been carried out on the following hypotheses concerning recruitment mechanisms:

1. Match/mismatch (Ellertsen *et al.*, 1987; Ellertsen *et al.*, 1989)
2. Microturbulence (Sundby and Fossum, 1990; Sundby *et al.*, 1994; Sundby, 1995; Sundby, 1997)
3. Predation (Øiestad, 1985; Melle, 1985)
4. Condition and age of spawning female cod (Kjesbu, 1988; Kjesbu *et al.*, 1991; Kjesbu *et al.*, 1992; Marshall *et al.*, 1998; Marshall *et al.*, 1999; Marshall *et al.*, 2000).

Evidence of long-term trends in recruitment

There is a tendency towards lower recruitment, although not as pronounced as for many other stocks. However, recruitment at age 3 from VPA shows that strong year classes (>1000 million individuals) were produced in 1948–1950, 1963–1964, and 1969–1970. After that only the 1983 year class has been close to that level at this age (Godo, 2003).

Is recruitment related to SSB or any environmental factors?

Recent studies of recruitment dynamics in Arcto-Norwegian cod suggest that SSB in tonnes is a poor index of the reproductive potential and that a bioenergetic index may improve prediction of future recruitment (Marshall *et al.*, 2000).

Recruitment is favoured by above average sea temperatures; strong year classes seldom, or never, occur during a cold year (Sætersdal and Loeng, 1987). Average re-

cruitment measured as 0-group was found to be nearly three times higher during warm years than cold (Ottersen *et al.*, 1994).

There are indications that the stock is more vulnerable to environmental fluctuations at present than it was previously. A closer link between temperature fluctuations and recruitment may be a result of structural changes in the spawning-stock. The average age of a spawner has decreased quite dramatically and the spawning-stock has recently been dominated by one, or a few, age classes (Ottersen *et al.*, 1994). Recruitment is thus now less resilient in adverse environmental conditions (low temperatures) compared with when the stock structure was more robust, e.g. during the 1950s.

Migration

Following spawning, eggs and larvae drift with the currents towards the north and east and are spread all over the southern Barents Sea and southwest of Spitsbergen, a distance of 600–1200 km from their spawning ground. They settle towards the bottom at an age of about 5 months. There is substantial interannual variation in the distribution of the pelagic juveniles; in some years there is a typical westerly distribution, in others an easterly distribution. The immature cod make seasonal east-west and north-south migrations. The range of these migrations increases with age, and at an age of 3–4 years, when capelin (*Mallotus villosus*) become a major food item, the cod follow the spawning migration of capelin to the coasts of Northern Norway and Murman (Ottersen *et al.*, 2002). Mature cod migrate even further, down the coast of Norway to spawn.

A consequence of these movements is that the majority of adults, more than 7 years of age, may experience a seasonal temperature variability of perhaps as much as 10°C during the annual migration from the summer feeding grounds in the cold north and northeastern parts of the Barents Sea to the milder spawning grounds along the west coast of Norway. This is a significantly higher variability than younger individuals from the same stock encounter (Ottersen *et al.*, 1998).

Temperature-related displacement has been reported on an interannual time scale as well as on both small and large spatial scales. In periods of warm climate, the cod distribution is extended towards the low-temperature eastern and northern parts of the Barents Sea as compared to colder periods when the fish tend to concentrate in the southwestern region (Nakken and Raknes, 1987; Ottersen *et al.*, 1998). However, there need not be a direct cause and effect relationship between variation in temperature and geographical distribution, other factors may be just as influential, e.g. temperature induced changes in distribution of prey organisms (Shevelev *et al.*, 1987). Alternatively, much of the interannual variability in distribution may already have been determined by transportation during the pelagic first half year of the cod's life and their location at bottom settlement (Ottersen *et al.*, 2002).

Adult growth

Mean length (cm) and weight (g) at age of Arcto-Norwegian cod from Norwegian surveys in January-March 2002:

Age	1	2	3	4	5	6	7	8
Length	12.4	19.9	31.4	43.8	52.4	62.1	71.6	78.0
Weight	16	68	280	750	1 240	2 047	3 169	4 308

There is on-going work on forecasting weight, condition and proportion mature for Arcto-Norwegian cod from indices of prey availability and temperature. This may lead to the development of new biological reference points that incorporate environmental and ecological factors and hence to harvest control rules that are sensitive to variation in growth rate (Andersen *et al.*, 2002).

Evidence for density-dependent growth

The question of density-dependent growth of Arcto-Norwegian cod is debated. Several authors have suggested that the observed year-to-year variability in growth is density-dependent (Rollefsen, 1953; Ponomarenko, 1967; Nilssen *et al.*, 1994). On the other hand, Jørgensen (1992) found no density-dependent growth, because no significant relationship between length increments and stock size could be established.

A number of authors have observed larger mean length-at-age in warmer years than in colder ones and have proposed a positive connection between temperature and growth (Dementyeva and Mankevich, 1965; Nakken and Raknes, 1987; Michalsen *et al.*, 1998). Mean lengths-at-age for cod age 2–6 increases with ambient winter temperatures. Mean individual growth was highest for year classes that had experienced high temperatures during the two first years of their life (Michalsen *et al.*, 1998). Since the range of the seasonal migrations increases with age it is expected that the amplitude of the annual temperature cycles experienced by the fish also will increase as they grow older. Through data storage tags, it has been shown that cod can experience just as large a difference in temperature within a single day as they experience between seasons. In order to arrive at reliable estimates of annual food consumption by cod, the extent of this diel temperature variation has to be studied more thoroughly and the magnitude quantified (K. Michalsen, IMR, pers. com.).

In a “common garden” experimental study which compared Norwegian coastal and Arcto-Norwegian cod Otterlei *et al.* (1994) found stock-specific difference in mean weight-at-age, but no counter gradient latitudinal variation in growth capacity of the two larval cod stocks. Differences in growth rate between these stocks were minor compared with the effects of temperature.

The environmental effects tend to override density-dependent effects on growth of larval Arcto-Norwegian

cod. High temperature will cause high production of prey items leading to higher growth rates and higher survival through the vulnerable larval and juvenile stages (Ottersen and Loeng, 2000).

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3.2 Baltic

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Introduction

The Baltic Sea is a brackish, semi-enclosed sea typified by an estuarine circulation. It is located in a transition area between continental and marine climates and the oceanographic conditions and their variability are strongly linked to the dominance of one of these “climatic modes”. The physical conditions in the Baltic Sea may respond to climate change through (i) direct air-sea interaction, (ii) the magnitude of freshwater run-off, and (iii) interactions with the ocean at the open boundary (Stigebrandt and Gustafsson, 2003). Surface temperatures are determined by the dominance of either westerly winds with mild “Atlantic air” (high NAO) or easterly winds with cold “continental air” resulting in low temperatures and extensive ice cover (low NAO). River run-off affects salinity in the Baltic by directly freshening surface waters. Renewal of the bottom water of the deep Baltic basins by inflows of saline and oxygenated water from the North Sea via the Kattegat and Belt Sea is indirectly prevented because increased zonal atmospheric circulation increases the freshwater input (Matthäus and Schinke, 1999). The period of high NAO-index values since the late 1980s resulted in an increase in average water temperatures (Fonselius and Valderrama, 2003). The dominance of “westerly weather” increased further the amount of run-off with the consequence of drastically decreasing salinities (Hänninen *et al.*, 2000).

Vertically a permanent halocline restricts the water exchange between the low-salinity surface layer and the deep saline layer, particularly in the central Baltic Sea i.e. east of Bornholm. Salinity and temperature in the upper water layers, as well as in the coastal areas, are thus more influenced by freshwater run-off and air temperature. A seasonal thermocline develops in spring due to surface heating and is maintained due to solar inputs until autumn. Between the thermocline and the halocline exists a cold intermediate layer originating from vertical convection in the preceding winter. In the autumn the thermocline deepens due to the combined effects of heat-loss due to surface cooling and wind induced entrainment and it eventually coalesces with the remnants of the previous winter’s cold intermediate water. This results in a relatively homogeneous surface mixed layer down to the permanent halocline, or to the bottom.

Biologically the Baltic Sea can be typified by five phytoplankton phases in the annual cycle. The initial phase is a diatom dominated period in April that is generally terminated by silica deficiency and followed by a late spring dinoflagellate maximum. During summer blue-green algae and dinoflagellates tend to dominate. There follows

an autumn peak when the phytoplankton biomass is composed of large diatoms and autotrophic ciliates. The final phase, in winter, largely comprises resting stages of the different species. A key to this system is that primary production during the summer nutrient-replete period is dominated by N-fixing blue-green algae. This phytoplankton production supports a high metazoan biomass, however, the degree of coupling and the processes that modify the degree of coupling are poorly understood. Whereas a general increase in chlorophyll *a* indicates an effect of increased eutrophication, a change in dominance from diatoms to dinoflagellates has been attributed to climate-related mild winters (Wasmund *et al.*, 1998).

The zooplankton community in and below the halocline is dominated by *Pseudocalanus elongatus*, due to its preference to higher salinity, while upper water layers are dominated by the copepods *Temora longicornis*, *Eurytemora hirundoides* and *Acartia* spp., and in summer by cladocerans (e.g. *Bosmina coregoni maritima*) (Ackefors and Hernroth, 1970). A consequence of the climate induced effect of increasing water temperatures/decreasing salinities is a change in the mesozooplankton community. The change favours species not dependent on a high salinity level, especially *Acartia* spp., whereas “marine” species e.g. *Pseudocalanus elongatus* have declined in abundance (Dippner *et al.*, 2000; Möllmann *et al.*, 2000).

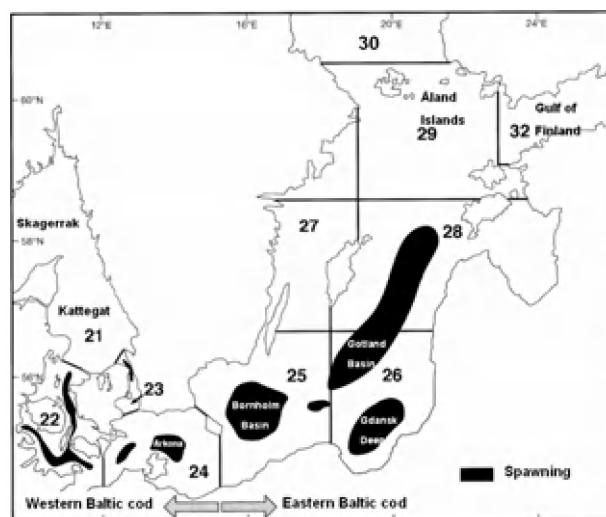


Figure 3.2.1. The Baltic Sea with ICES Subdivisions 21–32 and the distribution of the western and the eastern cod stock including main spawning areas.

The Baltic Sea is characterised by low fish species diversity. Apart from cod there are no gadoids, except occasional visits from the Kattegat by haddock and whiting. Other visitors are e.g. mackerel, garpike (which spawn in the Baltic, but do not stay there permanently as adults) and a number of other species which are in very low abundance. The most important resident fish species in addition to cod are herring, sprat, salmon, trout, flounder, plaice, dab, turbot, sticklebacks, gobids, sandeel and eel, with the first three species dominating open sea areas in terms of biomass and abundance (Sparholt, 1994). Also a number of freshwater species inhabit at least the coastal areas of the Baltic Sea (Voipio, 1981).

Clear relationships exist between the distribution and recruitment of the eastern Baltic cod and the salinities and oxygen levels in the deep basins as well as the reproductive success of sprat with water temperature (Köster *et al.*, 2003a). Intra- and interspecific interactions between the different fish stocks and life stages are relatively well documented with cod being the major top predator in southern and central Baltic areas (Sparholt, 1994). The upper trophic levels of the central Baltic changed during the last two decades from a cod- to a clupeid-dominated system (Köster *et al.*, 2003b). The decline of the cod stock, due to recruitment failure (caused by unfavourable salinity and oxygen conditions) and continuous high fishing pressure, released the sprat stock from predation pressure. High reproductive success, due to generally favourable temperature conditions, enhanced egg and larval survival, resulting in exceptionally high sprat stock sizes in the 1990s, which act as predators on cod eggs (Köster and Möllmann, 2000) and affect the dynamics of important zooplankton prey species of cod larvae (Hinrichsen *et al.*, 2002a). Apart from a relatively low number of seals, adult cod have no natural enemies in the Baltic Sea.

Stock and area of distribution

Evidence of stock discreteness

Stock separation and migration studies show that there are two cod stocks in the Baltic Sea. The eastern Baltic stock (ICES Subdivisions 25–32) exists in the central Baltic with its primary distribution south of the Åland islands (Subdivisions 25–28) (Figure 3.2.1). The western Baltic stock or stock complex is distributed in the Arkona Basin (Subdivision 24), the Sound (Subdivision 23) and the Belt Sea (Subdivision 22). The cod population in the Kattegat (Subdivision 21) seems to comprise two units: one in the area towards the southwest and one towards the north and east. The relationship between cod in north and east Kattegat, the Sound, and the western Baltic Sea is not fully understood, whereas migration studies and genetic analyses indicate that the southwest Kattegat component relates to the stock or stock complex in the western Baltic showing a high degree of mixing in the entire area (ICES, 2001a).

The earliest investigations of Baltic cod stock structure were based on differences in meristic and morphometric characteristics. Determination of the number of vertebrae and fin rays in the dorsal and pelvic fins were the basis for extensive studies comparing cod from the eastern and western Baltic and Kattegat (Schmidt, 1930; Poulsen, 1931; Kändler, 1949; Birjukov, 1969; Berner and Vaske, 1985). The studies demonstrated significant differences in these characteristics among cod populations, however this method does not reveal whether differences are genetically and environmentally induced.

Differences in shape and growth pattern of otoliths also have been used to characterise cod populations and to determine the extent of their mixing (Kändler, 1949; Berner, 1968; Bagge and Steffensen, 1980). Otoliths from western Baltic cod generally show normal well-defined seasonal growth zones, whereas differences between growth zones are less evident in otoliths from eastern Baltic cod. Recent investigations suggest that the differences in development of winter rings (ICES, 1999) between cod in these two areas are due to differences in their ambient water temperature. A smaller nucleus and a less evident juvenile ring in eastern Baltic cod otoliths reflects the later spawning time of the eastern stock that results in a shorter growth period for larvae and juveniles during winter (Hüssy *et al.*, 2003).

Comprehensive tagging experiments were conducted in the Baltic Sea during the period from 1950 to 1980 to study cod migration patterns of cod in the Baltic Sea and adjacent areas. (Bagge and Steffensen, 1989) and (Aro, 1989) have reviewed the available information. Migration patterns related to spawning and foraging were investigated as was the degree of mixing of cod between areas outside the spawning season. The results indicated that the eastern and western Baltic populations were separate stocks with limited overlap in the area around Bornholm and with separate spawning areas. The eastern Baltic cod has spawning areas in the Bornholm Basin (Subdivision 25), Gotland Deep (Subdivision 26) and the Gdansk Deep (Subdivisions 26 north and 28 south) (Figure 3.2.1). The stock, or stock complex, in the western Baltic has spawning areas in the Arkona Basin (Subdivision 24) and different areas in Subdivision 22. Also, ichthyoplankton studies have been carried out that identify the main spawning areas (see section below on “Location of spawning”).

Results of early population genetic investigations (Sick, 1965; Jamieson and Otterlind, 1971; Moth-Poulsen, 1982) supported the assumption that reproductively separate sub-populations existed in the eastern and western Baltic Sea. New studies using modern gene technology confirm these findings (Nielsen *et al.*, 2001). The exchange of genetic material between the eastern and western populations thus seems to be very limited. The eastern Baltic cod is in genetic terms highly divergent from North Sea cod, while western Baltic cod show intermediate genetic characteristics (Nielsen *et al.*, 2001). The reproductive separation is effective through limited overlap in spawning seasons between the two stocks and adapta-

tions in egg characteristics of eastern Baltic cod to survive in a low saline environment.

Assessment units

The assessment is performed separately for the western Baltic cod stock i.e. Subdivisions 22–24 and the Eastern Baltic cod i.e. Subdivisions 25–32 (Figure 1 in ICES, 2001a). Spawning stock biomass and recruitment time series are available for the period 1970–2003 and 1966–2003 for the each stock respectively (ICES, 2003a). The standard stock assessment uses an XSA covering age-groups 1–7+ and 2–8+ for the western and eastern stocks respectively, while Multi-Species models (MSVPA) developed separately for each of the two stocks provide recruitment estimates from age-group 0 onwards (ICES, 2003b). To establish time-series of spawning-stock sizes and recruitment in the different spawning areas of the eastern Baltic cod area-disaggregated MSVPAs are available for Subdivisions 25, 26, and 28 (Köster *et al.*, 2001b; ICES, 2001b). Despite the evidence of stock discreteness the two stocks are managed as one unit by the IBFSC, but this may be changed in the near future.

Time-series of catches, fishing mortalities, spawning-stock biomass and recruitment

The historical development in catch, fishing mortality, spawning-stock biomass and recruitment at age 1 of the western Baltic cod stock is presented in Figure 3.2.2. The landings were stable around 40 to 55×10^3 t until mid-1980s, but declined during the late 1980s to a historic minimum of 17×10^3 t in the early 1990s. After an intermediate increase in the mid-1990s, the stock size is at an intermediate level. The fishing mortality as determined by XSA was rather high, i.e. between 1.0 and 1.5 and showed large fluctuations especially in the 1990s, partly caused by enforced management measures. The western cod spawning-stock biomass largely follows the development in landings (Figure 3.2.2). Recruitment at age 1 shows a declining trend from early 1970s to late 1980s and intermediate year-class strength in most recent years.

Catches of the eastern Baltic cod stock fluctuated around 120 to 230×10^3 t during the 1970s followed by an increase to nearly 400×10^3 t in 1984 and a subsequent decrease to 45×10^3 t in 1993 (Figure 3.2.3). In most recent years catches have fluctuated between 70 and 120×10^3 t. The fishing mortality declined throughout the 1970s from 1.1 to 0.5, but reversed during the 1980s to reach a historic high value of 1.4 in 1991. F sharply decreased to the lowest level on record in 1993 (Figure 3.2.3). This reduction was caused by enforced management measures, i.e. a TAC reduction for the entire Baltic (the management unit) from 171×10^3 t in 1991 to 100×10^3 t in 1992 and 40×10^3 t in 1993. Since then a pronounced increase in fishing mortalities to the former high level is indicated due to increasing fishing effort at declining stock size (ICES, 1998).

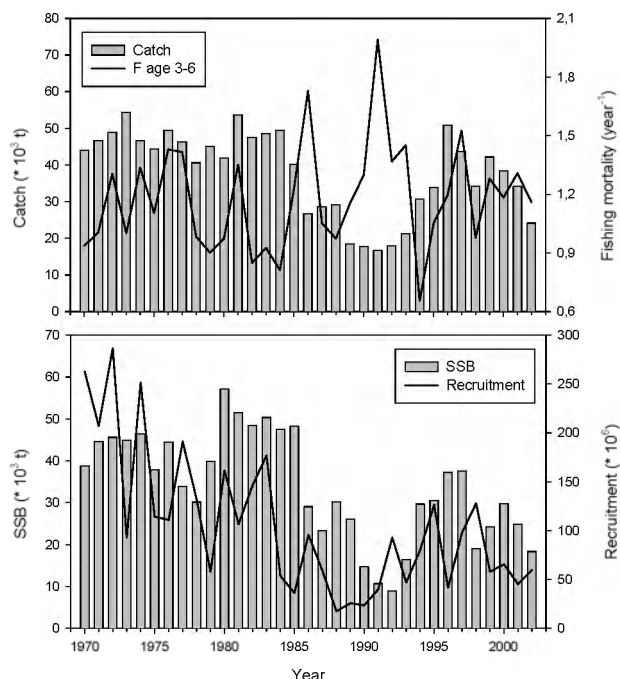


Figure 3.2.2. Catch, fishing mortality (average ages 3–6), spawning-stock biomass and recruitment (age 1) of western Baltic cod.

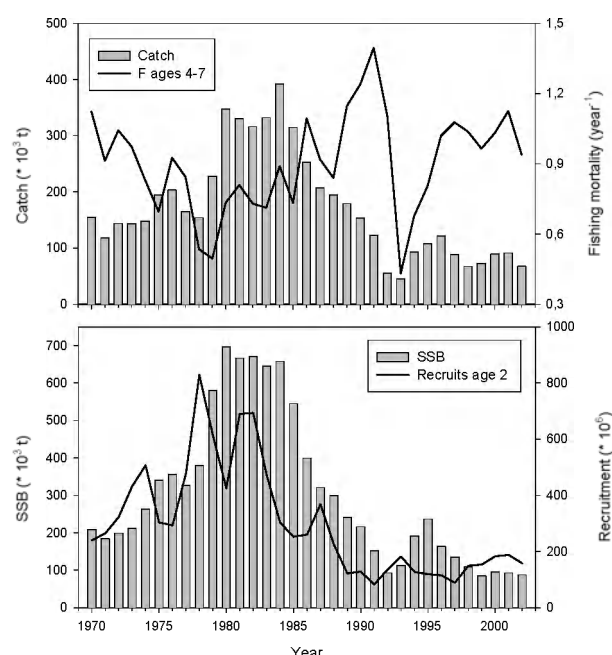


Figure 3.2.3. Catch, fishing mortality (average ages 4–7), spawning-stock biomass and recruitment (age 2) of eastern Baltic cod.

The stock abundance of eastern Baltic cod is characterised by a pronounced increase from 1976 to 1980, remaining high until 1983, followed by a steady decline to its lowest level on record in 1991. Despite some fluctuations during the 1990s, the stock remains at a low level. The SSB followed a similar time trend, but remained

longer at a high level and recovered to a higher degree after its minimum in the early 1990s (Figure 3.2.3). The time-series of recruitment at age 2 show a high reproductive success at intermediate SSB values during the 1970s, followed by a significant decline in reproductive success at historically high spawning-stock levels from 1981 to 1985.

Estimates of SSB for eastern Baltic cod in Subdivisions 25, 26 and 28 based on the area disaggregated MSVPA displayed a substantial decrease in all three areas from 1983 onwards. The SSB increased again in the early 1990s in Subdivisions 25 and 26, due to enhanced reproductive success and a reduction in fishing mortality, however, no recovery is evident for the stock component in Subdivision 28 (Köster *et al.*, 2001b; ICES, 2001b). A declining trend in recruitment is obvious in the 1980s for all areas. The abundance of 1-group cod was estimated to be lowest in Subdivision 28 throughout the time-series, with extremely low values in this Subdivision since 1990. During the second half of the time-series, cod recruitment was estimated to be highest in Subdivision 25 (with the exception of the 1993 year class). When evaluating these area-specific data against research survey results, the overall trend is confirmed, but clear indications exist that cod during different life stages are transported or migrate between basins (Köster *et al.*, 2001b).

Apart from XSA and MSVPA output, time-series of spawning-stock size and recruitment indices are available from the Baltic International Trawl Survey (BITS) conducted annually since 1982 (ICES, 2002). The survey has been conducted by national research vessels in the 1st quarter of the year, but with limited coordination in coverage and gear until a revision of the survey strategy and survey gear took place in 2001 when an additional 4th quarter survey was established. However, the impact of the changed gear on catchability especially of age-group 1 and 2 is presently not resolved (ICES, 2002). In addition, benthic-pelagic trawl surveys addressing spawning aggregations have been conducted in the Gotland Basin throughout the 1980s and in the Bornholm Basin since 1994. Specific pelagic trawl surveys targeting 0-group cod were conducted in the Gotland Basin during the 1980s and in the Bornholm Basin from 1993–2000.

There is a 4th quarter German survey time-series for the western Baltic cod that started in the beginning of the 1980s and which is more consistent than the BITS. Additionally, a long-term trawl data series exists from the early 1950s to 1999 based on Danish and German surveys utilising a standard gear.

Commercial CPUE data are only used in the western Baltic cod assessment, but also exist for the eastern Baltic in a standardised form since the early 1980s and for specific trawler fleets for earlier periods (Lablaika and Lishev, 1961).

Time of spawning

Date of spawning and interannual variability or trend

The western Baltic stock spawns from January to May with their main spawning period from February to April (Bagge *et al.*, 1994). The eastern stock has an even more prolonged spawning period, which historically extends from March to September. This behaviour is likely to be an adaptation to the variable, and sometimes critical, environmental conditions in the Baltic Sea (MacKenzie *et al.*, 1996). The time of peak spawning as identified on the basis of egg abundance estimates in the Bornholm Basin was between the end of April and mid-June in the 1970s and 1980s (MacKenzie *et al.*, 1996). During the 1990s, the time of peak egg production gradually changed to the second half of July (Wieland *et al.*, 2000) with the start of the main spawning period being delayed until May. The duration of the spawning period depends on sex and size with males generally ripening earlier than females, and large females ripening earlier and spawning longer than smaller females. However, the time of peak spawning of both sexes is similar (Tomkiewicz and Köster, 1999). The observed shift in the main spawning time of cod might be affected by the age structure of the stock but other processes must also be involved. Potential causes include removal of early spawners by the commercial fishery, which is largely directed towards prespawning and early spawning concentrations (ICES, 1999), and low ambient water temperatures delaying the ripening process (Wieland *et al.*, 2000).

Timing of spawning season in relation to environmental conditions

Timing and duration of spawning are important sources of variability in reproductive success of eastern Baltic cod. Variability is due to seasonal changes in: i) abiotic environmental parameters, most importantly declining oxygen concentrations in the bottom water layer from winter to summer affecting egg survival rates (MacKenzie *et al.*, 1996), ii) overlap with pelagic fish acting as predators is high in spring at which time sprat concentrate in the deep Baltic basins for spawning (Köster and Möllmann, 2000), iii) temporal/spatial pattern of nauplii production determining the food availability of first-feeding larvae (Hinrichsen *et al.*, 2002a) and iv) transport of larvae into suitable nursery areas (Hinrichsen *et al.*, 2002a). For further information, see section on Recruitment below.

Location of spawning

Horizontal distribution of spawning

Since the beginning of the last century the location of the cod spawning areas in the Baltic Sea has been studied by surveying the horizontal distribution of eggs and larvae (Strodtmann, 1906; Mielck, 1926; Kändler, 1949; Grauman, 1974; Bagge and Muller, 1977; Wieland, 1988; Karasjova, 1997; Makarchouk, 1997). The Born-

holm Basin, the Gdansk Deep and the Gotland Deep have been identified as the major spawning areas in the eastern Baltic (Figure 3.2.1). The most important spawning areas in the western Baltic are located in southern Subdivision 22, with less important spawning grounds in the Danish Straits (northern Subdivision 22) and the Arkona Basin (Subdivision 24).

In the central Baltic Sea with its permanent stratification into an upper low salinity layer (approximately 7‰) and a deeper saline layer (approximately 12–16‰) both the vertical and horizontal distribution of cod is related to its salinity preference, it being a marine species. Outside the spawning period cod are distributed mainly near the bottom at intermediate depths i.e. below the halocline (Neuenfeldt, 2002). However, prior to spawning ripe cod migrate to the deep basins and during spawning there is a significant difference in the distribution of mature and immature cod (Tomkiewicz and Köster, 1999). The spawning cod mainly aggregate in the pelagic zone below the halocline but avoid the low oxygen concentrations which often prevail in the deeper, central parts of the basins. Immature and spent cod remain demersal at intermediate depths (Tomkiewicz *et al.*, 1998). Accordingly, the highest concentrations of the youngest egg stages occur in the deepest parts of the basins with considerably lower abundances at intermediate depths (Bagge and Muller, 1977; Wieland, 1988). The vertical distribution of cod eggs is related to the density characteristics of the eastern Baltic cod. Eastern Baltic cod have eggs that reach neutral buoyancy at salinities of around 12–14 psu, which is an adaptation to the brackish water of the eastern Baltic Sea. These conditions are fulfilled only within and below the halocline and eggs are virtually absent from the water layers above the halocline (Nissling and Vallin, 1996; Wieland and Jarre-Teichmann, 1997). In the western Baltic where the water has higher salinities and is more mixed, the eggs of cod do not show such adaptations.

Spawning intensity in different spawning areas

Studies of the gonadal maturation pattern of western Baltic cod based on trawl surveys conducted monthly from February to June during the years 1996–1999 confirmed that Kiel Bight is the major spawning area of the western stock, but also Mecklenburger Bay is of importance (Bleil and Oeberst 2002).

In the eastern Baltic, the abundance of cod eggs during main spawning period is generally higher in the Bornholm Basin than in the Gdansk and Gotland basins (Köster *et al.*, 2001b) (Figure 3.2.4). Egg abundances vary considerably from year to year, especially in the Gdansk Deep and the Gotland Basin. Since the mid-1980s, the contributions of these easternmost spawning areas to the total egg production have been marginal. The intermediate increase in egg abundance which was observed during the mid-1990s relates only to the Bornholm Basin.

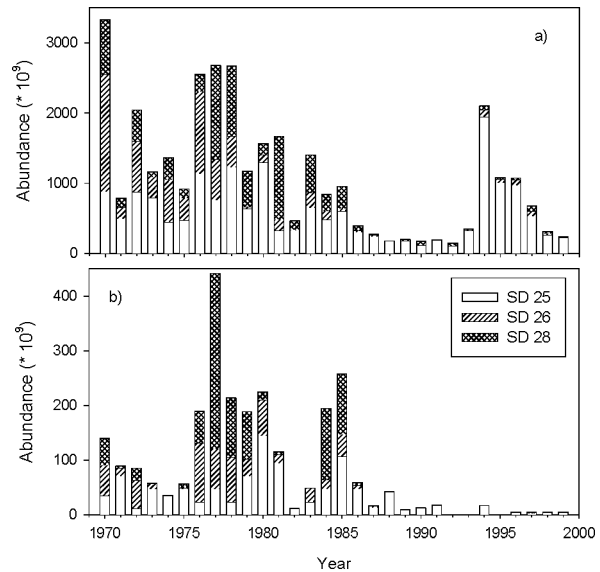


Figure 3.2.4. Abundance of cod eggs (a) and larvae (b) in Subdivisions 25 (Bornholm Basin), 26 (Gdansk Deep and southern Gotland Basin) and 28 (Central Gotland Basin) during main spawning time 1970–1999 data from Karasiova 1999; Köster *et al.*, 2001b, Makarchouk 1997; Karasiova, Köster, and Makarchouk unpubl.

This indicates low spawning intensity in the Gdansk Deep and Gotland Deep, however, the egg abundance estimates could also be influenced by adverse hydrographic conditions in these areas. If the oxygen concentration in the water layer where the cod eggs flow is below approximately 2 ml/l then the eggs will die and sink to the bottom which would result in low egg abundance estimates (Köster *et al.*, 2001a). These conditions occur in the eastern spawning areas during stagnation periods i.e. limited inflows of saline oxygenated water from the North Sea via the Kattegat and the western Baltic Sea. Under these conditions the egg abundance may not accurately reflect the egg production and spawning-stock size.

Catch rates from the Baltic International Trawl Survey conducted annually in February/March (Aro, 2000), i.e. before the spawning migration, confirm that the spawning-stock biomass was low in the Gotland Basin during the 1990s. Catch rates in the Gdansk Deep were similar or even higher than in the Bornholm Basin, which contradicts the distribution as inferred from the egg abundance as well as the spawning-stock biomass estimates obtained by area disaggregated MSVPA runs (Köster *et al.*, 2001b).

In addition, benthic-pelagic trawl surveys conducted in different months of the spawning season in 1996 indicate spawning migration from the Gdansk Deep and the Gotland Basin to the Bornholm Basin. While catch rates of adult cod in the Gdansk Deep and the Gotland Basin decreased from spring until peak spawning time in July/August, they increased in the Bornholm Basin

(STORE, 2003). A similar spawning migration pattern has been reported previously (Netzel, 1974; Lablaika and Lishev, 1961) and would explain the deviations between the estimates of large-scale horizontal stock distribution from (i) winter trawl surveys (ii) spawning-stock biomass estimates (iii) area disaggregated MSVPA based on quarterly catches and (iv) egg abundance estimates from ichthyoplankton surveys (Köster *et al.*, 2001b). Whether this spawning migration is triggered by unfavourable hydrographic conditions in easternmost spawning areas or by homing into areas of origin is unknown. Spawning migrations to the Bornholm Basin may also occur in years of favourable environmental spawning conditions in Gdansk and Gotland Deep (Netzel, 1974), but the intensity of the spawning migration seem to be related to environmental conditions (Lablaika and Lishev, 1961).

Biological details

Fecundity

Cod fecundity data exist from various years and areas of the Baltic Sea. Within the western stock, the relative fecundity (number of eggs per g body weight) varies only a little from year to year. The variation between spawning areas is also insignificant (Bleil and Oeberst, 1996; Bleil and Oeberst, 1999). It has been shown that the relative fecundity of the eastern Baltic cod is independent of body length and that it does not vary either between the spawning areas or between the different months of the spawning period; but it does vary significantly between years (Kraus *et al.*, 2000). Fecundity models have been established for this stock based on a significant relationship between the relative fecundity and either growth anomaly and temperature or the food availability relative to stock size (Kraus *et al.*, 2000; Kraus *et al.*, 2002).

Sex ratios and maturity ogives

Time-series of age-specific sex ratios and maturity ogives have been established based on data from the Baltic International Trawl Survey, western Baltic surveys and the International Bottom Trawl Survey in Kattegat (Tomkiewicz *et al.*, 1997; STORE, 2003). These data show: i) a general dominance of females with increasing age, ii) that males generally mature at a younger age than females, iii) that the age at which sexual maturation occurs increases with the distance from the Kattegat and the Danish Straits and iv) that maturity-at-age tends to vary between years or time periods. The time-series of combined female and male ogives have been applied in the stock assessment estimate of SSB since 1998. But the combined ogives do not allow for the strong influence of both the age structure of the stocks and the changes in environmental conditions (e.g. food availability) on the relative size of the female spawning-stock and the stock egg production.

Variability in maturation of the eastern Baltic cod appears to be coupled to growth rates, reflected in decreasing age at sexual maturity concurrent with increasing

weight-at-age both over time and from west towards east (STORE, 2003). Thus, an increase in weight-at-age resulting from a decreasing stock size and increasing prey availability as seen in the 1990s tends to promote a decline in length/age of attaining sexual maturity and an increase in individual fecundity which has a compensating effect on the total egg production of the stock (Kraus *et al.*, 2002).

Potential egg production

For the eastern Baltic cod stock, time-series of potential egg production have been established on the basis of estimates of the female-only spawning-stock size and composition at the time of spawning, weight-at-age and the fecundity model (Kraus *et al.*, 2002; Köster *et al.*, 2003a). The studies show a significant relationship between the potential egg production and estimates of the realized egg production in Subdivision 25 based on egg surveys. The estimated difference between the potential and realised egg production was around 15% (Kraus *et al.*, 2002) which apart from uncertainties in the input data series (Köster *et al.*, 2003a) may result from i) atresia, i.e. resorption of oocytes before spawning (Kraus, submitted), ii) variable fertilization success in relation to salinity changes (Westin and Nissling, 1991) and iii) differences in egg mortality already in the first developmental stage (Wieland, 1995).

The potential egg production by the western stock estimated by (Bleil and Oeberst, 1996) for 1993 and 1994 attained a level of 15–16% of the potential egg production by the eastern stock (Köster *et al.*, 2001a). This is slightly higher than would be expected from the ratio between the relative sizes of the spawning-stock biomass in the two areas, and the high individual fecundity of western cod (Bleil and Oeberst, 1996).

Parental effects on offspring viability

For eastern Baltic cod significant positive relationships between i) egg size and female size, ii) egg size and larval size/growth, iii) egg size and survival during the yolk-sac stage, and iv) egg size and egg buoyancy, have been documented (Nissling *et al.*, 1998; Vallin and Nissling, 2000). This implies that the survival rates of eggs and larvae originating from large females are higher than for those from smaller females, especially because larger and more buoyant eggs have a higher chance of avoiding the often oxygen-depleted bottom water layers in the deep basins of the eastern Baltic Sea. Consequently, the significant reduction in the share of older females in the spawning-stock from the mid-1980s to the early 1990s caused by heavy fishing pressure (Wieland *et al.*, 2000), has had a negative effect on the reproductive success of the eastern Baltic cod stock (Vallin *et al.*, 1999; Hjerne *et al.*, 2004). Furthermore, the size of eggs from individual fish varies during the spawning period, with an early maximum and a subsequent decrease, which suggests higher survival probabilities of early spawned cohorts (Vallin and Nissling, 2000).

Recruitment

By relating observed abundance and production data between successive life stages, (Köster *et al.*, 2003a) confirmed recruitment of eastern Baltic cod to be dependent on egg survival, with low oxygen concentrations in dwelling depths being a major cause of egg mortality. Production of surviving eggs and larval abundance was weakly correlated, indicating that the late egg and early larval stage is critical for cod recruitment. In contrast larval abundance is significantly related to year-class strength (Köster *et al.*, 2003a). Processes affecting these critical life stages are reviewed below and possibilities of incorporating significant environmental factors into recruitment predictions and stock recruitment relationships are discussed.

Egg survival in relation to hydrographic conditions

Cod early life stage survival is known to be highly influenced by hydrographic conditions in spawning areas (Bagge *et al.*, 1994; Grauman and Yula, 1989; Plikshs *et al.*, 1993; Nissling, 1994; Wieland *et al.*, 1994). The observation that live cod eggs are only encountered in water layers with oxygen concentrations $>2\text{ml/l}$ and temperatures $>1.5^\circ\text{C}$ and that a salinity of 11 psu is necessary for successful fertilization leads to the definition of the so called reproductive volume (RV), i.e. the water volume that can sustain cod egg development (Plikshs *et al.*, 1993). Processes affecting the RV are: i) the magnitude of inflows of saline oxygenated water from the western Baltic, ii) temperature regimes in the western Baltic during winter, which affect the oxygen solubility prior to advection, iii) river run-off and iv) oxygen consumption by biological processes (MacKenzie *et al.*, 2000; Hinrichsen *et al.*, 2002b).

Resolving the potential egg production by cod spatially, showed that in some years a substantial fraction of the total annual egg production has been unsuccessful (in terms of recruit production), because eggs were released in spawning areas with virtually no RV (Figure 3.2.5). This mismatch in egg production and suitable environmental conditions for egg development explains the drastic decline in reproductive success of cod from 1981 to 1985 despite high egg production (Köster *et al.*, 2003c).

However, the reproductive volume may be not the best proxy for egg survival, as it i) does not take into consideration the impact of sub-lethal oxygen deficiency on egg and larval survival, ii) neglects the possibility that eggs float outside the reproductive volume in water layers not sustaining their development and iii) ignores a potential horizontal mismatch in spawning activity and the presence of reproductive volumes. The influence of oxygen concentration on the proportion of viable hatch in relation to the surviving fraction at norm-oxic conditions derived from controlled laboratory experiments showed indeed that oxygen concentrations above the threshold level of 2 ml/l that is utilized in the definition

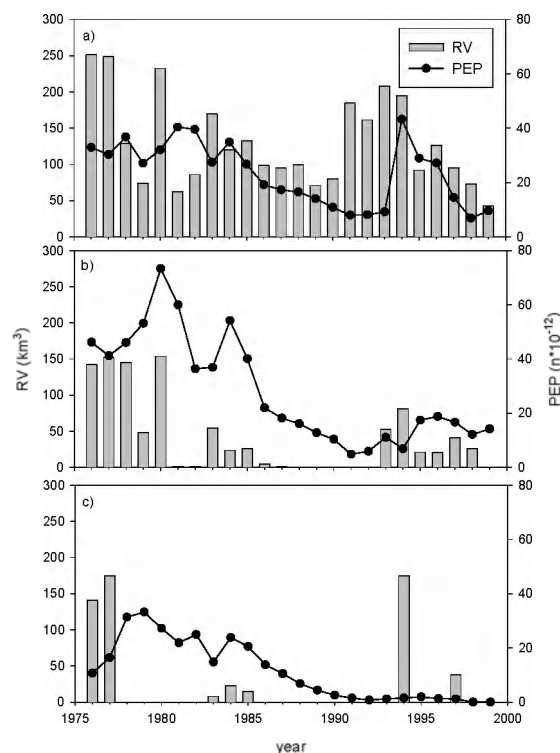


Figure 3.2.5. Reproductive volume (RV) of cod eggs during main spawning seasons 1976–1999 and potential egg production of central Baltic cod (PEP) in ICES Subdivisions 25 (a), 26 (b) and 28 (c).

of the RV, still have a pronounced impact on egg survival (Wieland *et al.*, 1994; Rohlf, 1999).

Coupling an oxygen - egg survival relationship obtained from laboratory experiments to modelled vertical egg distributions and ambient oxygen conditions at depths of incubation enabled the estimation of an oxygen related egg survival factor (Köster *et al.*, 2001a). This survival factor compares favourably with the survival observed *in-situ* by successive ichthyoplankton surveys, following egg cohort developmental and seasonal egg production curves in relative terms. The absolute magnitude of observed egg survival is, however, significantly lower *in-situ*, indicating that other causes of mortality affect egg development success (STORE, 2003).

For the western Baltic a similar dependence on hydrographic conditions for reproductive success has been proposed on basis of an exploratory statistical analysis (Berner *et al.*, 1989). However, recent monitoring of hydrographic conditions on the spawning grounds did not indicate unfavourable conditions that would explain the observed variability in recruitment success (Bleil and Oeberst, 2002).

Predation on eggs

Substantial predation by clupeids on cod eggs has been described for the Bornholm Basin, which is at present the only important spawning area of the eastern Baltic cod stock. Egg predation is most intense at the beginning of the cod spawning season, with sprat being the major

predator (Köster and Schnack, 1994). At this time spring spawning herring concentrate in their coastal spawning areas and do not contribute to the predation-induced egg mortality of cod. Sprat spawn in the Bornholm Basin from March to July, thus concentrating in cod spawning areas at times of high cod egg abundance. After cessation of spawning, part of the sprat population leaves, resulting in reduced predation pressure on cod eggs. With the return of the herring from the coastal areas to their feeding grounds in the Bornholm Basin, the predation on cod eggs by herring increases to considerable levels (Köster and Möllmann, 2000).

The shift of cod peak spawning time from spring to summer (Wieland *et al.*, 2000) resulted in decreasing predation pressure on cod eggs by sprat, due to a reduced temporal overlap between predator and prey. Additionally a decline in predation on cod eggs by individual sprat was observed from 1993–1996, despite the relatively high abundance of cod eggs in the plankton. This is partly explainable by a reduced vertical overlap between predator and prey. Due to the increased salinity after the 1993 major Baltic inflow (Matthäus and Lass, 1995), cod eggs floated in the shallower water layers, while clupeids occurred deeper, due to enhanced oxygen concentration in the bottom water (Köster and Möllmann, 2000). Thus, predation pressure on cod eggs appears to be higher in stagnation periods, characterised by the absence of inflows of oxygenated saline water from neighbouring western Baltic basins.

Cod egg predation by clupeids appears to be less important in the more eastern spawning areas. This has been explained by a more limited vertical overlap between predator and prey in these areas (STORE, 2003).

Larval survival in relation to hydrographic conditions

Low oxygen concentration does not only impact on egg survival, but also the vertical larval activity is affected by the oxygen concentration at incubation (Rohlf, 1999). Even when hatching successfully, larvae incubated at low oxygen concentrations are less active, which is of importance in the Baltic as hatching occurs in deep water layers and the larvae have to ascend to the upper water layers where the food supply is (Grønkjær and Wieland, 1997). The vertical distribution of early larvae within and below the halocline implies that oxygen conditions affect larval survival as demonstrated by Nissling (1994).

Larval diet composition

Copepod nauplii and copepodites are the dominating prey organisms of cod larvae in the central Baltic (Voss *et al.*, 2003). In contrast to other stocks outside the Baltic, phytoplankton does not comprise a significant proportion of the cod larval diet. This is confirmed by results obtained from the eastern Baltic spawning areas in 1978–1985 (Grauman *et al.*, 1989). The difference might be explained by the special environmental conditions in the Baltic, which lead to a temporal as well as spatial

mismatch of larvae and high concentrations of phytoplankton. Cod larvae appear in the plankton after the spring bloom of diatoms has ended and before the autumn bloom occurs. Additionally, the vertical overlap during spring is rather limited, i.e. the highest concentrations of diatoms are encountered in 5–15 m depth (Dahmen, 1995), whereas feeding cod larvae show highest concentrations at ca. 30–35 m depth and only very few are found in the upper 15 m of the water column (Grønkjær and Wieland, 1997).

Food availability for larvae and early juveniles

Investigations on the seasonal distribution of mesozooplankton in the central Baltic revealed seasonal trends in abundance to be characterised by the general life-cycle patterns of the abundant meso-zooplankton species. The univoltine *Pseudocalanus elongatus* (Line, 1979; Line, 1984) had a peak in abundance in April and May. There is a clearly visible shift in stage-structure from April (high copepod egg, CI-III and CVI abundance) to May/June (increasing CI-III and CIV as well as decreasing CVI abundance). Conversely *Temora longicornis* and *Acartia* spp. have multiple generations and accumulated CVI in June to produce the next summer generations. *Centropages hamatus*, preferring higher temperatures (Ackefors and Hernroth 1970; Sidrevics 1984), as well as *Oithona similis* were found in low quantities early in the season. A rise of cladoceran abundance from April to June illustrates the affinity of this taxonomic group to increased temperature (Dippner *et al.*, 2000; Möllmann *et al.*, 2000).

Horizontal distribution patterns of *P. elongatus* in the Bornholm Basin are associated with their vertical distribution. CVI, which prefer higher salinities, (Dippner *et al.*, 2000; Möllmann *et al.*, 2000) were found in deeper parts of the water column. This explains the concentrations in the centre of the Basin. Younger stages were found in the shallower water layers from where they are moved by currents to shallower regions. In contrast, *T. longicornis* and *Acartia* spp., not confined to high salinities but to warmer waters, were generally found in the upper 50 m of the water column and also in shallower regions. Nauplii of *C. hamatus* were observed mainly in the centre of the Basin which suggests a spawning in deeper layers, similar to *P. elongatus*. The general concentration of *O. similis* is similar to *P. elongatus* and associated with their deeper distribution, whereas cladocerans dwelling in the upper water layer were found all over the Basin.

Larval and early juvenile transport

(Hinrichsen *et al.*, 2001a) performed a modelling exercise on the transport of early life stages between the western and eastern Baltic. The potential for early life stages from the western Baltic cod stock to drift into the Arkona Basin and the Bornholm Basin, where they contribute to the juvenile population, has been recognised as being caused mainly by strong westerly winds. During cold and calm winters, the retention of eggs, larvae and

juveniles within their original spawning grounds predominates.

(Jarre-Teichmann *et al.*, 2000) demonstrated that the cumulative wind energy at peak spawning time impacts on eastern cod recruitment success. The suggested process being transport of larvae and pelagic juveniles to coastal nursery habitats, where there is high plankton production, during periods of high transport, and retention in the central basins during periods of low wind stress and variable wind direction (Hinrichsen *et al.*, 2001b). (Köster *et al.*, 2001a) incorporate these transport processes into their exploratory analysis of cod recruitment processes by modifying the wind energy index to explicitly bring the direction of transport into consideration (larval transport index). Hydrodynamic modelling studies by (Voss *et al.*, 1999) and (Hinrichsen *et al.*, 2001b) demonstrated that larval drift towards the west and north is caused primarily by winds of westerly and southerly direction, whereas winds of opposite direction result in larval transport to the south and east. Periods of low wind energy or varying direction in turn cause retention in the spawning areas.

(Hinrichsen *et al.*, 2003) compared the seasonally averaged distribution of drifters with the actual distribution of 0-group cod as determined from bottom and pelagic trawl surveys in and around the Bornholm Basin conducted in the autumn from 1993 to 2000. The results suggest that juveniles caught in different areas can be assumed to have hatched at different times in the spawning season. Because of seasonal differences in the circulation pattern, the southern coastal environment is on average the most important for larvae from early and late spawned eggs. Larvae that hatched in mid-summer were usually either transported towards the north or retained to a higher degree than normal on the spawning ground, where there were poorer feeding opportunities than in the more shallow coastal areas, see below.

Impact of food availability on larval growth and survival

The effect of food availability on growth and survival of cod larvae has been investigated using a coupled tropho-/hydrodynamic individual-based model (IBM) (Hinrichsen *et al.*, 2002a). Model results based on idealised three dimensional prey fields and realistic atmospheric forcing conditions suggest the necessity of co-occurrence of peak prey (nauplii) and early larval abundances as well as favourable oceanographic conditions for high survival rates. The strong decline of the *P. elongatus* stock during the last two decades as a result of low salinities (Möllmann *et al.*, 2000), meant that early cod larvae changed from a non-food limited to a food limited state. If *P. elongatus* nauplii were present in the model, high survival rates occurred during spring and early summer, whereas omitting *P. elongatus* resulted in high mortality rates and only late hatched larvae or larvae transported rapidly out of the basins into shallow water areas survived (Hinrichsen *et al.*, 2002a). Thus, low *P. elongatus* availability is likely to have contributed to the reduced recruitment of cod since the late 1980s.

Predation on larvae

In contrast to cod eggs, cod larvae are very rarely found in clupeid stomachs in the central Baltic. Insufficient sampling may be one reason, but it appears to be an unlikely explanation, because high numbers of other fish larvae were encountered, with sprat obviously specialising in larval prey (Köster and Möllmann, 1997). The low predation pressure on cod larvae may be explained by a combination of limited vertical overlap between larger larvae and a size selection (at least in herring) favouring these larger larvae as prey. Other potential predators of cod larvae, e.g. scyphomedusae, show a temporal and spatial mismatch in occurrence with cod larvae. This makes high predation pressure rather unlikely, at least in the eastern Baltic (CORE, 1998).

Predation on juveniles

Juvenile cod suffer from cannibalism (Sparholt, 1994; Neuenfeldt and Köster, 2000). As in other cod stocks, the intensity of cannibalism is related not only to predator abundance, but also to the concentrations of juveniles, which depends upon the habitat volume occupied and on the overall abundance of cod. Apart from medium- to long-term distribution changes related to stock size, interannual variability in cannibalism may be also influenced by changing hydrographic conditions. (Uzars and Plikshs, 2000). For example, low oxygen concentrations in the deep Baltic basins may force the adults into shallower slope areas, and low temperature in shallow waters may force juveniles into deeper water thus increasing the spatial overlap between predator and prey, and hence cannibalism. This suggests that the process is most pronounced in stagnation periods, especially after cold winters and at high predator stock sizes.

Predicting recruitment

Cod larval abundance and recruitment are significantly correlated in Subdivisions 25 and 26, but not in Subdivision 28. Here recruitment occurred regularly despite the lack of larvae in the ichthyoplankton surveys in some years (Figure 3.2.4). This can be explained either by a problem in sampling efficiency of the gear in use at low, and probably patchy, larval abundance or a transport/migration of juvenile life stages into the Gotland Basin. Evidence exists for both passive transport of larvae/pelagic juveniles from the Bornholm Basin into the eastern basins (Aro, 2000) as well as active migration or habitat expansion into the Gotland Basin of demersal juveniles during the second year of life (Plikshs, 1996).

Larval abundance integrated over all spawning areas however is significantly associated with cod recruitment at age 0 as output of the MSVPA and recruitment at age 2 as output of the regular stock assessment. Adding prey availability for early larvae (the product of *P. elongatus* nauplii abundances and turbulent velocity) as an additional variable significantly enhances the statistical relationship between larval abundance and recruitment, ex-

plaining 72% of the variability in recruitment at age 2 (STORE, 2003).

Stock recruitment relationships

Investigation of the link between environmental factors, spawning-stock features and reproductive success of Baltic cod has been performed by several investigators (Berner *et al.*, 1989; Kosior and Netzel, 1989; Lablaika *et al.*, 1989; Grauman and Yula, 1989; Plikshs *et al.*, 1993; Sparholt, 1996; Jarre-Teichmann *et al.*, 2000; Vallin and Nissling, 2000; Köster *et al.*, 2001a). All studies revealed an impact of hydrographic conditions on recruitment, specifically the impact of oxygen concentration within and below the halocline. Most of the studies also detected an impact of spawning-stock size on recruitment.

Few of these studies considered refined measures of the stock reproductive potential, e.g. potential egg production (Kraus *et al.*, 2002), offspring viability in relation to parental characteristics (Vallin and Nissling, 2000; Hjerne *et al.*, 2004), or explored the explanatory power of measures of predation on early and juvenile life stages (Sparholt, 1996; Köster *et al.*, 2001a). None of them so far directly tackled food availability for larvae, but some incorporated wind energy (Jarre-Teichmann *et al.*, 2000) or a larval transport index (Köster *et al.*, 2001a) as indirect factors. Considering spatial heterogeneity of egg production and environmental conditions has likewise been addressed by only a few studies (Köster *et al.*, 2001a; Hjerne *et al.*, 2004).

The environmentally sensitive and spatially explicit stock-recruitment relationship established by Köster *et al.* (2001a) has been further explored by predicting most recent year-class strength and subsequent comparison to updated MSVPA results and survey derived recruitment indices (Köster *et al.*, 2003a). Furthermore, an update of these stock recruitment relationships was conducted by (STORE, 2003). The most recent statistical model includes: the product of potential egg production and oxygen related egg survival factors in each spawning area, and prey availability for first-feeding larvae as the product of *P. elongatus* nauplii abundance and turbulent velocity. If, when predicting recruitment at age 1 and 2, area specific cannibalism rates on 0- and 1-group fish are additionally applied then the statistical model is highly significant and explains 73% of the variability in age-group 0 recruitment (ICES, 2003b).

Migration

Tagging experiments show that cod from the western Baltic may migrate eastwards and enter the Bornholm Basin, Slupsk Furrow, the Gdansk Deep and even the southern part of the Gotland Deep, however these observations are very rare. Similarly, migration rates of cod

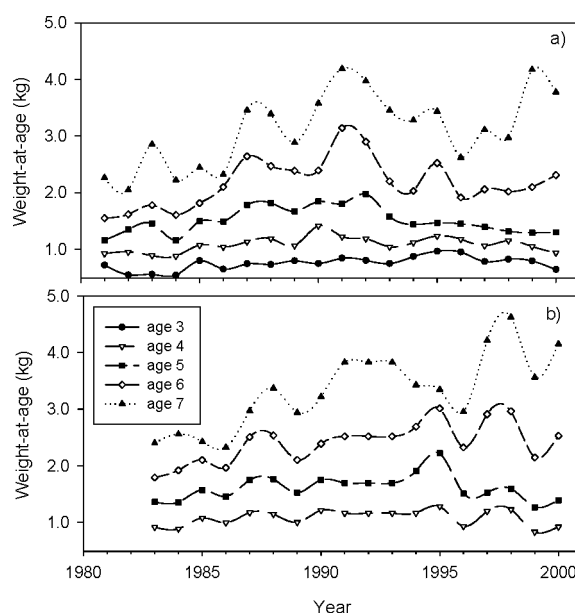


Figure 3.2.6. Average weight at age of cod in the central Baltic (1. quarter) as obtained from sampling the commercial fishery (a) and from the international bottom trawl survey (b) (Köster *et al.*, 2003c, ICES, 2001).

from the eastern Baltic to the western Baltic Sea and from the western Baltic to northwest Kattegat were negligible, while substantial movement occurs within the western and eastern Baltic (for review see (Aro, 1989; Aro, 2000)).

During the feeding period adult cod spread over large areas and may move long distances. In the eastern Baltic, the feeding migration after spawning is in general from deeper waters towards more shallow areas. Also northward migrations along the east coast of the Baltic off Klaipeda and Liepaja have been observed. During the period with large stock size, cod migrated into the Botnian Bay, an area without any spawning areas due to very low salinity in the entire water column (Aro, 2000; Aro, 1989).

Previously spawning migration started in February-March but it now tends to be mainly in April-May. The cod that migrate to the Bornholm Basin to spawn come mainly from the feeding grounds in Hanö Bay, Slupsk Furrow, around the Gdansk Deep and the Gotland Basin (Netzel, 1974). Spawners aggregating in the Gdansk Deep originate from areas south of the Bornholm Basin and from southern parts of the Gotland Basin. The homing behaviour of eastern Baltic cod is uncertain and the fish may use different spawning areas in successive years. See also the section on Location of spawning for a description of spawning migrations in relation to spawning intensity in different spawning areas.

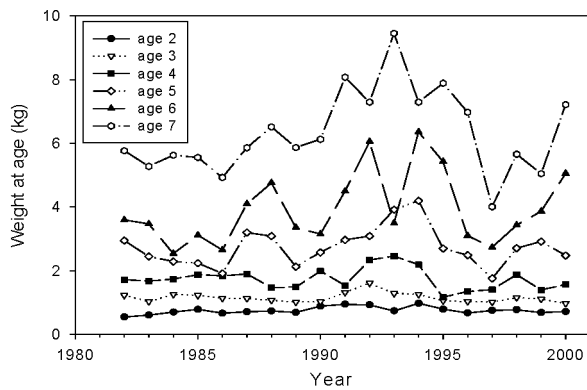


Figure 3.2.7. Average weight-at-age of cod in the western Baltic as obtained from sampling the commercial fishery (ICES, 2001).

Within the western Baltic stock, spawning migrations take place mainly westwards from the Arkona Basin to Mecklenburg Bay, Kiel Bay, Little Belt Sea and the Great Belt Sea and into the southern Kattegat.

Growth

Bagge *et al.* (1994) summarised the available information on growth of Baltic cod with focus on i) estimation of von Bertalanffy growth parameters and ii) reliability of these estimates in relation to sampling procedures and bias caused by age determination problems. As in many fish species, weight-at-age in Baltic cod differs between the sexes and evidence from the international bottom-trawl survey shows that weight-at-age differs between immature and mature fish (STORE 2003).

Growth of Baltic cod has been described as density dependent and affected largely by the relative availability of clupeid prey (Baranova and Uzars, 1986; Baranova, 1992). Thus, concurrent with the decline in stock size of the eastern Baltic stock (Figure 3.2.3) an increase in weight-at-age from both the commercial catch and the international bottom-trawl surveys is observed (Figure 3.2.6). The increase continued until the beginning of the 1990s, followed by a decline in age specific weight. This was seen earlier in the commercial data than in survey data. But this decline did not continue in most recent years for the oldest age groups in both data series. A considerable interannual variability in weight-at-age is evident especially in the older age groups. This is likely to indicate inadequate sampling sizes during surveys or problems in age determination (Bagge *et al.*, 1994) and for the commercial data changes in the relative contributions of trawl and gillnet catches to the total landings.

For the western Baltic cod, a similar increase in weight-at-age with decreasing stock size until the early 1990s is observed (Figure 3.2.7) with a decline in the subsequent 5 years and an increase in most recent years. The changes in weight-at-age thus inversely follow the stock development (Figure 3.2.2).

Similarly, the condition (Fulton's K based on gutted weight as an indication of somatic growth) of individuals

from the eastern stock has varied over time. During the late 1960s, condition tended to be at a relatively high level and was at a low level in mid-1980s. During the early 1990s, condition tended to be above average, but has been near the average since then (STORE, 2003). Condition differs significantly between different length groups, with the highest values in smaller fish. Condition also varies significantly on a seasonal basis, being highest in quarters 4 and 1 and lowest in quarters 2 and 3. This seasonal variation relates to the reproductive cycle with energy allocated to maturation of gonads and spawning and the seasonal variability in food intake, which for adult cod is generally lower in quarters 2 and 3 (during the spawning time) than in quarters 4 and 1 (ICES, 2001b).

Variation in condition was found to be coupled to inter-annual variation in prey abundance (STORE, 2003), which supports the results of (Baranova and Uzars, 1986) and (Baranova, 1992). Condition seems to be particularly strongly correlated with prey availability during years when relative food abundance was lowest. When the relative food availability was higher, condition tended to be better and less variable.

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3.3 Celtic Sea and western English Channel (ICES Divisions VII e-k)

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Environment

The Celtic Sea is situated to the south of the British Isles and Ireland and represents a transition zone between the Atlantic waters at the margins of the European continental shelf and the coastal waters of the Bristol Channel and the Irish Sea. The area of the English Channel considered here is located from the boundary at the western entrance of the English Channel to approximately 2°W (see Figure 3.3.1).

Topography and tidal amplitude vary considerably throughout the region. A deep trough exceeding 130 m within the deep basin of the Celtic Deep extends via St. Georges Channel into the southern Irish Sea. Tidal amplitudes are less than $0.25 \text{ m} \times \text{s}^{-1}$ in the southwest and exceed $2.0 \text{ m} \times \text{s}^{-1}$ in the Bristol Channel and the margins of St. Georges Channel. The variability in topography and tidal force determines the water column structure which from May – November is dominated by thermal stratification. A distinct tidal mixing front marks the boundary between the stratified Celtic Sea and the mixed waters of the Bristol Channel where tides dominate and depths are shallower (Brown *et al.*, 2003 and references therein).

Sea surface temperatures on the shelf, both to the west and south of Ireland, are several degrees warmer in winter than those found in the comparatively shallow Irish Sea. These waters are both deeper and influenced by warmer Atlantic water derived from the North Atlantic Drift. During the summer, bottom temperatures in stratified areas may be 5–6°C cooler than the overlying surface water. Frontal systems tend to develop in late spring at the confluence of mixed and stratified areas, for example the Celtic Sea front to the south of the Irish Sea and the Irish Shelf front to the west of Ireland (Figure 3.3.1; OSPAR, 2000). These break down with the onset of winter cooling and increased wind-induced mixing. This stratification is due primarily to the strong temperature differences that develop between surface and bottom waters because the tides are not strong enough to cause mixing throughout the water column. The resultant thermocline lies at a depth of between 20 and 40 m depending on the year and breaks down in autumn and rebuilds in spring (OSPAR, 2000).

The general pattern of water transport around and within the region is shown in Figure 3.3.1. On the basis of current measurements it is known there is a persistent northwesterly current, which averages about 6 cm^{-1} and follows the slope edge from the Bay of Biscay to the southwest of Ireland. There is also known to be a weak, variable but persistent flow from the coast of Brittany

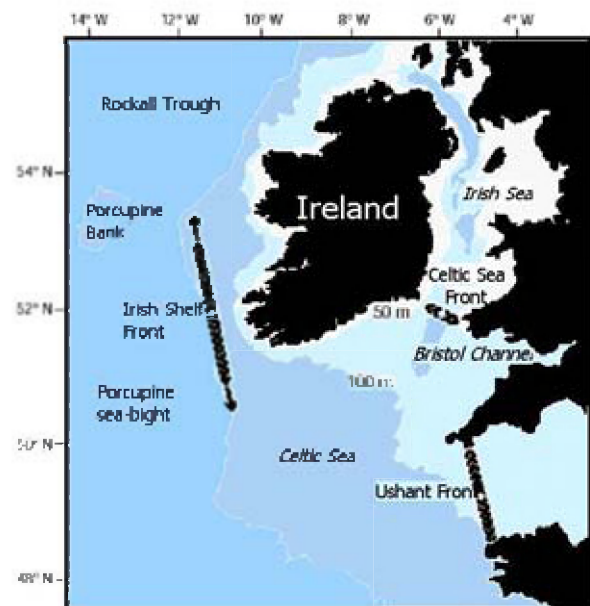
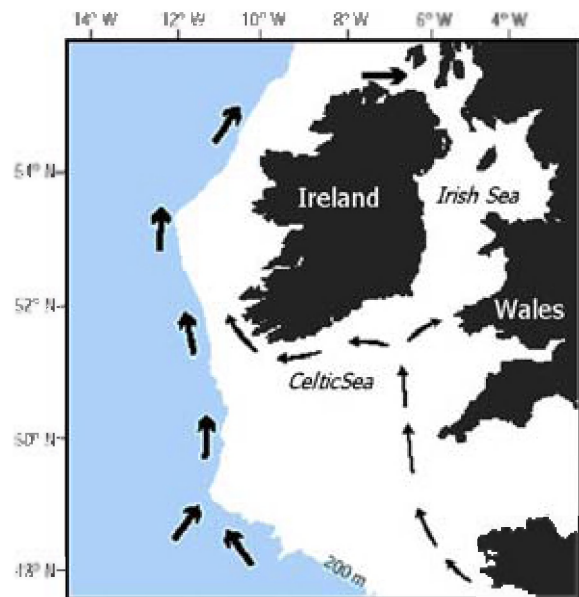


Figure 3.3.1. (upper) General circulation in and around the Celtic Sea (from OSPAR, 2000; adapted from Pingree and LeCann, 1989) and (lower) Frontal systems of the Celtic Sea and Atlantic seaboard (OSPAR, 2000).

across the mouth of the Channel. North of the Isles of Scilly part of this flow moves west along the south coast of Ireland with the remainder flowing weakly northwards.

A general overview of the physical and biological characteristics of the Celtic Sea and English Channel is given in OSPAR (2000) and more detailed descriptions of the physical structure and circulation are available in Brown *et al.* (2003) and Pingree (1980).

Stock and geographic distribution

Evidence of stock discreteness

Since 1997, the cod of the Celtic Sea and western English Channel (ICES Divisions VII e-k) have been assessed as a single stock unit. There is, however, limited evidence to support the discreteness of the stock based on tagging and genetic studies. Although cod in the Celtic Sea and western Channel are distinct from cod in the eastern Channel and the North Sea, the degree of isolation from the Irish Sea is less clear.

Brander (1975) reported that a substantial number of immature cod tagged in various parts of the Irish Sea undertook migrations into the Celtic Sea, but that mature fish were primarily recaptured on and around the spawning grounds of the Irish Sea. Pawson (1995) described the results of several tagging studies from various locations around the British Isles and reported that cod released in the Celtic Sea have been recaptured in the Irish Sea and vice versa (see Figure 3.7.5 in the section on Irish Sea Cod). Although there seems to be an association between the cod of the Celtic and Irish Seas, tagging results (Pawson, 1995) have suggested that there is limited migration between the western Channel and Celtic Sea. Hutchinson *et al.* (2001) reported that there was no evidence of genetic sub-structuring within the Irish and Celtic Seas, although the populations remained divergent from the western Channel. These findings corroborate anecdotal evidence that cod of the western English Channel seldom move out of the area and only undertake localised seasonal migrations from deeper water in the summer to warmer inshore waters during the winter (Pawson, 1995).

More recent tagging results have been described in an abstract on tagging research that was carried out from 1997–2000 (2220 tagged cod) which stated that although there was some movement of cod between the Irish Sea and Celtic Sea, the component of Irish Sea cod in the Celtic Sea was low and that no cod tagged in the Celtic Sea were recovered in the Irish Sea (Connolly and Officer, 2001). One of the reasons these results are thought to differ from those from the 1970s is due to the large difference in abundance compared to the current status of both of the stocks.

Meristics have shown that the mean vertebral number for cod was 51.72 off of southeastern Ireland, 51.58 for the

Bristol Channel and 52.13 for the western Channel (Brander, 1979). The western Channel value was considered to be anomalous as it deviated somewhat from the general equation between mean vertebral number and temperature that was developed for cod stocks across the North Atlantic (Brander, 1979).

Units for which assessment of spawning-stock biomass and recruitment are available

Recruitment indices from the 2002 assessment are based on relative abundance of age 1 cod (thousands). Biomass (B) and spawning-stock biomass (SSB) (tonnes) is calculated using a time invariant maturity ogive and incorporates international landings data with abundance indices from groundfish surveys carried out by French (IFREMER), Irish (MI), and UK (CEFAS) research institutes.

Time-series of spawning-stock biomass and recruitment data

B and SSB increased steadily from 1971 until reaching a peak in 1988 and 1989. Since 1989 biomass has been variable although current biomass is comparable to that during the early 1970s. Recruitment (at age 1) has been variable over the 1971–2001 time period with the strongest year class observed in 1986. This also corresponds to the same year for which the largest year class was observed for cod in the Irish Sea and strong correlations have been reported in the recruitment trends for cod in the Celtic and Irish Seas (Myers *et al.*, 1995). Average fishing mortality (F) has significantly increased over the 1971–2001 period.

What is the geographical location of the stock and does it change seasonally?

Spring survey results have shown that in years of high abundance, cod appear to be spread across the Celtic Sea, western Channel and shelf edge areas. During years of reduced abundance the distribution seems to be more concentrated in the area of the northeastern Celtic Sea, the western English Channel, and the shelf edge.

Over the 1971–2003 period presence/absence data from the English groundfish survey show that there is a large degree of spatio-temporal variability in these observations (Anon., 2000).

What is the depth range and temperature associated with the stock and does it change seasonally?

Bottom temperature data from English groundfish surveys were available for March and April for the following years: 1991, 1992, 1995, and 1997 (CEFAS, unpublished data). Based on these data, cod were observed in the temperature range of 7.4 to 10.6°C. The depth range over the entire series was from 50 to 291 metres with no significant difference in the range of depths in which cod were caught during different the months in which the

survey was carried out, although English groundfish surveys have not routinely taken place during summer months (CEFAS, unpublished data).

Time of spawning

Date of spawning and interannual variability or trend

Brander (1994) reported on the timing and location of cod spawning around the British Isles by synthesising data that were collected over different temporal and spatial scales. The best coverage of spawning areas within ICES Divisions VII e-k was in the Bristol Channel where the mean spawning date was day 83 (S.D. 15.7) based on the distribution and densities of stage 1 eggs. Much less is known about the spawning areas to the south of Ireland and in the western Channel.

Several egg and larvae surveys have been carried out historically. Simpson (1959) describes results for egg surveys that took place during mid-February and March of 1953. The survey in March was the only one to cover the area off the southeastern coast of Ireland where extensive spawning has been known to occur but has not been extensively studied. Two surveys in the Bristol Channel were carried out in March 1971 and these were consistent with the findings from the 1953 surveys (Brander, 1994).

The most comprehensive data, in terms of spatial coverage, for cod spawning in the Bristol Channel area are from five surveys reported by Horwood (1993), a study directed at surveying the sole spawning area. Brander (1994) summarises the results for cod based on surveys carried out during mid-February to late April 1990 that showed most of the eggs occurred throughout the area west of 4°30'W, although during middle to late March eggs were centred on 50°50'N, 5°15'W.

Although the western Channel has not been well studied in terms of egg and larval surveys, the limited information that exists has shown that eggs were present on the spawning grounds in the western Channel in February of 1971 (Brander, 1994).

Larval surveys that were carried out across the Celtic Sea and English Channel during 1938 and 1939 were compared with more recent results. It is suggested that although the density of eggs changes temporally, the spatial location of spawning seems to be persistent through time (Brander, 1994). Cod larvae also appear to remain close to the spawning areas; therefore transport of eggs is thought to be limited. Larval surveys carried out for the entire ichthyofauna community on the western and shelf edge area of the Celtic Sea (48° to 52°N and 8° to 12°W) during April-June of 1980 and 1983 showed that cod larvae were relatively rare but those found were located in a transitional zone between the continental shelf and central Celtic Sea, an area where 85% of the fish larvae detected were mackerel (Horstman and Fives, 1994).

Time of day when spawning occurs.

Not known.

Timing of spawning season in relation to planktonic production cycle

The Bristol Channel spawning area is one of the most southerly spawning grounds and water temperature is usually around 10°C during March. Spawning in this area has been shown to take place relatively later in the year compared to other stocks around the British Isles. The lateness of spawning may be due to the later occurrence of the production cycle in the area, due to strong tidal mixing (Brander, 1994), and is not influenced primarily by temperature.

Timing of spawning season in relation to hydrographic events

It is not known whether other hydrodynamic events also influence the timing of spawning, particularly in the less well-studied areas of the western Channel and southeast of Ireland.

Timing of spawning season in relation to other fish species that spawn in the same location

The Bristol Channel is an important spawning area for several other commercial species. The area off Trevoze Head is a particularly important spawning ground for sole and is also important for the commercial fishery (Horwood, 1993). Many other species of flatfish and gadoids, as well as several pelagic species, spawn in the area. There is an overlap in the timing and distribution of copepod species with fish eggs and larvae in the area.

Location of spawning

Geographic location and extent of spawning area

The main spawning grounds for cod in the Celtic Sea and western English Channel are located in the Bristol Channel throughout the area west of 4°30'W, in the western Channel and the southeast Irish coast (Figure 3.3.2). According to Brander (1994) there is very little temporal variability associated with the Bristol Channel spawning grounds. The degree of temporal variability in the spawning areas in the western Channel and southern Irish coast is much less well understood.

Does spawning regularly begin in one part of the spawning area and then move to other parts?

Spawning appears to be localised (Brander, 1994).

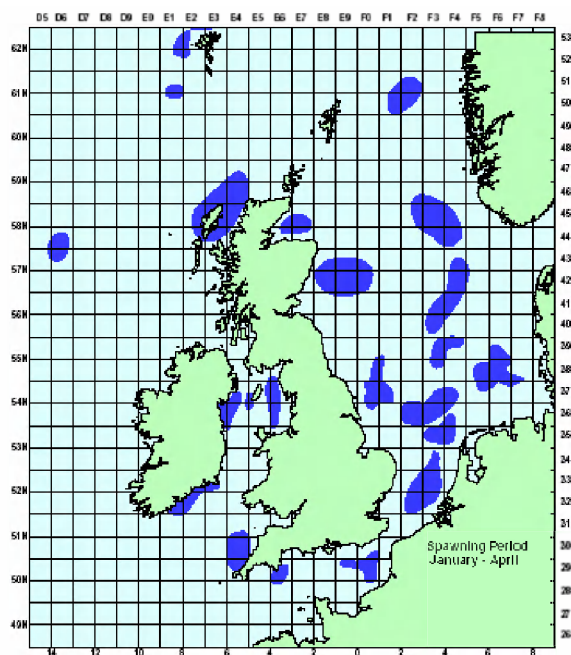


Figure 3.3.2. Spawning “sensitivity areas” for cod around the British Isles (Coull *et al.*, 1998).

Can the location be described in relation to hydrographic features?

The spawning area in the Bristol Channel can be characterised as having high tidal amplitude. There was no apparent transport of eggs out of the Bristol Channel from results of surveys carried out in 1990 (Brander, 1994). The spawning grounds near the southwest coast of Ireland and off of Start Point in the English Channel are close to the coast but little is known about the exact spatial and temporal extent of cod spawning in these areas.

Can location be described in relation to other species, including food organisms and predators?

The area is an important spawning ground for many species and the seasonal abundance of plankton with eggs and larvae in the area are closely linked.

Can location be described in relation to water mass circulation?

See above in the section under “location of spawning”.

Biological details

Fecundity

There has been no published fecundity study dedicated to cod in ICES Divisions VII e-k to date.

Evidence of changes in fecundity with time

Not known.

Percentage mature-at-age

The maturity ogive below is the one currently used in the VII e-k cod assessment and is based on data collected during the UK Westerly Groundfish Surveys in spring from 1996 up to 1999 for both sexes combined (ICES, 2004).

Age	1	2	3	4	5+
Maturity	0.00	0.39	0.87	0.93	1.00

Is there evidence of changes over time in maturity?

A preliminary analysis of length at 50% maturity values for Celtic Sea cod (L_{50}) derived from logistic regression models indicated that L_{50} underwent significant inter-annual changes over the period for which maturity data were available (Anon., 2002; CEFAS data, unpublished). Omitting the value for 2001 results in an apparent but non-significant declining trend over time (Figure 3.3.3, Mann Kendall test, $p > 0.05$). It is possible that there are different maturity ogives for different spatial components of the Celtic Sea and that the relative abundance of different areas is influencing these inter-annual differences but this has not yet been investigated.

Egg size and evidence of changes with age and with time during the spawning season. Specific gravity of eggs and larvae

There is no knowledge of egg sizes in relation to maternal age and body size.

Typical densities, i.e. number per m^3 of eggs and larvae

Average densities of eggs and larvae in areas of presence during the 1990 Bristol Channel surveys ranged from 0.0023 to 0.155 numbers per m^3 for cod eggs and from 0.002 to 0.3 numbers per m^3 for cod larvae depending on the time of year (CEFAS, unpublished data).

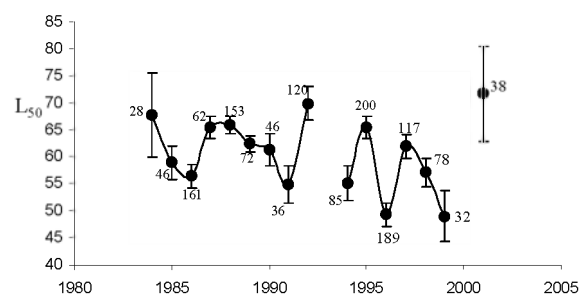


Figure 3.3.3. Length at 50% maturity (L_{50}) of Celtic Sea cod (CEFAS data, unpublished) over 1984–2001. Data labels indicate number of individuals observed (n) for each year's estimate and error bars represent the standard error associated with each L_{50} value.

Incubation rate of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larvae

No knowledge of this

Larval development rate as a function of temperature

No knowledge of this.

Condition factor and nutritional status

There are limited data for individual weights-at-length from the CEFAS groundfish surveys (1986 and 1993–1995 and 1996–2003; CEFAS unpublished data). Condition and nutritional status of larvae is not known.

Egg and larval mortality rates

No knowledge of this.

Time of first-feeding of larvae and food at first-feeding

No knowledge of this.

Food of larvae during development

No knowledge of this.

Evidence of predation during the egg and larval stage

No known evidence of cannibalism of cod eggs or larvae in the Celtic Sea was recorded based on stomach contents data from 949 cod stomachs spanning the 1977–1994 period (Pinnegar *et al.*, 2003).

Recruitment

Are there several spawning sites (sub-populations) that contribute to the same stock unit?

There are three spawning areas within the management unit. The degree to which each of these contributes to the “stock unit” is unknown.

Earliest time in the life history when year-class strength can be predicted

Recruitment units have historically been based on either age 1 or age 0 (ICES, 2004).

Hypotheses which have been put forward to account for year-to-year variability in year-class strength

The detrended recruitment series for cod recruitment in the Irish and Celtic Seas are highly correlated in terms of year-to-year variability (Myers *et al.*, 1995). Although the causes of this are not known, hypotheses are that due to the stocks proximity to one another there is similar forcing of environmental variables influencing recruit-

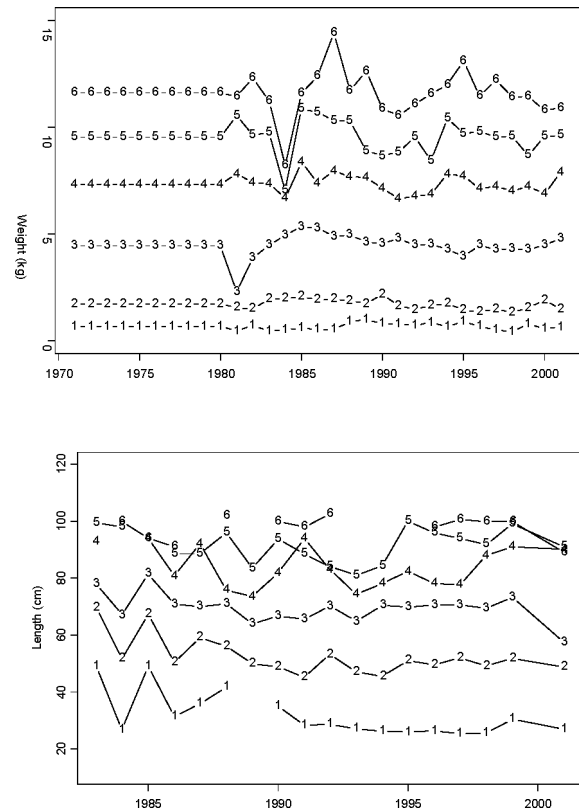


Figure 3.3.4. (upper) Mean estimated weights at age over the 1971–2001 for Celtic Sea and western English Channel cod as used in the assessment (ICES, 2004). (lower) Mean length-at-age in spring derived from English groundfish surveys (CEFAS, unpublished data).

ment and/or that cod from the two areas are actually part of the same stock.

Evidence of long-term trends in recruitment

There has been a long-term increase in log transformed recruitment series for Celtic Sea cod over time. This has been shown in Myers *et al.* (1995) for the 1971–1990 period and the increasing long-term trend is still apparent using estimates up to 2001.

Evidence that variability in recruitment is linked to variability of other species in the same area, the same species in other areas or other species in other areas

Not known.

Evidence of inter- or intraspecific competition

Not known.

Is recruitment related to SSB or any environmental factors?

Recruitment is related to SSB and the long and short-term trends in recruitment could be linked to environmental variability (Myers *et al.*, 1995).

Adult growth

What are the general growth characteristics?

In the ICES Assessment (ICES, 2004) constant weights-at-age are used from 1971–1980 and time variant weights-at-age are used thereafter (Figure 3.3.4 upper). Cod in the Celtic Sea are fast growing and Brander (2000) showed the specific growth rate of cod at a ‘standard size’ of 3 kg in the Celtic Sea was rapid (101%) compared to other cod populations in the northeast Atlantic. The length-at-age of Celtic Sea cod has remained relatively stable over time for older ages, although slight declines are evident for ages 1 and 2 (Figure 3.3.4 lower).

Evidence for density-dependent growth

Not known.

Evidence of temperature-dependent growth

Not known.

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3.4 East and West Greenland

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Stock and geographic distribution

Due to exceptional warm conditions during the 1920s and 1930s the Atlantic cod extended its northern limit of distribution at West Greenland from the Nuuk area (64°N) to the Upernavik district (73°N) (Jensen, 1939). In the 1920s cod occurred in small schools at East Greenland in the Angmassalik area (65°30'N) (Schmidt, 1930) and during the 1930s became more widely distributed on the shelf south of 67°N (Jensen, 1939). However the usual range of distribution is between 59–70°N at West Greenland and between 59–66°N at East Greenland. Four stock components with different spawning, larval drift and migration patterns (Figures 3.4.1 and 3.4.2) are involved.

Icelandic cod: Spawning takes place off southwest Iceland (Jónsson, 1982) and the Irminger current carries some of the offspring across the Denmark Strait to East and West Greenland (Tåning, 1943). The transport of eggs, larvae and early juveniles (0-group) towards Greenland is very variable but has been pronounced in a few years, for instance in 1945, 1956, 1961, 1973, and 1984 (Schopka, 1993, 1994; Shepherd and Pope, 1993). Tagging experiments at Iceland showed that migration of adult cod from Iceland to Greenland waters occurs very seldom (Jónsson, 1965, 1986). In contrast, cod tagged in southwest and East Greenland waters return to Iceland (Hansen, 1949; Harden-Jones, 1968). This is true for almost all year classes (Riget and Hovgård, 1989) but is especially pronounced for those that as young were observed drifting in large quantities from Iceland to Greenland (Schopka, 1993, 1994; Shepherd and Pope, 1993).

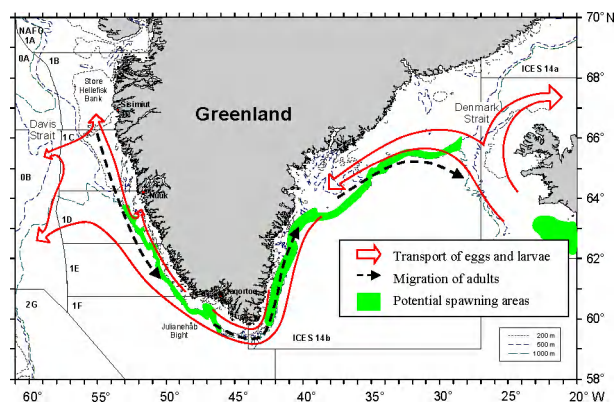


Figure 3.4.1. Cod spawning migration and transport of eggs and larvae in the Iceland – Greenland area (modified after Wieland, and Hovgård, 2002).

East Greenland cod: Spawning occurs offshore between approximately 62–66°N (Jónsson, 1959; Meyer, 1963), and eggs and larvae are transported towards southeast and West Greenland (Wieland and Hovgård, 2002). In addition, migration of immature cod from East to West Greenland has been seen in some years (Rätz, 1994). Cod tagged at East Greenland are often recaptured at Iceland, but very rarely at West Greenland (Riget and Hovgård, 1989).

West Greenland offshore cod: Spawning has been observed at the offshore slope of Fylla Bank at 64°N but more frequently at the various fishing banks further south including the northern part of Julianehåb Bight at 61°N (Jónsson, 1959; Meyer, 1963; Diaz, 1969). Eggs and larvae are transported along the coast towards Store Hellefisk Bank at about 67–68°N (Wieland and Hovgård, 2002). Cod tagged in the northern areas, i.e. NAFO Divisions 1A–1D, were mostly recaptured at West Greenland (Rasmussen, 1959; Hovgård and Christensen, 1990). However in 1989–1991 there was a very strong and rapid emigration of maturing cod from West to East Greenland (Rätz, 1994; Storr-Paulsen *et al.*, 2004).

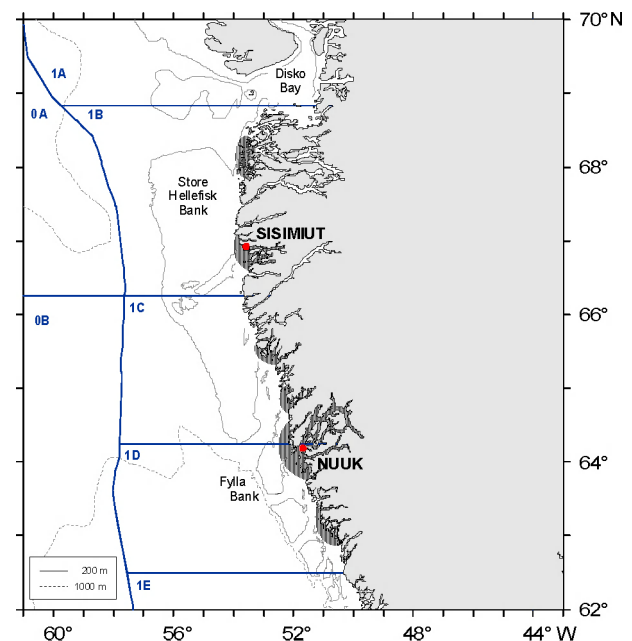


Figure 3.4.2. Geographical distribution of inshore populations of Atlantic cod at West Greenland (redrawn after Engelstoft, 1997).

West Greenland inshore cod: A number of local populations exist. Spawning has been reported in several West Greenland fjords and the offspring remain within the nearby fjord and coastal areas (Engelstoft, 1997; Hansen, 1949; Storr-Paulsen *et al.*, 2004). Cod from these inshore areas were caught mostly within the fjords where they were tagged (Hovgård and Christensen, 1990; Storr-Paulsen *et al.*, 2004).

Links to Labrador

In some years during the 1950s and 1960s considerable numbers of cod larvae were observed in the southwestern part of Davis Strait far off the West Greenland coast (Wieland and Hovgård, 2002). These larvae might have been transported further to the northern and middle parts of the Labrador shelf (Dickson and Brander, 1993; ICES, 2002b) in particular during the 1950s, when their distribution in the western Davis Strait was more southerly than in the 1960s. This interpretation is supported by the occurrence of cod with unusually low mean vertebral numbers in the corresponding year classes off Labrador (Templeman, 1981). This situation, however, has been regarded as abnormal, because it was associated with an extreme westward spreading of warm water off West Greenland. There is very little information about the magnitude of larval transport between West Greenland and Labrador, and the evidence for a return migration is mainly indirect (Dickson and Brander, 1993).

Landings

In the past decades Atlantic cod in Greenland waters has shown large variations in abundance and distribution (Figure 3.4.3). Prior to 1920 annual catches of cod were less than 500 t (Horsted, 2000) and were restricted to inshore areas at West Greenland (Buch *et al.*, 1994). Thereafter an offshore stock developed which gave rise to a large fishery, which frequently yielded annual catches considerably above 300 000 t through the mid-1950s to the early 1970s, with a record high level of 480 000 t in 1962 (Horsted, 2000). At the same time, the spawning-stock biomass was gradually reduced and the catches declined dramatically in the late 1970s. During the 1980s annual catches were generally poor and dependent on single strong year classes, which gave rise to an intermediate fishery with catches of about 100 000 t in 1988–1990. Since then Atlantic cod has almost disappeared from the offshore waters (Rätz, 1999). Offshore catches were taken exclusively off East Greenland since 1992 and became less than 500 t in 1994. At present only a small inshore fishery takes place at West Greenland (ICES, 2003).

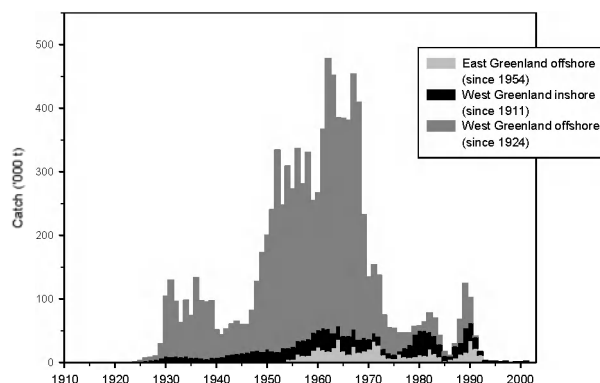


Figure 3.4.3. Catches of Atlantic cod in Greenland waters (see Table 3.4.1 for references).

Assessment

Several attempts have been made to assess the cod stocks off Greenland, in which they have either been divided into East and West Greenland or treated as one stock unit with or without the inclusion of the West Greenland inshore component. Hence, no consistent time-series of recruitment and spawning-stock biomass exist for the different stock components (Table 3.4.1). Assessments for West Greenland were carried out by NAFO and for East Greenland by ICES until 1991. Since then the ICES North Western Working Group has dealt with both areas and advice for East and West Greenland cod is provided through the ICES Advisory Committee on Fishery Management (ACFM).

The cod stock in East Greenland is difficult to assess, as it includes Icelandic cod grown up in East Greenland waters, cod on migration from West Greenland to Iceland and 'true' East Greenland cod. No analytical assessment exists and stock size estimates are based on area swept in research surveys.

A historical VPA for West Greenland comprising the inshore and offshore components is given in Buch *et al.* (1994). Here, data back to 1924 were considered. However, no attempts were made to correct for emigration.

The offshore population off East and West Greenland was assessed as one stock unit and distinguished from the West Greenland inshore component for the first time in 1996 using data back to 1955 (ICES, 1996). Disregarding conflicting data for the years 1993–1995, the final year of the VPA was 1992. The effect of emigration was only covered for the 1973 and 1984 year classes, through an increase of the natural mortality for age 5 and older. Due to the severely depleted status of the offshore component, the directed cod fishery was given up in 1992, and since then no adequate data have been available to update the analytical assessment (ICES, 2003).

For the assessment of the West Greenland inshore component, a Schaefer general production model has been fitted using commercial CPUE data for 1993 to 1999, but lack of contrast in the data impeded successful results (ICES, 2003).

Survey information

In the absence of analytical assessments, research surveys are actually the most important source of information on the state of the different stock components.

A stratified random groundfish survey covering the shelf area outside the 3 nautical mile limit and the continental slope down to a depth of 400 m off East and West Greenland (ICES area 14 and NAFO Divisions 1B–1D) has been conducted by Germany annually since 1982. The survey is primarily targeted at cod, and the fishing gear used is a groundfish trawl rigged with a heavy (rubber disc/bobbin) ground gear. The survey provides abundance and biomass indices for the East and the West Greenland offshore component (Table 3.4.1), which form the primary basis for the current assessment. However, area coverage at East Greenland has been incomplete in three years and at West Greenland the northernmost area (NAFO Division 1B) was not covered in 1995 and 2001–2002 due to technical problems.

Greenland introduced a stratified random survey for northern shrimp in 1988, covering the West Greenland shelf and continental slope down to 600 m (NAFO Divisions 1A–1E). In this survey a shrimp trawl with a heavy (bobbin) ground gear was used, and the main effort was allocated to depths between 150 and 600 m. Area coverage was extended in 1992 to southwest Greenland (NAFO divisions 1E and 1F) and the survey is now considered to be a combined groundfish/shrimp survey. However, cod abundance and biomass indices from this survey were not included in the present report due to the short time-series.

A gillnet survey using gangs of different mesh-sizes has been conducted since 1985 in three West Greenland inshore areas: Sisimiut (NAFO division 1B), Nuuk (NAFO division 1D) and, occasionally, Qaqortoq/Julianehåb Bight (NAFO division 1F). The links of gillnets contain separate sections with mesh-sizes from 16.5 to 33 mm bar length and are set in shallow waters at depths of mainly between 2 and 20 m. The survey provides primarily recruitment indices for age 2 cod, in particular for the West Greenland inshore populations in the Sisimiut and Nuuk area (Table 3.4.1). However, the Sisimiut area was not covered in 1995, 1999, and 2000, and no survey was conducted in 2001 due to technical problems.

Life history information for stock components

Available life history information for the different stock components of Atlantic cod in Greenland waters (see Table 3.4.2 for data summaries) is as follows:

East Greenland cod

Spawning period and location

Spawning has been observed from March to June (Meyer, 1958, 1962, 1963; Jónsson, 1959, 1961, 1975; Serebryakov, 1967) along the offshore slope of the shelf from about 62 to 66°N. Spawning depth ranged from 170 to 400 m (Jónsson, 1959; Meyer, 1963) at which temperatures were between 3.2 and 5.2°C (Jónsson, 1959, 1961). Jónsson (1959) found cod with maturing gonads as late as the end of June and hence assumed that spawning continued into July. Serebryakov (1967) and Jónsson (1961) noted that spawning was somewhat later in the more northern area compared to the south and attributed this to a higher proportion of first-time spawners in the north.

Early life stages

Egg and larval distributions covering the entire East Greenland shelf area are available from the NORWESTLANT surveys conducted in 1963 (Anon., 1968). Eggs were found along the slope of Dohrn Bank (66°N) down to Cape Farewell (60°N) in April/May. The mean egg concentration off southeast Greenland (59–63°N) was about 10 times higher than in the area further north (Wieland and Hovgård, 2002). Few larvae were found in the entire East Greenland shelf area in June/July, which indicates either an extremely high mortality or, more likely, a rapid transport of the offspring towards southwest Greenland in this year. No further information on the distribution of early life stages (eggs to settled juveniles) of East Greenland cod is available, in particular not for the period in which a self-sustained spawning-stock was presumed to exist in this area.

Other biological observations

Jónsson (1961) reported some first-time spawning at age 4 but 50% maturity is first attained at age 8. However, maturity has become earlier and condition as well as mean length- and weight-at-age varied considerably during the 1980s and 1990s. This has been attributed to environmental changes (ICES, 2003; Lloret and Rätz, 2000; Rätz *et al.*, 1999). Survey results indicate that variability in recruitment is much higher than variability in spawning-stock biomass (Table 3.4.1).

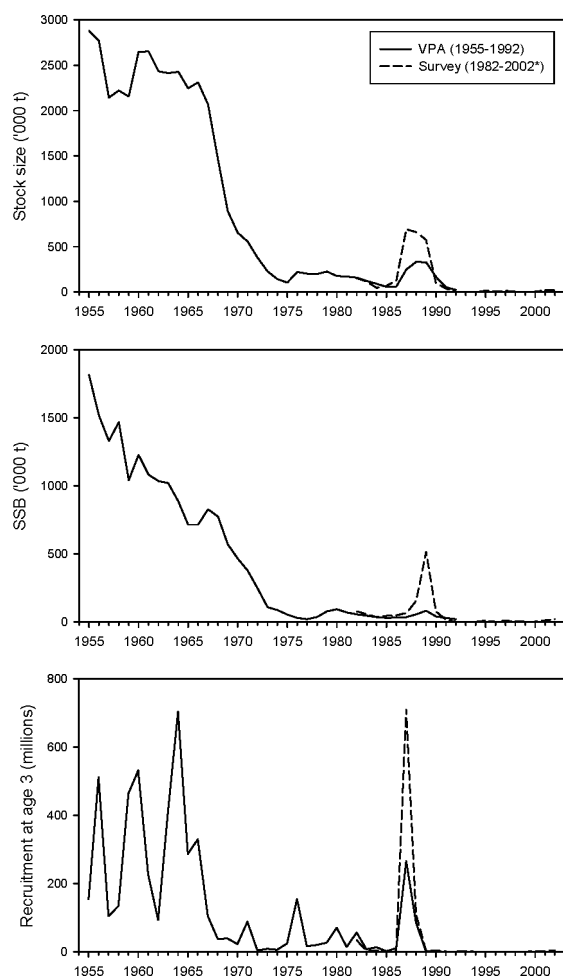


Figure 3.4.4. Time-series of stock size, SSB and recruitment at age 3 for East and West Greenland offshore cod (*: three years with incomplete coverage off East Greenland excluded, see Table 3.4.1 for references).

West Greenland offshore cod

Spawning period and location

Jónsson (1959) found that 50% of the mature fish were spawning and 38% had finished spawning by the end of April. Bratberg (1965) noted that 40% of cod caught in the middle of April had not yet finished spawning. In 1961 and 1966 spawning peaked at the end of March to the beginning of April (Meyer, 1963, 1967). A high proportion of spawning cod were observed in March 1967 during a Russian survey (Konstantinov and Noskow, 1968). However, information on cod maturity from a Portuguese survey in 1968 revealed that spawning was nearly completed by the beginning of June, except for a small fraction of males, which were in running condition (Diaz, 1969). Also Serebryakov (1967) reported spawning as late as June. Spawning was observed at locations on the offshore slope of Fylla Bank (64°N) at a depth of 120 m and a temperature of 1.5°C (Jónsson, 1959), but more frequently off the various fishing banks further south at depths below 350 m in the warmer Atlantic water (Meyer, 1963, 1967; Meyer and Lenz, 1972; Konstantinov and Noskow, 1968).

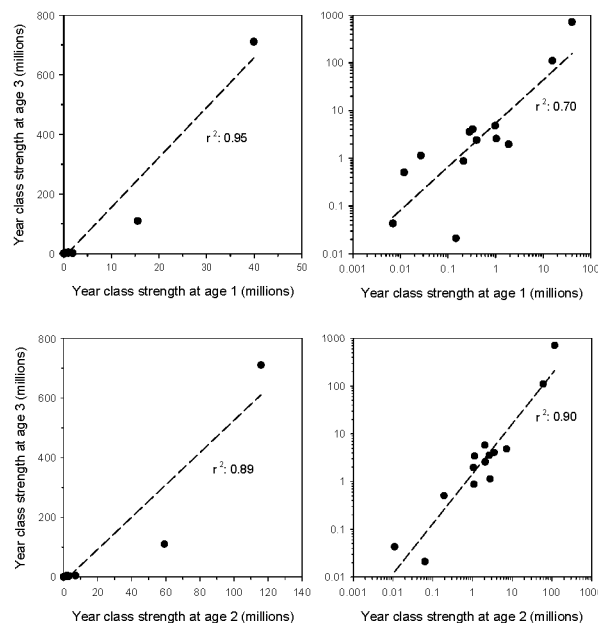


Figure 3.4.5. Comparison of survey estimates of abundance at age 3 in a given year with age 1 two years earlier and with age 2 one year earlier for East and West Greenland offshore cod (three years with incomplete coverage off East Greenland excluded). Data from Rätz, 2003.

Early life stages

Results from a series of ichthyoplankton surveys carried out in West Greenland offshore waters have shown that the distribution of eggs extends from about 59 to 67°N, but with declining densities in the northern part and a pronounced maximum off southwest Greenland (Wieland and Hovgård, 2002). Egg abundance showed a pronounced peak in late April and diminished during June. Larvae occurred from March to August, but predominantly in June. Mean larval length increased from 4.6 mm in April and 5.4 mm in May to 8.1 mm in June and to 13.9 mm in July (unpubl. data, Greenland Institute of Natural Resources). In June/July, the larvae were usually found in the vicinity of the fishing banks between 64 and 67°N, and very few larvae were ever seen in the shelf and continental slope area south of approximately 64°N. This indicates a northward drift of the offspring from southwest Greenland towards Store Hellefisk Bank (67–68°N) during late spring and summer (Wieland and Hovgård, 2002).

0-group cod are regularly taken in the German ground-fish bottom-trawl survey in November, although always in small quantities due to trawl selection, but they have also been caught with pelagic trawls at that time of the year (Wieland, 1991). Settling therefore does not seem to

occur before October/November and might take place at the Store Hellefisk Bank where a large nursery area was observed during the 1950s and 1960s (Horsted, 1967; Buch *et al.*, 1994).

Other biological observations

50% maturity occurred at age 6 to 7 in the years 1960–1983 (Horsted *et al.*, 1983), but has become earlier and more variable since then. Also, condition and mean length- and weight-at-age varied considerably during the 1980s and 1990s, which has been related to changes in the environment (Hansen, 1987; ICES, 2002a; Lloret and Rätz, 2000; Rätz *et al.*, 1999). Survey results indicate that variability in recruitment is much higher than variability in spawning-stock biomass, in particular if recruitment at age 3, instead of age 2, is considered (Table 3.4.1).

West Greenland inshore cod

Spawning period and location

Inshore spawning is documented for several fjord and coastal areas between 64 and 67°N (Jensen and Hansen, 1931; Hansen, 1949), i.e. Ameralik fjord (64°15'N), Nuuk fjord (64°30'N), Atangmik (64°45'N), Hamburger-sund (65°40'N) as well as Igertoq and Amerdloq fjords (66°45'N). The most intense spawning was observed in small, shallow-water fjord branches (Smidt, 1979) where ambient temperature ranged between 0.5 and 4.0°C (Hansen, 1949).

Early life stages

Eggs were found in the Nuuk area from February to July with a peak in April. Locally, very high egg catches were taken, with the eggs being concentrated in the uppermost water layers at a depth of less than 30 m (Smidt, 1979; Storr-Paulsen *et al.*, 2004). Larvae were seen to emerge in April or early May. Mean larval lengths were 4.7 mm in April, 5.8 mm in May, 8.1 mm in June and 10.4 mm in July (unpubl. data, Greenland Institute of Natural Resources). In Nuuk fjord, the highest larval concentrations were found in June, which averaged 0.3% of the mean egg concentration in April.

First settling, as inferred from beach seine catches, was in mid-September at a length between 49 and 90 mm (Jensen and Hansen, 1931).

Other biological observations

During the 1930s 50% maturity was reached by age 5 to 6 in the Sisimiut and Nuuk areas (Hansen, 1949). No recent information on maturity for the inshore populations exists.

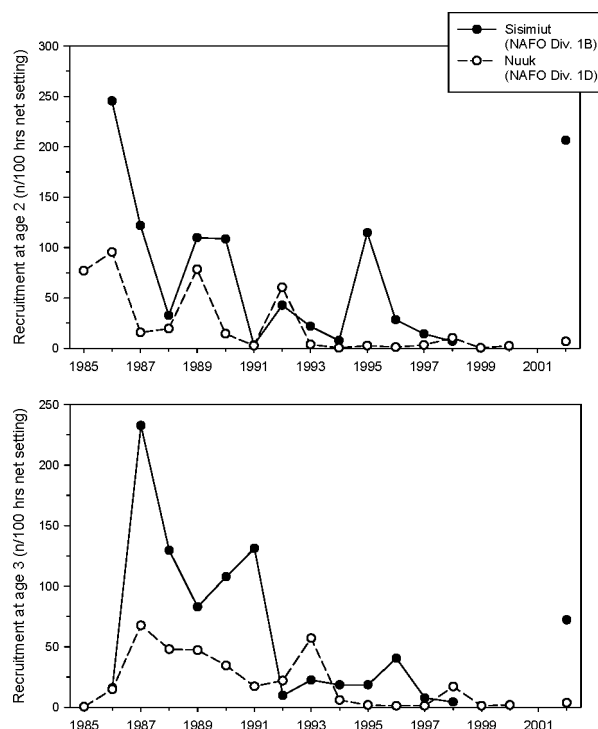


Figure 3.4.6. Time-series of recruitment at age 2 and at age 3 for West Greenland inshore cod in NAFO division 1B and 1D. ICES, 2004.

Time-series of stock size, SSB and recruitment

East and West Greenland offshore

Stock size was about 2 500 000 tons in the 1960s and declined drastically thereafter when the spawning-stock biomass was gradually reduced (Figure 3.4.4). Several strong year classes emerged during the 1950s and 1960s, whereas in past 30 years only the 1973 and the 1984 year classes reached the long-term mean recruitment level at age 3 (Figure 3.4.4). Survey estimates illustrate that an intermediate rise in stock size and SSB in the late 1980s was followed by a rapid decline of the stock to a very low level in the early 1990s and from which it has not yet recovered.

Pelagic 0-group abundance recorded in the Denmark Strait and off East Greenland (Dohrn Bank) during Icelandic surveys since 1970 correlated well with subsequent year-class strength off East and West Greenland and a return migration was found in most years, which indicates that offspring from Iceland contributed regularly, even if not always in large quantities, to the recruitment at Greenland in the 1970s and 1980s (ICES, 2002a).

Neither age 1 nor age 2 fish are fully retained in the German groundfish survey, but it has been suggested that the survey estimate of age 1 abundance represents a reasonable recruitment index based on its strong correlation with age 3 two years later (ICES, 2002a).

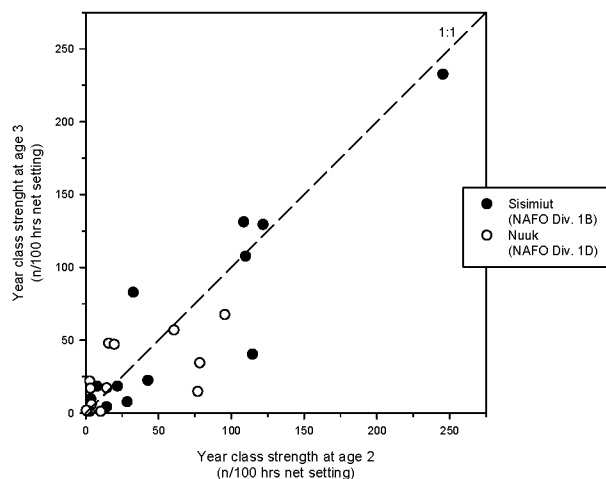


Figure 3.4.7. Comparison of survey indices for age 2 in a given year with that for age 3 one year later for West Greenland inshore cod in NAFO division 1B and 1D. ICES, 2004.

However, this correlation is mainly determined by two high observations and it diminishes when a log-log scale is used (Figure 3.4.5). In contrast, a strong correlation between year-class strength at age 2 and at age 3 in the following year is evident, both on a linear and on a log-log scale (Figure 3.4.5). Hence, age 2 appears to be the earliest possible life stage when year-class strength can be predicted with sufficient robustness.

West Greenland inshore

With the different mesh-sizes used in the Greenland gill-net survey individuals of between approximately 15 and 50 cm are caught, which includes cod at age 2 and 3, while older and larger fish are subject to low efficiency (Nygaard and Pedersen, 1991). Age 4+ cod are present in the catches but the survey index comprises mainly age 2 and age 3 (Table 3.4.1) and thus provides only a very rough estimate of total stock size.

Abundance indices for age 2 and age 3 were on average higher for the Sisimiut than for the Nuuk area (Figure 3.4.6). The strong 1984 year class was seen at age 2 in 1986 and at age 3 in 1987 in the Sisimiut area, but it was less prominent in the Nuuk area. Recruitment fluctuated considerably in the early 1990s but with a downward trend in both areas. A year class of intermediate strength emerged in the Sisimiut area at age 2 in 1995 and a similar situation is indicated from the preliminary results of the 2002 survey, whereas recruitment remained poor in the Nuuk area.

Comparison of year-class strength at age 2 and at age 3 (Figure 3.4.7) reveals low, or even negative, mortalities in many cases including e.g. the 1984 year class in the Sisimiut area. This may indicate that the survey is more efficient for age 3 than for age 2. On the other hand, relative high abundance indices for age 3 may also be, at least to some extent, due to immigration from the off-

shore area. The immigration might be most pronounced in years with good recruitment offshore and a relative northerly distribution of the 2-group as it has been observed for the 1984 year class (ICES, 1990). However, an analysis providing evidence for a general link between the inshore and the offshore population is lacking.

Variations in maturity, condition and growth

East and West Greenland offshore

Age at 50% maturity varied between 3.9 and 6.6 years in 1982 to 1991 and maturation became earlier thereafter when the temperature in the near bottom layer began to increase (Figure 3.4.8). Pronounced early maturation was observed in the past three years, probably as a reaction to the continuing favourable temperatures (Rätz, 2003). These results, however, should be interpreted with caution because the maturity-at-age was examined during autumn surveys, when the gonads were in resting stages, which can make it difficult to distinguish immature from mature individuals (Rätz, 2003).

Lloret and Rätz (2000) reported mean annual Fulton's condition factors from 0.82 to 0.95 for the 1980s and 1990s (Figure 3.4.9). The average for the entire period was 0.89 (sd: 0.15), which is among the lowest observed for any cod population.

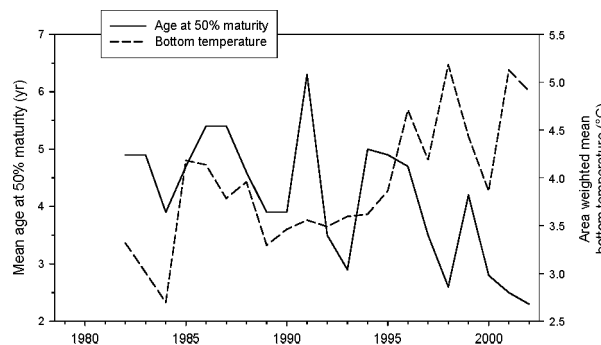


Figure 3.4.8. Mean age of 50% maturity of East and West Greenland offshore cod and mean bottom temperature (weighted for stratum areas) from the German groundfish survey off East and West Greenland. Data from Rätz (2003).

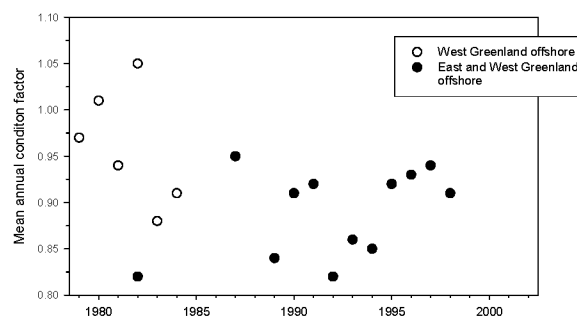


Figure 3.4.9. Mean annual condition factors for East and West Greenland offshore cod. Data from Hansen (1987) for West Greenland offshore and from Lloret and Rätz (2000) for East and West Greenland offshore combined.

For 22 year classes born in the period 1955–1981, Rätz *et al.* (1999) reported von Bertalanffy growth coefficients between 0.05 and 0.34 accompanied by values of L_{∞} of between 87 and 226 cm. If year classes with L_{∞} values < 100 and > 150 cm are excluded then the number of included year classes is reduced to 14, and the range for k and L_{∞} becomes 0.09–0.25 (mean: 0.15) and 101–139 cm (mean: 114 cm), respectively (Table 3.4.2c).

Factors affecting larval survival and recruitment variability at West Greenland

Links have been investigated on the one hand between surface temperature, density stability of the water column and windstress and on the other hand between larval abundance or year-class strength at age 3 of cod in the West Greenland offshore area Hermann *et al.* (1965), Hansen and Buch (1986), and Stein and Lloret (1995), but consistent and significant correlations were not detected. Pedersen and Rice (2002) found stronger association between cod larval and zooplankton, or copepod, abundance than between cod larvae and hydrographic factors. Although the correlations were not significant, this may suggest that larval abundance was more strongly determined by system productivity than by hydrographic conditions, or that both cod larvae and zooplankton were aggregated and dispersed by the same mechanisms (Pedersen and Rice, 2002).

Considering that larval transport from Iceland to East and West Greenland is a major factor affecting the variability of year-class strength at age 3 off West Greenland, Borokov and Stein (2001) presented multiple linear regressions on the recruitment of West Greenland cod using SSB of Icelandic cod, sea surface and air temperatures around Greenland as well as zonal wind components between Iceland and Greenland. An extension of this analysis, which additionally includes meridional wind components off southwest Greenland, yielded a regression model that explains 79% of the variability in cod recruitment off West Greenland from the 1950s to the 1990s (Stein and Borokov, 2004). However, the final model considerably underestimates the strong 1984 and 1985 year classes and predicts much higher recruitment than was observed in the late 1990s.

The 1999 year class is the strongest observed in the past 14 years, but amounts only to 5.5% of the strength of the 1984 year class at age 2 although temperature conditions have been favourable (Figure 3.4.10) and spawning-stock biomass of Icelandic cod, as well as 0-group abundance, in the Denmark Strait has been at, or even above, the level reported for the 1980s (ICES, 2002a). A stock-recruitment plot indicates that the 1999 year class is of Icelandic origin and has obviously not been a product of spawning off East and West Greenland (Figure 3.4.11). However it remains speculative whether or not the generally relative low recruitment level in the late 1990s was due to less intense 'advective' situations at the relevant time of the year or due to high larval mortality related to low food abundance off East Greenland (ICES, 2002b).

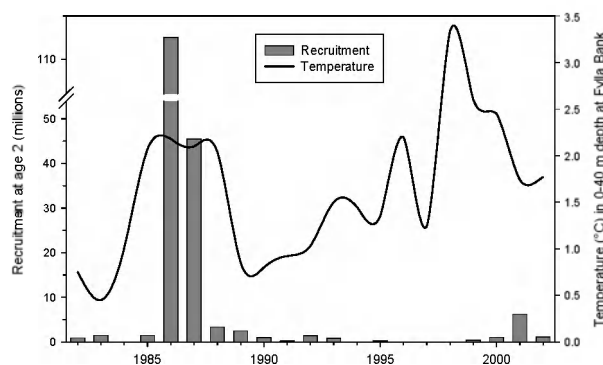


Figure 3.4.10. Time-series of recruitment at age 2 of West Greenland offshore cod (see Table 3.4.1 for reference) and mean temperature in the surface layer at Fylla Bank in summer (Data from Buch and Ribergaard, 2003).

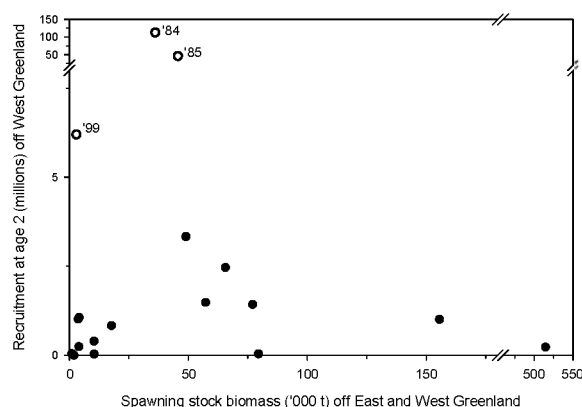


Figure 3.4.11. Recruitment at age 2 off West Greenland and spawning-stock size off East and West Greenland combined (three years with incomplete coverage off East Greenland in the German groundfish survey included). Open symbols indicate year classes, which are assumed to be mainly of Icelandic origin. Data from Rätz, 2003.

Another factor, which may be relevant here, is the amount of bycatch of juvenile cod in the shrimp fishery off East and West Greenland. In this context, it is further noteworthy that the strength of the 1999 year class decreased from 5.5 to 0.4% of that of the 1984 year class if age 3 is considered instead of age 2. This, however, may not necessarily have been due to high bycatch mortality by the shrimp fishery. Migration of juveniles out of the area covered by the German groundfish survey in 2002 towards NAFO division 1B offshore and inshore in the Sisimiut area could also have been at play.

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Table 3.4.1. Stock summaries for Atlantic cod in Greenland waters.

Stock component:		East Greenland																								
		Landings (000 t)					Stock biomass (000t)				SSB (000t)				Recruitment (millions), Age 2				Recruitment (millions), Age 3							
Code	Area	max	min	mean	actual		max	min	mean	actual	max	min	mean	cv	actual	max	min	mean	cv	actual	max	min	mean	cv	actual	Reference
E1	ICES 14	35.6 (1984)	0.1 (1999)	12.1 (1954-2002)	0.4 (2007)	Assess ¹ (11 yrs)	134 (1980)	72 (1915)	42 (1980-1990)	-	115 (1990)	16 (1985)	32 (1980-1990)	0.89	-	-	-	-	-	-	-	-	-	-	-	ICES CM 1990/Assess 12 (WG on Cod Stocks off East Greenland)
						Survey ^a (16 yrs)	240 (1989)	4 (1996)	37 (1982-2002)	20 (2002)	189 (1989)	2 (1996)	26 (1982-2002)	1.62	20 (2002)	13.8 (1987)	< 1 (1996)	1.4 (1982-2002)	2.32	0.4 (2002)	17.8 (1987)	< 1 (1996)	2.1 (1982-2002)	1.99 (2002)	1.8 (2002)	ICES CM 2003/ACPM 24 (North Western WG) *
Stock component:		West Greenland offshore and inshore																								
		Landings (000 t) **					Stock biomass (000t)				SSB (000t)				Recruitment (millions), Age 2				Recruitment (millions), Age 3							
Code	Area	max	min	mean	actual		max	min	mean	actual	max	min	mean	cv	actual	max	min	mean	cv	actual	max	min	mean	cv	actual	Reference
W1	NAFO 1	460.7 (1982)	< 1 (1998)	103.2 (1911-2001)	1.7 (2001)	VPA ² (66 yrs)	4129 (1949)	38 (1986)	1451 (1924-1989)	-	3034 (1949)	17 (1986)	883 (1924-1989)	1.03	-	-	-	-	-	-	631.5 (1950)	0.7 (1989)	143.0 (1924-1989)	1.07	-	Buch et al 1994
Stock component:		West Greenland offshore																								
		Landings (000 t) **					Stock biomass (000t)				SSB (000t)				Recruitment (millions), Age 2				Recruitment (millions), Age 3							
Code	Area	max	min	mean	actual		max	min	mean	actual	max	min	mean	cv	actual	max	min	mean	cv	actual	max	min	mean	cv	actual	Reference
W1a	NAFO 1	425.0 (1982)	0.0 (1992)	102.0 (1924-2002)	0.0 (2002)	Survey ^{a,2} (21 yrs)	639 (1987)	< 1 (1996)	95 (1982-2002)	2 (2002)	338 (1987)	< 1 (1996)	33 (1982-2002)	2.28	2 (2002)	112.53 (1986)	< 1 (1998)	8.6 (1982-2002)	3.00	1.1 (2002)	632.6 (1987)	< 1 (1998)	40.6 (1982-2002)	3.72 (2002)	3.0 (2002)	ICES CM 2003/ACPM 24 (North Western WG) *
Stock component:		East and West Greenland offshore																								
		Landings (000 t)					Stock biomass (000t)				SSB (000t)				Recruitment (millions), Age 2				Recruitment (millions), Age 3							
Code	Area	max	min	mean	actual		max	min	mean	actual	max	min	mean	cv	actual	max	min	mean	cv	actual	max	min	mean	cv	actual	Reference
E1 & W1	ICES 14 & NAFO 1	442.6 (1982)	0.1 (2000)	126.3 (1954-2002)	0.4 (2002)	VPA ² (38 yrs)	2682 (1965)	26 (1992)	1017 (1955-1992)	-	1617 (1965)	21 (1997)	479 (1955-1992)	1.12	-	-	-	-	-	-	783.4 (1964)	0.2 (1992)	132.5 (1965-1992)	1.36	-	ICES CM 1996/Assess 15 (North Western WG)
						Survey ^{a,2} (18 yrs)	180 (1987)	4 (1996)	146 (1982-2002)	22 (2002)	615 (1989)	2 (1996)	63 (1982-2002)	1.90	21 (2002)	115.9 (1986)	< 1 (1996)	11.3 (1982-2002)	2.60	1.5 (2002)	710.4 (1987)	< 1 (1998)	49.3 (1982-2002)	3.39 (2002)	4.8 (2002)	ICES CM 2003/ACPM 24 (North Western WG) *
Stock component:		West Greenland inshore																								
		Landings (000 t) **					Stock biomass (000t)				SSB (000t)				Recruitment (000), Age 2				Recruitment (000), Age 3							
Code	Area	max	min	mean	actual		max	min	mean	actual	max	min	mean	cv	actual	max	min	mean	cv	actual	max	min	mean	cv	actual	Reference
W1b	NAFO 1	39.7 (1981)	< 1 (1912)	14.7 (1911-2002)	3.7 (2002)	Survey ^a (15 yrs)	203 (1987)	12 (1997)	75 (1966-2002)	89 (2002)	-	-	-	-	-	124.0 (1986)	1.4 (1994)	29.7 (1986-2002)	1.17	63.2 (2002)	119.8 (1987)	2.7 (1997)	27.6 (1986-2002)	1.15	19.60 (2002)	ICES CM 2003/ACPM 20 (North Western WG)
W1b-1	Sisimiut (18)	9.9 (1980)	< 1 (1919)	2.9 (1915-2002)	1.8 (2002)	Survey ^a (14 yrs)	361 (1987)	23 (1988)	181 (1986-2002)	340 (2002)	-	-	-	-	-	245.4 (1986)	3.4 (1991)	76.1 (1986-2002)	1.02	208.5 (2002)	232.6 (1987)	4.3 (1988)	63.8 (1986-2002)	1.06 (2002)	72.10 (2002)	
W1b-2	Narsuk (10)	9.8 (1980)	< 1 (1912)	2.6 (1911-2002)	0.2 (2002)	Survey ^a (17 yrs)	165 (1986)	4 (1996)	64 (1985-2002)	14 (2002)	-	-	-	-	-	95.5 (1986)	0.4 (1994)	23.2 (1986-2002)	1.11	6.80 (2002)	67.6 (1987)	0.4 (1997)	20.2 (1986-2002)	1.11 (2002)	3.70 (2002)	
{ } Year																										
* German Bottom Trawl Survey, years with incomplete coverage off East Greenland (1984, 1992 and 1994) excluded; ^b Greenland Gillnet Survey, years with incomplete coverage (Sisimiut: 1985, 1999, 2000, 2001; Narsuk: 2001) excluded																										
¹ Stock biomass for age 4+ (based on survey estimates of trawlable biomass); ² Stock biomass for age 3+; ³ Stock biomass for all ages																										
^a maturity ages from RNEZ (2003); ** historical landings from Husted (2000); *** number/100 h net setting																										

Table 3.4.2. Spawning, egg, larval and adult data summaries for Atlantic cod in Greenland waters.

a) Spawning and egg data summary													
Code	Stock component	Area	Spawning date			Spawning depth (m)	Temperature (°C)		Egg		conc. (n/m ³)	mortality (%)	production
			mean	sd	duration		Adults	Eggs	diam. (mm)	density			
E1	East Greenland	ICES 14	April	-	March - July	120 - 400	3.2 - 5.2	-1 - 6	-	-	< 1.5	-	-
W1a	West Greenland offshore	NAFO 1	mid April	25 days	March - June	120 - 800	1.4 - 5	-0.5 - 5	-	-	< 1	-	-
W1b	West Greenland inshore	NAFO 1	March/April	-	Feb - July	> 20	0.5 - 4	0.5 - 4	-	-	< 15	> 99	-
b) Larval stage summary													
Code	Stock component	Area	Size (mm TL) at			Growth (mm/month)	Mortality (%)	Date at		Distance from			
			hatch	metamorph.	settling			hatch	metamorph.	settling	spawn to settle (km)		
E1	East Greenland	ICES 14	-	-	-	-	-	April - June	-	Oct - Nov	900	(SW Denmark Strait - SE Greenland)	
W1a	West Greenland offshore	NAFO 1	3 - 4	-	-	2 - 6	-	April - June	-	Oct - Nov	1000	(Julianahåb Bight - Store Hellefisk Bank)	
W1b	West Greenland inshore	NAFO 1	4 - 5	-	49 - 90	2 - 6	-	April - June	-	Sept - Oct	retention		
c) Adult stage summary													
Code	Stock component	Area	Mean Latitude	Recruits, age 2 ^a	Recruits, age 3 ^a	Stock biomass ^a	SSB (000 t) ^a	Landings (000 t) ^b	Maternity ^c , 50 % at age	length (cm)	Condition factor ^d	Growth ^d coefficient	L _∞ (cm)
E1 and W1a	East and West Greenland offshore	ICES 14 and NAFO 1	63	11	49	146	65	17	2.9 - 6.3	35 - 65	0.82 - 0.95	0.09 - 0.25	101 - 139
W1b-1	West Greenland inshore - Sisimiut	NAFO 1B	67	76	64	181	-	3	-	-	-	-	-
W1b-2	West Greenland inshore - Nuuk	NAFO 1D	64	23	20	84	-	3	-	-	-	-	-
d) Factors affecting survival of early life stages (Hypothesis being tested)													
Code	Stock component	Area	Starvation	Predation	Advection	Other							
E1	East Greenland	ICES 14	-	-	(+)	(Climate)							
W1a	West Greenland offshore	NAFO 1	-	-	(+)	(Climate, Stratification, Zooplankton)							
W1b	West Greenland inshore	NAFO 1	-	-	-	-							

^a mean survey indices; offshore 1982-2002 (except 1984, 1992, 1994), recruits in millions, stock size and SSB in 000t, inshore 1985-2001, recruits and stock size in number/100 in net hauling

^b 1962-2002, age at 50% maturity from sigmoidal functions fitted to annual maturity curves given in Raiz (2003)

^c Fulton's condition factor for the years 1982, 1997 and 1999-1999 (Ljorset and Raiz 2000)

^d von Bertalanffy growth coefficient k and L_∞ for year classes 1955-1961 (Raiz et al. 1999), year classes with L_∞ < 100 and > 150 cm excluded

3.5 Cod in Faroese waters

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Background and physical environment

Commercially, cod is the most important demersal species in the catches from the Faroe area. Catches back to 1903 are shown in Figure 3.5.1. Since 1906, total catches have fluctuated between 6000 and 45 000 tonnes. With the exception of the World War periods, the proportion caught by the Faroese was rather low until 1970, but it then increased.

The habitat of cod, as well as the whole ecology of Faroese waters, is dominated by the location of the islands on the submarine ridge system between Scotland and Greenland, which separates the warm Atlantic waters from the cold waters of northern origin. In the northern part of the area, the Iceland-Faroe Ridge has a sill depth around 500 m while the southern part of the ridge system, the Wyville-Thomson Ridge, has a sill depth around 600 m (Figure 3.5.2). The Faroe-Shetland Channel separates the Faroe Plateau from the Scottish

continental shelf, whereas the Faroe Bank Channel, with sill depth around 840 m, separates the Faroe Plateau from the Faroe Bank.

The upper layers of the waters surrounding the Faroes are dominated by "Modified North Atlantic Water" (MNAW) which derives from the North Atlantic Current (Hansen and Østerhus, 2000). This water has typical temperatures of around 8°C and salinities of around 35.25. The general circulation pattern of the area (Figure 3.5.3) transports this water past the Faroes on all sides, but in the Norwegian Sea, north of the Faroes, the Iceland-Faroe Front separates it from the water carried by the East Icelandic Current. This water is much colder (temperature around or below 4°C) and fresher (salinity below 34.9). In the upper layers, it is only found north of the Iceland-Faroe Front, but at deeper levels to the north and east of the Faroes, this water may be found mixed into the MNAW in increasing amounts down to depths of 300 to 500 meters. Deeper than 500–600 m (Figure 3.5.3, bottom panel), the water northeast of the ridges is cold ($T < 0^{\circ}\text{C}$) with salinities close to 34.9. Only the region north of the Faroe Bank and west of the Iceland-Faroe Ridge is in the deeper parts dominated by Atlantic water, and even in that region, one finds colder water derived from overflow through the Faroe Bank Channel and across over the Iceland-Faroe Ridge.

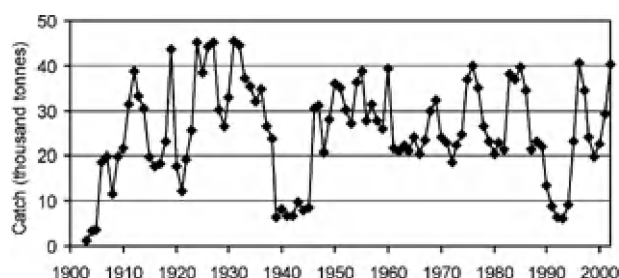


Figure 3.5.1. Annual catches of cod for the Faroe area (ICES Division 5).

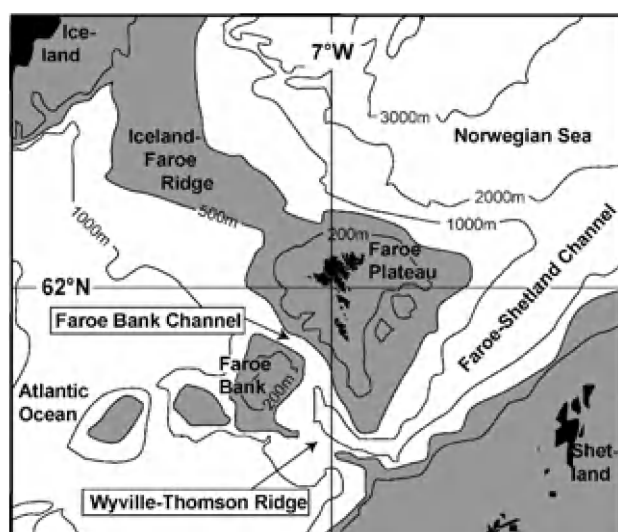


Figure 3.5.2. Bottom topography of Faroese waters (gray areas are shallower than 500 m).

All the hydrographic observations, that have been made during more than a century, have shown the Iceland-Faroe Front to be so far north of the Faroes, that the waters on the Plateau and on the banks have had comparatively small variations in temperature and salinity, although cold intrusions from the frontal region may occasionally reach the shelf region (Hansen and Meincke, 1979). Contributing to this stability are the almost closed anticyclonic circulation systems (Figure 3.5.3, top panel), which are known to dominate the shallower regions at least on the Faroe Bank (Hansen *et al.*, 1986) and on the Faroe Plateau (Hansen, 1992). The persistence of these flows results in long retention times for both the water and the planktonic organisms over the shallower regions; and the fact that the circulation over the Faroe Bank is separate from the circulation over the Plateau may explain how the two cod stocks can remain distinct. On the Faroe Plateau, there are indications that there may be more than one gyre, but detailed knowledge on this is lacking, as is knowledge on the vulnerability of the gyre systems to storms or abnormal weather conditions.

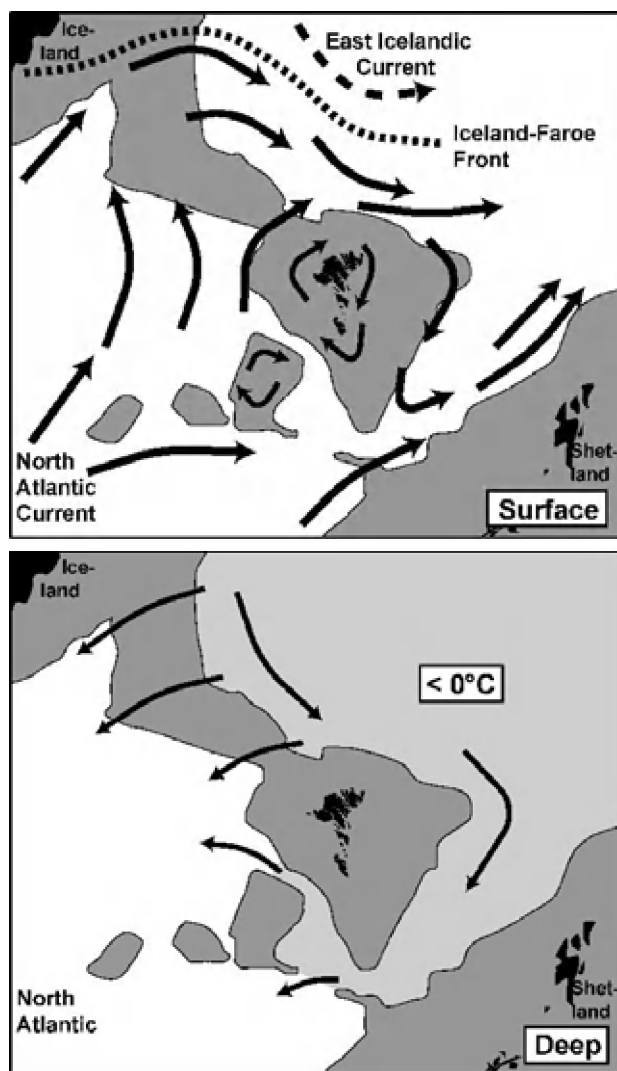


Figure 3.5.3. Circulation and water masses at the surface (top panel) and at depths greater than about 500 m (bottom panel). On top panel, thick continuous arrows indicate flow of Atlantic water. Thin continuous arrows indicate quasi-closed circulations on the shallow parts of the Faroe Plateau and Faroe Bank. On bottom panel, light grey areas indicate cold water flowing towards and across the ridges. Dark grey areas on both panels are shallower than 500 m.

In the shallow regions, there are strong tidal currents, which mix these waters very efficiently. This results in a difference between the vertically almost homogeneous shelf water and the offshore waters, which become stratified in the warmer seasons (Figure 3.5.4). On infrared satellite pictures the border between these two regimes is seen as a distinct front both on the Faroe Bank and on the Plateau. These three regimes (well-mixed, frontal, and stratified) give different conditions for primary production, but little is known about production cycles in Faroese waters, except for the shallow parts of the Faroe Plateau, and much more work is required to establish an understanding of these cycles and their dependence on the very variable weather conditions in the region.

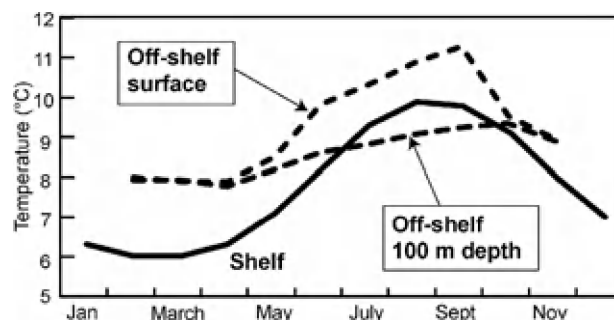


Figure 3.5.4. Seasonal temperature variation on the shallow parts of the Faroe shelf 1914–1969 (continuous curve) and at two depths on a station off-shelf (in the Faroe Bank Channel) 1982–1997.

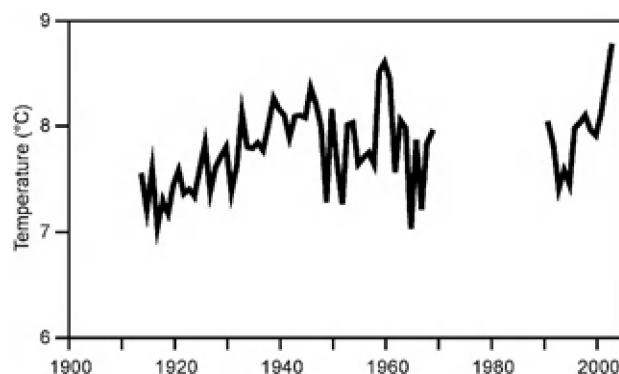


Figure 3.5.5. Annually averaged temperature on the shallow parts of the Faroe shelf based on measurements at two coastal stations.

From the beginning of the 20th century, hydrographic investigations have been made in Faroese waters, but irregularly. In the late 1980s three standard sections were established and one more was added in 1994. They are occupied at least four times a year. These sections were designed to coincide as closely as possible to the sections often occupied in the historical data set. Shore-based daily temperature measurements were initiated in 1875 in Tórshavn and moved in 1914 to Mykines, where they continued until 1969. A critical analysis (Hansen and Meincke, 1984) indicates that the Mykines series gives reliable annual averages for the shallow waters on the Faroe Plateau. These measurements were discontinued in 1969, but an automatic temperature recording station was established in 1989, close to the Mykines site. Together, these series give a long-term perspective on the temperature development on the Faroe shelf (Figure 3.5.5).

Stock and geographic distribution

Extensive tagging experiments have demonstrated the existence of two cod stocks in the Faroe area, one on the Faroe Plateau and one on Faroe Bank (Strubberg, 1916; Tåning, 1940; Joensen, 1954; Jones, 1966). Schmidt, (1930) has shown that cod on the Faroe Bank have a lower number of vertebrae than cod on the Plateau and concluded that the stock on Faroe Bank and that on the

Plateau are two different stocks. Analysis of serum protein by Jamieson and Jones, 1967) supports this thesis. In the assessment of cod in the Faroe area, the cod on the Faroe Bank and that on the Plateau are therefore treated as two different stocks.

The catch figures shown in Figure 3.5.1 are for the total Faroe area between 1903–1960 and for the Faroe Plateau between 1961–2002. Catches on the Faroe Bank since 1965 are shown in Figure 3.5.6. They reached a maximum of 5000 tonnes in 1973. The cod fishery in the Faroe area collapsed in 1990 and was historically low in 1991–1994. The cod stock recovered in the mid-1990s and the catch figures have shown the normal pattern since then.

Data to assess the cod stock on the Faroe Plateau are available back to 1961 and limited attempts have been made to assess the Faroe Bank cod stock. Mean fishing mortalities for the age groups 3 to 7 of Faroe Plateau cod, estimated by virtual population analysis are shown in Figure 3.5.7. From 1961–1973 the fishing mortality decreased from 0.6 to 0.3 and fluctuated between 0.4 and 0.8 from the mid-1970s to 1990. After the collapse, the fishing mortalities were especially low (< 0.34) but they increased steeply after the recovery of the cod stock and have fluctuated between 0.36 and 0.9 since then. With the present exploitation pattern, $F_{\max}$ is estimated to be 0.41 and $F_{0.1}$ to be 0.25.

The estimated recruitment as two year old and the estimated spawning-stock biomass are shown in Figure 3.5.8. With the exception of the 1972, 1973, 1982, 1993, and 1999 year classes, the recruitment has fluctuated between 3 and 30 million. The long term recruitment is estimated at 18 million. A series of poor, or average, year classes during 1984–1991 was observed prior to the collapse of the fishery. The spawning-stock biomass increased from 1961 to 1976 when it reached the highest observed value (116 000 tonnes). It peaked again in the mid-1980s when the strong 1982 year class became sexually mature. During the collapse in 1990–1994, the spawning-stock reached the lowest observed value of 22 000 tonnes in 1992. The spawning-stock biomass then increased spectacularly and reached 86 000 tonnes in 1996 when the strong 1993 year class entered the fishery. At the beginning of 2002, the spawning-stock was estimated at 69 000 tonnes.

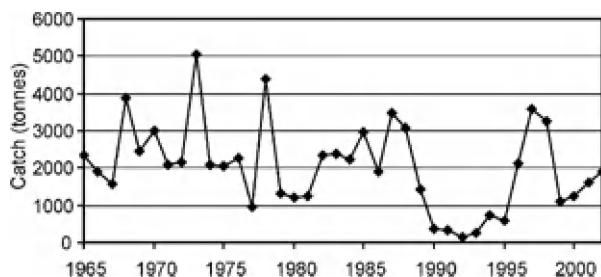


Figure 3.5.6. Annual catches of Faroe Bank cod.

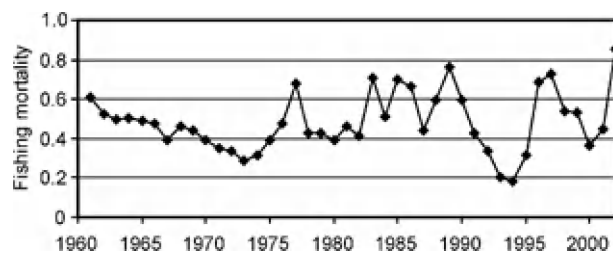


Figure 3.5.7. Mean fishing mortality for Faroe Plateau cod of age 3–7 years.



Figure 3.5.8. Spawning-stock biomass and recruitment as 2 year old for Faroe Plateau cod.

Time of spawning

Tåning (1943) and Joensen and Tåning, (1970) state that spawning takes place from February to May with April being the most important month. Analysis of roelandings (Hoydal and Reinert, 1978) and length distributions of pelagic larvae and juveniles (Reinert, 1979; Hansen *et al.*, 1990) verified this spawning period but indicated a mean spawning in the second half of March. Data from the Faroese Groundfish Surveys 1982–1989 have been used to estimate the timing of gonadal development and spawning. According to these data, spawning on the Plateau starts at a low level in February. In the second half of March, most of the sampled cod have been spawning. No data are available for the first half of February for the Faroe Bank but in the second half, the proportion spawning is at the same level as that on the Plateau. The lower proportion of spawning cod and higher proportion of maturing cod in March on the Faroe Bank compared to the Plateau indicates a prolonged spawning period on the Faroe Bank.

Location of spawning

Spawning takes place all around the Faroe Plateau at depths of about 80–180 m and at temperatures of 6–7°C. By far the most important spawning grounds are to the north and west of the islands (Figure 3.5.9). It should be mentioned that there seems to be a delay of about one month between the main spawning of the three main demersal gadoids in the area, with main spawning time of saithe in the second part of February, of cod in the second part of March and of haddock in mid-April (Joensen, 1954; Joensen and Tåning, 1970).

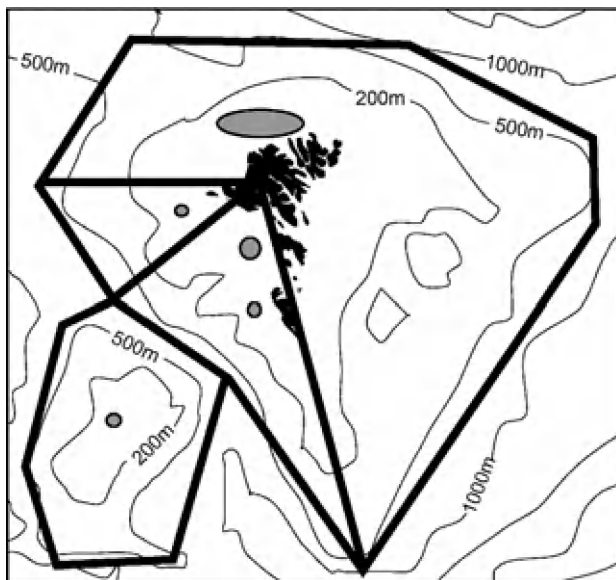


Figure 3.5.9. Spawning of Faroese cod. Thick lines roughly divide the waters shallower than 500 m into four regions. Mature cod in each of these regions, migrate to the spawning areas, indicated by gray ellipses within each region.

Biological details

After fertilization, the eggs ascend towards the upper layers. The eggs are advected by the clockwise circulation around the islands and are dispersed by the strong tidal currents (Reinert, 1979; Gaard, and Steingrund, 2001). On their way from the spawning grounds, the eggs hatch and the cod start feeding. The feeding seems to coincide fairly well with the onset of the spring bloom and the first-feeding larvae predate mainly on copepod eggs. As the larvae and pelagic juveniles grow, they consume progressively larger prey items, which may be copepod nauplii and small- to medium-sized copepods (Gaard and Steingrund, 2001). In mid-summer, having attained a length between 20 and 40 mm, the juveniles to a large extent predate on large-sized plankton, mainly the largest copepods and decapod larvae (Gaard, and Reinert, 2002).

In June and early July, the distribution of juveniles shows a characteristic picture on the Plateau, with heavy concentrations near the islands to the north and more scattered in other areas (Jákupsstovu, and Reinert, 1994). The Faroe Plateau seems to be a retention area for eggs and larvae, created by the anticyclonic current system, and a subdivision of this system into several minor gyres could be responsible for the characteristic distribution of the juveniles in June and early July. The current system around the Faroe Bank creates a retention area there as well.

The information on growth in the pelagic phase is scarce. Samples from Bongo, Gulf III and capelin trawl in the late 1970s (Reinert, 1979) indicated a logarithmic growth in agreement with Saville (1956). At lengths of about 3.5-40 cm, the juveniles leave the pelagic phase and most

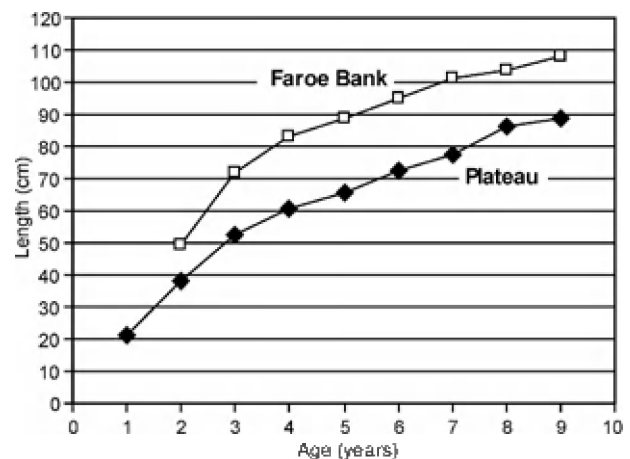


Figure 3.5.10. Mean length-at-age for cod on Faroe Plateau (1994–2004) and Faroe Bank (1999–2003).

of them migrate into the littoral zone of the fjords. This usually happens after the first week of July. On the Faroe Bank, however, the juveniles settle on the Bank proper, i.e. in relatively deep water.

In late July, the demersal stages, now about 4.5 cm long, are found in the seaweed in the littoral zone. In the middle of August, the mean length is about 5 cm, and in mid-September, it is about 7 cm (Joensen and Tåning, 1970). The growth of cod from 1-year and onwards is shown in Figure 3.5.10.

After 1–2 years in the littoral zone of the fjords, the cod migrate towards deeper waters. Tagging experiments show, however, that the cod is rather stationary while sexually immature, i.e. up to about 3 years (Strubberg, 1916). The food in the littoral zone is mainly crustaceans and the young of other fish species, e.g. saithe and sandeel.

Recruitment

The year-class strength seems to be determined rather late in life, i.e. during the second winter which coincides with the migration towards deeper waters (Steingrund and Gaard, 2005). The bottleneck seems to be food availability in the area, which is determined by the new phytoplankton production (about 6 months before) and the abundance of older cod, i.e. competition. The new primary production during spring and early summer may vary by a factor of five (Gaard, 2003) and the production of cod (numbers $\times$ individual growth summed up for all age groups), which is highly correlated to phytoplankton production (Figure 3.5.11), may vary even more (Steingrund and Gaard, 2005). Thus, the collapse and rapid recovery of the cod stock in the 1990s seems to a large extent to be explained by variation in phytoplankton production.

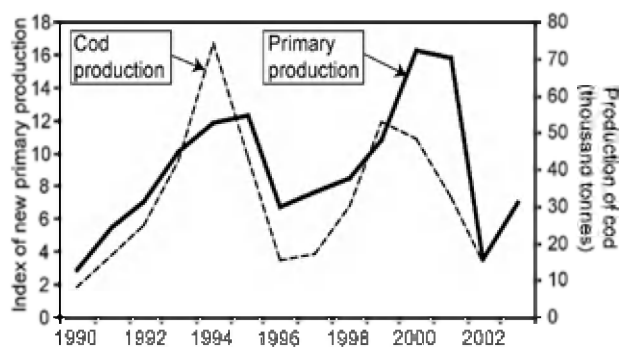


Figure 3.5.11. Index of new primary production on the Faroe shelf and corresponding production of Faroe Plateau cod older than 1.5 years. Updated from Steingrund *et al.*, 2003.

The mechanisms controlling the primary production on the shelf are not well understood. Earlier studies have shown no correlation between primary production (timing of spring bloom or production level) and light irradiance (Gaard *et al.*, 1998; Gaard, 2003). Also, modelling indicates that the spring bloom would have occurred earlier, than it does in nature, if light was the only controlling factor. Hence, other controlling mechanisms appear to be present. Gaard *et al.* (1998) and Gaard (2003) have shown a clear inverse relationship between new primary production and zooplankton biomass (variable influx of the copepod *Calanus finmarchicus* from offshore areas) and it has been hypothesized that the observed plankton variability could be due to variable grazing from *C. finmarchicus*. However, recent modelling studies indicate that the variable exchange rate between on-shelf and off-shelf waters may also be a main controlling factor for the timing and intensity of the spring bloom (Hansen *et al.*, 2004).

Migration

The geographical location of the stock depends on season. During spawning in March, the majority of the sexually mature part of the cod stock is located in two main spawning areas north and west of the Faroe Islands at 80–120 m depth, but other spawning areas also exist (Figure 3.5.9). Earlier tagging results showed that after spawning the fish disperse all over the Plateau (Joensen, and Tåning, 1970). An extensive tagging program, initiated in 1997, has confirmed that after spawning, the cod disperse all around the Faroe Plateau following the prespawning migration routes the opposite way, i.e. the cod move “back home”. The postspawning migration is considered to be a feeding migration. There is evidence of sub-populations, but no data on the genetic relationship between them are available. As cod grow larger, they gradually select deeper waters. Thus, the mean size increases with increasing depth. During summer, the cod have the maximum dispersion covering depths from 10–500 m, but the bulk are normally at depths of 60–150 m.

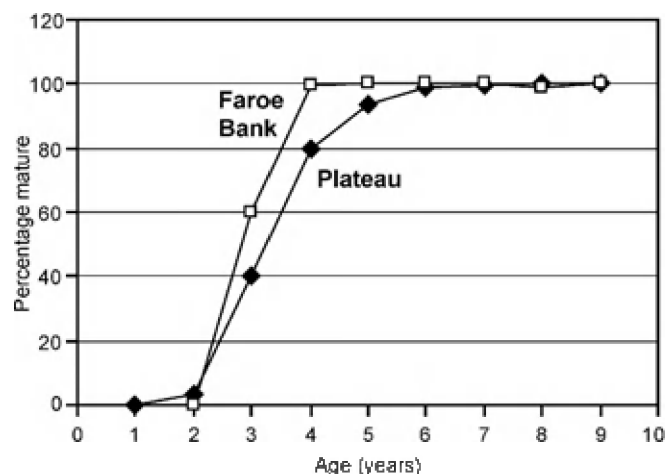


Figure 3.5.12. Average maturity ogives by age for Faroe cod during the period 1999–2003.

Data on feeding and predation are scarce. Joensen and Tåning (1970) describe the cod as feeding on nearly everything they come across and mention fish, crustaceans, worms, mussels, echinoderms, ascidians and hydroids. The most favoured fish species in the food are probably sandeel and herring, but also Norway pout. The abundance of these fish species and their migrations may at times be decisive for the cod migration. Cod stomachs have regularly been collected during March and August since 1997. The results are not published, but they show that cod prey on Crustaceans (Portunidae, Pandalidae, Crangonidae, *Hyas coarctatus*, *Pagurus bernhardus* and *Pagurus pubescens*) as well as fish (Ammodytidae, *Trisopterus esmarkii* and juvenile *Melanogrammus aeglefinus*).

Adult growth

In Figure 3.5.10, the mean lengths-at-age for the two cod stocks in the Faroe area are shown. The figure is based on ages determined from otoliths collected over the period 1994–2004 (Faroe Plateau) or 1999–2003 (Faroe Bank). The Faroe Bank cod grow more rapidly than the Plateau cod. At an age of 3 years, the average length of cod on the Faroe Bank is around 72 cm, while on the Faroe Plateau it is around 53 cm. Cod on the Faroe Bank is one of the cod populations with the fastest growth.

The individual growth of Faroe Plateau cod is density-dependent, but not in the typical sense of the word (many fish – slow growth). The phytoplankton production sets the limits for overall cod production (number of fish $\times$ individual growth summed up for all age groups). Within those limits, individual growth depends on the abundance of cod and may be regarded as density-dependent. Since the annual variation in phytoplankton production is so great, no relationship is found between stock size and individual growth.

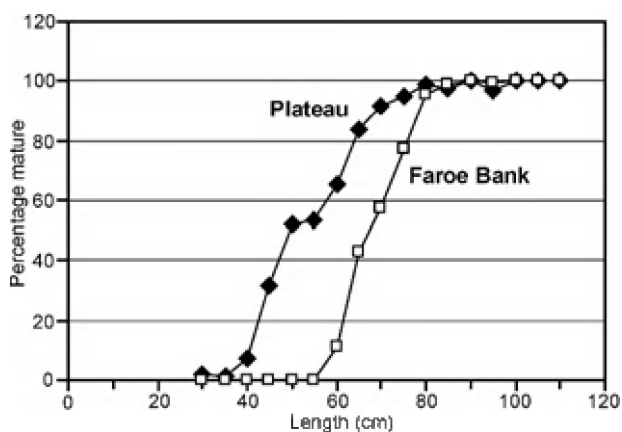


Figure 3.5.13. Average maturity ogives by length (5 cm groups) for Faroe cod during the period 1999–2003.

Very little data have been published on the maturation of cod at the Faroes. Tåning (1943) and Joensen and Tåning (1970) state that, on average, the cod on the Faroe Plateau becomes mature at an age of 4 years while the Faroe Bank cod reaches maturity at 3 years old. Since 1982, samples have been collected during the Faroese ground-fish surveys in February and March to estimate maturity ogives. Some of the results are shown in Figure 3.5.12. According to these investigations, there is no large difference in the maturity ogives by ages for cod on the Plateau and the Faroe Bank cod. In both cases, 50% of the cod became mature at an age of 3 years, i.e. one year younger than stated by Tåning (1943) and Joensen and Tåning (1970). The rapid growth of cod on the Faroe Bank and the similar maturity ogives by ages must imply that cod on the Faroe Bank become mature at a larger length as compared to cod on the Plateau, and this is demonstrated in Figure 3.5.13. The 50% maturation length of the Faroe Bank cod was around 65–70 cm while for the Plateau cod it was around 50–55 cm.

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3.6 Iceland

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Species, stock and area of distribution

Evidence of stock discreteness, e.g. genetic distance, tagging

Tagging experiments have demonstrated that the Icelandic cod stock is virtually discrete from the other North Atlantic stocks. Both mature fish tagged on the spawning grounds and immature fish tagged on the nursery grounds have only been caught in the Icelandic shelf area during later years (Jónsson, 1996). During some years there have been migrations of cod from Greenland to the spawning grounds at Iceland, but these are mainly believed to be made up of individuals which originally drifted as larvae to Greenland from the Icelandic spawning grounds (Jamieson and Jónsson, 1971). More recently, microsatellite DNA analysis has shown that cod in Icelandic waters is genetically different from cod in the Barents Sea, North Sea and Newfoundland (Pogson *et al.*, 1995).

Units for which assessment of spawning-stock biomass and recruitment are available

Cod in Icelandic waters are distributed over all of the continental shelf (Figure 3.6.1). For stock assessment, advisory and management purposes this cod has, historically, been assumed to belong to a single unit. Information on stock size and recruitment is available from ~1950 (VPA estimates) and these have been reported in ICES assessment working group papers (ICES, 2002) and in Icelandic stock status reports (Anon., 2002). However, recent studies have shown that the Icelandic cod stock may consist of distinct spawning populations (Marteinsdóttir *et al.*, 2000b; Begg and Marteinsdóttir, 2000) and at least two populations spawning in adjacent areas on the south coast have been shown to be genetically distinct (Jónsdóttir *et al.*, 1999, 2001, 2002). Studies on the genetic composition of the Icelandic cod stock and construction of databases for assessment based on the revealed sub-stock structure are ongoing (METACOD; QLRT-2000-0953; www.hafro.is/metacod).

Time-series of spawning-stock biomass and recruitment data, e.g. from commercial catch and effort data, fishing surveys or VPA

Indices of biomass and recruitment based on VPA exist back to ca. 1925 (Schopka, 1994). Indices based on data obtained in the stratified groundfish surveys exist for the time periods 1985 – present (spring survey); (Pálsson *et al.*, 1989; ICES, 2002; Begg and Marteinsdóttir, 2003) and 1995–present (fall survey). Indices of spawning-stock biomass based on CPUE data obtained in a gillnet survey conducted on the spawning grounds south and west of the country exist for the time period 1996–present (Thorsteinsson *et al.*, 1998; Gudmundsdóttir *et al.*, 1998). Indices of 0-group abundance exist back to 1972 (Ástþórsson *et al.*, 1994; Begg and Marteinsdóttir, 2000).

Timing of spawning

Date of spawning and interannual variability or trend

Spawning of cod on the main spawning grounds at the south and southwest coast generally starts in middle of March and is completed in the first week of May (Jónsson, 1982; Marteinsdóttir and Björnsson, 1999). Time and duration of spawning in this area varies between size groups of cod where larger cod start spawning earlier and spawn over a longer time period than smaller cod (Marteinsdóttir and Björnsson, 1999). Time of spawning at other locations may vary. In general, spawning at the west and east coast starts in late March and is completed

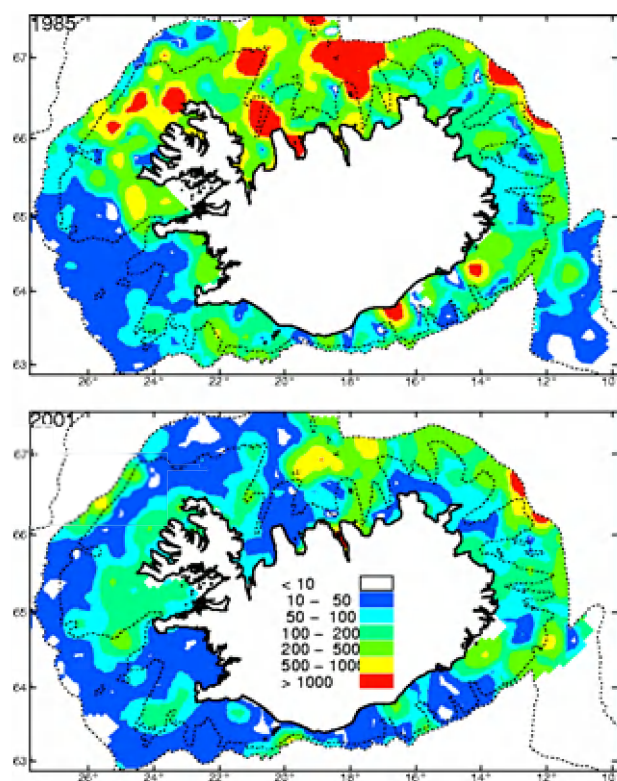


Figure 3.6.1 Mean catch (kg/tow) of cod in the 1985 and 2001 ground fish survey conducted by the Marine Research Institute in March each year (figure provided by Hoskuldur Björnsson, MRI).

in late April while spawning at the north and northeast coast starts early April and may extend into late May or early June (Marteinsdóttir *et al.*, 2000b) and unpublished observations). In turn, time of hatching varies between areas with most of the hatching completed by early June at the south coast but not until June and July at the north and east coasts (Marteinsdóttir *et al.*, 2000b).

Time of day when spawning occurs

Observations made with DST tags have indicated an increase in vertical movements, generally associated with spawning behaviour, during periods of slack water occurring twice every 24 hours during the course of the tidal cycle (V. Thorsteinsson in prep).

Time of spawning season in relation to plankton production cycle and

Time of spawning season in relation to hydrographic events

Spawning appears closely related to the onset of the phytoplankton spring bloom and the spawning of the zooplankton in the spawning areas along the south and southwest coast. Further, in the coastal area the onset of the spring phytoplankton bloom occurs earlier than in the waters farther offshore, and appears mainly to depend on stratification due to the outflow of fresh water from several large rivers dissipating there (Fridgeirsson *et al.*, 1979; Thordardottir, 1986; Olafsson, 1985; Gislason *et al.*, 1994; Gislason and Astþórsson, 1995; Astþórsson, and Gislason, 1999). The extension of the low salinity water, from the coast and on to the shelf, is highly variable and depends very much on the direction and strength of winds.

Time of spawning season in relation to other fish species which spawn in the same location

Other commercially important fish stocks (haddock, saithe, capelin, and herring) also spawn off the southwest coast of Iceland. The information on these species is rather limited but one can state that during the period from February to May the spawning sequence is the following: saithe, capelin, cod and haddock. Later in the summer, Icelandic summer spawning herring also spawn on these same or nearby grounds. The presence of capelin on the main spawning grounds of cod at the south and southwest coast of Iceland in the weeks preceding the spawning of cod is thought to play an important role in facilitating the physical condition of spawning cod (Marteinsdóttir and Björnsson, 1999; Astþórsson and Vilhjálmsson, 2002).

Location of spawning

Geographic location and extent of spawning area and evidence of its variability from year-to-year. Does

spawning regularly begin in one part of the spawning area and move to other parts?

The main spawning grounds of cod in Icelandic waters are located at the south- and southwest coast of Iceland (Sæmundsson, 1924; Fridgeirsson, 1982; Jónsson, 1982; Marteinsdóttir *et al.*, 2000a; Begg and Marteinsdóttir, 2002a). (Figure 3.6.2). Additional spawning occurs also within fjords of the west, north and east coasts although it is generally considered to be on a much smaller scale than the spawning at the south coast (Sæmundsson, 1929; Fridgeirsson, 1982; Jónsson, 1982; Marteinsdóttir *et al.*, 2000b). Distribution and abundance of spawning cod on the main spawning grounds is influenced by the composition of the spawning-stock. In general, size of spawning cod varies distinctly between areas, where larger cod spawn closer to the shore and smaller cod further out in deeper water (Marteinsdóttir and Pétursdóttir, 1995; Marteinsdóttir *et al.*, 2000a). Therefore, during periods of impaired size distributions certain spawning grounds become less populated than others. This is confirmed by a general decline in stock abundance in spawning areas close to the shore at the southwest coast in recent years (Gudmundsdottir *et al.*, 1998).

Can location be described in relation to hydrographic features?

The main spawning areas are located close to the shore within or at the boundary of the low salinity coastal current and the more saline Atlantic water farther ashore (Fridgeirsson, 1984). Additionally, most spawning sites, e.g. on the main spawning grounds as well as within fjords west, north and east of the country are likely to be influenced by the stratification due to freshwater run-off.

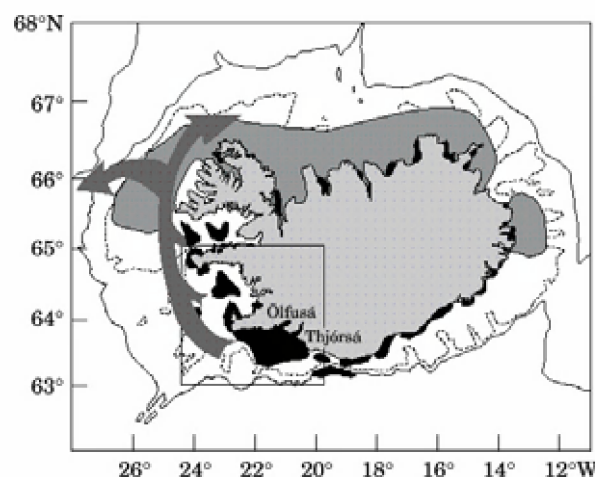


Figure 3.6.2 Spawning sites (in black) of cod in Icelandic waters and the expected drift route of eggs and larvae from the main spawning sites at the southwest coast. The dark grey area represents a typical distribution of 0-group cod, although the size of the total area occupied by juvenile cod may vary depending on the year class. Locations (in black) along the west, north and east coast represent areas where samples of spawning cod have been obtained by the Marine Institute since 1979 as well as areas that have been fished historically for spawning cod by local fishermen. Main spawning grounds are located within the box (from Marteinsdóttir *et al.*, 2000a).

Can location be described in relation to other species, including food organisms and predators?

Limited information is available on the location of the main spawning grounds with respect to other species and possible predators. However, it can be stated that in the coastal area where the spawning is usually most intensive relatively large densities of zooplankton are usually also encountered (Gislason and Astþórsson, 1991, 1996; Astþórsson and Gislason, 1995). Further, as discussed by Astþórsson and Gislason (1999), due to their proximity to the main source areas of *Calanus* the southern and western banks may be particularly suitable as spawning areas of fish.

The abundance and the timing of the spring spawning of *Calanus finmarchicus* near the main spawning grounds of cod (*G. morhua*) south of Iceland may vary between years, as a result of year-to-year variability in the timing of spring blooms (Astþórsson *et al.*, 1994; Astþórsson and Gislason, 1999). The peak spawning of *C. finmarchicus* was estimated to have taken place in April in 1991, while in 1990 and 1992 this probably took place in May. This may influence the success of first-feeding and survival of cod larvae.

Can location be described in relation to water mass circulation?

From the main spawning grounds off the southwest coast of Iceland (within the coastal current or at the boundary between the Atlantic water and the coastal current) the majority of the eggs and larvae are transported clockwise around the island to the nursery grounds off the north-west, north and north-east coasts of Iceland. The drift of eggs and larvae from the coastal areas in the south is influenced by a westward flowing coastal current fed by the freshwater run-off from the two major rivers on the coast, Þjórsá and Ölfusá (Ólafsson, 1985). This drift of eggs and larvae from the main spawning grounds around the Reykjanes Peninsula and into the outer part of Faxaflói Bay has been confirmed by Fridgeirsson (1984). From there the eggs and larvae are believed to drift with the coastal current and the warm saline Atlantic water of the Irminger Current, flowing northward along the west coast (Astþórsson *et al.*, 1994). As such, southerly winds will tend to favour this transport and confine the drifting larvae close to the west coast and within the shelf area. On the other hand, northerly winds will distribute the low salinity water on to the western shelf (Stefánsson and Gudmundsson, 1978) and probably lead to more extensive distribution of larvae at lower densities. The Irminger current splits into two branches off the Vestfirðir peninsula, one flowing to the west towards Greenland and one continuing northeast onto the northern shelf (Stefánsson, 1962, 1981). The interannual variation in the relative strength and direction of the coastal and Irminger currents has been shown to influence the general distribution of larvae and juvenile cod (Begg and Marteinsdóttir, 2002b). For example, in years when the coastal current was strong, more abundant and larger pelagic juveniles derived from the main spawning

component were found on the main nursery grounds north of the country.

Biological details

Fecundity

Potential fecundity of Icelandic cod ranges from 0.23–31.7 million vitellogenic oocytes and relative (or specific) fecundity ranges from 51–1327 oocytes g⁻¹ of whole body weight (Marteinsdóttir and Begg, 2002). The relationship between potential fecundity and total length is best described with a power equation

$$(F = 0.0118 \times L^{4.372})$$

$r^2 = 0.81$, $n = 869$; data from cod on the main spawning ground during 1995–2000), while the relationship between potential fecundity and weight is linear:

$$(F = -1491732 + 778 \times W(g))$$

$r^2 = 0.85$, $n = 869$; (Marteinsdóttir and Begg, 2002).

Evidence of changes in fecundity with time

The relationship between potential fecundity and total length varies annually (Marteinsdóttir and Begg, 2002). During 1960, 1967, and 1995–2000, the greatest slopes were obtained in 1997 and 1998, and the smallest in 1960, 1967, and 1999 (Joakimsson, 1969; Schopka, 1971; Marteinsdóttir and Begg, 2002). Potential fecundity varied between years from $836\text{--}1726 \times 10^3$ for a standard fish of 70 cm length, $3236\text{--}4835$ for 90 cm fish and $8748\text{--}15\,822 \times 10^3$ for a 120 cm fish. Potential fecundity is influenced by somatic and liver condition. In some years, more variation in relative fecundity was explained by liver condition than by length (Marteinsdóttir and Begg, 2002).

Percentage mature-at-age (including the population not on the spawning grounds). Length at 50% maturity

Female cod attain 50% maturity at a greater length and age (75.6 cm and 6.6 years) than males (67.2 cm and 5.8 years) (Marteinsdóttir and Begg, 2002). Size and age at maturity varies also spatially. Cod in waters off the north coast mature at a greater size and age than cod at the south coast. In the north, 50% of female cod reached maturity at 80.2 cm and 7.3 years, while in the south L50 and A50 were 71.0 cm and 5.9 years, respectively (Marteinsdóttir and Begg, 2002). In contrast, 50% of male cod in the north reached maturity at 72.8 cm and 6.6 years, while in the south L50 and A50 were 61.5 cm and 5.0 years, respectively.

Egg size and evidence of changes with age and with time during the spawning season. Specific gravity of eggs and larvae.

Size of eggs varies from 1.2–1.6 mm (Marteinsdóttir and Steinarsson, 1998). Egg size is positively related to female size and condition but negatively related to female spawning experience (Marteinsdóttir and Steinarsson,

1998; Marteinsdóttir and Begg, 2002). As such, size of eggs from females of all size classes decreased during the spawning season. Absolute density of eggs varies from 1.02256 to 1.02657 g cm⁻³; (Marteinsdóttir and Begg, 2002). Egg density is positively related to female length, liver condition and egg diameter while the variation in egg density within each batch is negatively related to female size and egg size (Marteinsdóttir and Begg, 2002).

Typical densities, i.e. number per m³ of eggs and larvae

Density of larvae varies with age and area. Patches of newly hatched larvae observed along the main drift route south-west of the country are often relatively dense, 1–5 m⁻³. Patches of older larvae are, however, less dense, 0.01–0.8 larvae m⁻³ (Marteinsdóttir *et al.*, 2000b; Fridgeirsson, 1984; unpublished data)

Incubation rate of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larvae

Mean incubation time for eggs at 7°C is 13.3 days (Marteinsdóttir, unpubl). Size of larvae at hatching is 4.3–4.7 mm and 0.06 – 0.08 mg (Marteinsdóttir and Begg, 2002). No information is available on the size of yolk sac in relation to the size of the larvae.

Larval development rate as a function of temperature

No information available.

Condition factor and nutritional status

Not available.

Egg and larval mortality rates

Hatching success varies between 0–100%, with an average of 57.8–64.3% (Marteinsdóttir and Steinarsson, 1998). Hatching success is marginally related to larval size but not to egg size (Marteinsdóttir and Steinarsson, 1998). However, larval survival is related to egg size and larval swimbladder occurrence. As such, the frequency of larvae with functional swimbladder varies from 0–100% between batches and is positively related to the egg size (Marteinsdóttir and Steinarsson, 1998).

Time of first-feeding of larvae and food at first-feeding

Larvae start feeding on day 4–7. The time of first-feeding and larval feeding success increased with egg size (Marteinsdóttir and Steinarsson, 1998). In nature, the smallest larvae eat mainly copepod eggs and copepod nauplii (Bainbridge and McKay, 1968; Fridgeirsson, 1984; Jónsson and Fridgeirsson, 1986; Thorisson, 1989).

Food of larvae during development

The following summary is based on studies made by Pálsson (1974, 1976, 1980) and by Thorisson (1989) during the summer of 1985. In May, copepod eggs and nauplii are the most important food for the smallest larvae while larger larvae (5–10 mm) eat euphausiid, naupli and small copepods (*Acartia*, *Temora*) and the copepod stages of *C. finmarchicus*. In June, the diet of 10–24 mm larvae is dominated by *C. finmarchicus* and other copepods. In July, larvae between 10–20 mm were mainly eating copepods while larger larvae (30–40 mm) also had euphausiids and capelin larvae as components of the diet. In August, the pelagic juvenile cod (ca. 40–80 mm) feed mainly on euphausiids, capelin larvae and *C. finmarchicus*.

Evidence of predation during the egg and larval stage

No information available.

Are there several spawning sites which contribute to the same stock unit?

Recent studies modelling back-calculated birth date distributions of pelagic juvenile (0-group) cod (*Gadus morhua*) have indicated different regional spawning components in waters off the west, north and east coasts of Iceland (Marteinsdóttir *et al.*, 2000b; Begg and Marteinsdóttir, 2000). The relative proportions of pelagic juvenile cod that are estimated to originate from these regional components in contrast to those from the main spawning grounds are hypothesized to vary in response to the inflow of Atlantic water from the main spawning grounds to the north Icelandic shelf (Begg and Marteinsdóttir, 2002b). The contribution of the different spawning sites is highly variable and in some years, the majority of the surviving 0-group cod appear to have originated from the regional components on the west, north and east coasts.

Earliest time in the life history when year-class strength can be predicted

An estimate of year-class strength can be obtained at the age of two years from data collected in a stratified groundfish survey incorporating about 600 trawling stations and which cover the whole shelf area all around Iceland (Pálsson *et al.*, 1989; Steinarsson, personal communication). The relationship between recruitment (number of 3 year old) and abundance of 0-group cod is relatively weak but is improved by the addition of zooplankton biomass, strength of the coastal current and spawning-stock biomass (Asthórsson *et al.*, 1994; Begg and Marteinsdóttir, 2002b).

Hypotheses which have been put forward to account for year-to-year variability in the year class

Recruitment success derived from individual spawning components is dependent upon favourable environmental and stock effects that influence the dispersal and survival of early life-history stages. It has been hypothesized that

the formation of large year classes will depend on successful production of eggs and larvae at the main spawning areas as well as successful transport from there to the northern located nursery grounds (Asthórrsson *et al.*, 1994; Marteinsdóttir *et al.*, 2000b; Begg and Marteinsdóttir, 2000, 2002b). Therefore, a potential important source of interannual variability in the relative contribution of the main spawning sites is hypothesized to be related to the strength and timing of the coastal current and Atlantic inflow from the main spawning grounds to the nursery sites in the north (Begg and Marteinsdóttir, 2002b). It has been demonstrated that the existence of multiple spawning components, each governed by distinct environmental and stock effects, is important for successful recruitment as the risk of mortality of early life-history stages is spread both temporally and spatially (Marteinsdóttir *et al.*, 2000b). It is therefore hypothesized that the population richness of the Icelandic cod stock may be responsible for the relative low fluctuations in recruitment in this stock compared with many other cod stocks in the North Atlantic. Therefore, the production of the regional in-fjord units are thought to supplement the recruits derived from the main spawning grounds (Marteinsdóttir *et al.*, 2000b; Begg and Marteinsdóttir, 2002b).

Evidence of long term trends in recruitment

Except for a couple of extremely large year classes during the first half of last century, the recruitment of cod in Icelandic waters varies from $50\text{--}430 \times 10^3$ three-year-old individuals. During the second half of last century, recruitment peaked systematically at periods shown to coincide with high age diversity of the spawning stock (Marteinsdóttir and Thorarinnsson, 1998). However, during this period a distinct declining trend is demonstrated by increasingly longer time intervals between strong year classes and more frequent occurrence of below average recruitment (Marteinsdóttir and Thorarinnsson, 1998). Today, recruitment has been at or below average since 1984 (ICES, 2002).

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3.7 Irish Sea (ICES Division VIIa)

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Environment

This section is intended as a brief introduction to the physical environment of the Irish Sea to allow the biological data to be placed in context. Fuller treatments of Irish Sea oceanography can be found in Simpson and Hunter (1974); Robinson (1979); Bowden (1980); Proctor (1981); Dickson and Boelens (1988); and Hill *et al.* (1997).

The bathymetry of the Irish Sea (Figure 3.7.1) plays an important role in determining the physical and biological processes that occur in it. The area is characterised by a deepwater trough (>80 m) running centrally between the Irish coast and a line from the southern end of the Isle of Man to the western edge of Anglesey. This trough continues northwards through the North Channel, joining the Malin Shelf, and reaches a depth of 315 m at Beauforts Dyke. To the south the trough links with the Celtic Sea via St George's Channel. In the central area the trough shoals rapidly to the west whilst to the east it slopes more gently to generate a relatively shallow bay (<50 m) bordered by the North Wales coast, Cumbria and the Isle of Man (eastern Irish Sea).



Figure 3.7.1. Bathymetry of the Irish Sea (from Dickson and Boelens, 1988).

Three primary forces are responsible for the movement of water within the Irish Sea, namely water density differences, tides and the weather (Bowden, 1980). Based on numerical models Heaps and Jones (1977); Heaps, (1978); and Proctor (1981), movement of seabed drifters Ramster and Hill (1969), current meter records and radioactive tracer distributions, a tentative scheme was presented for surface and bottom residual currents by Dickson and Boelens (1988). However, time-averaged circulation in the Irish Sea is relatively weak and shows no particular directionality over large areas. In addition, large seasonal changes can be expected. Due to the uncertainty about the patterns of residual flow in the Irish Sea, calculations of average flushing and residence times are at present unreliable. Of interest in relation to cod egg and larval dispersal is the possible existence of a south-going residual current along the Irish coast (see section on biological data below).

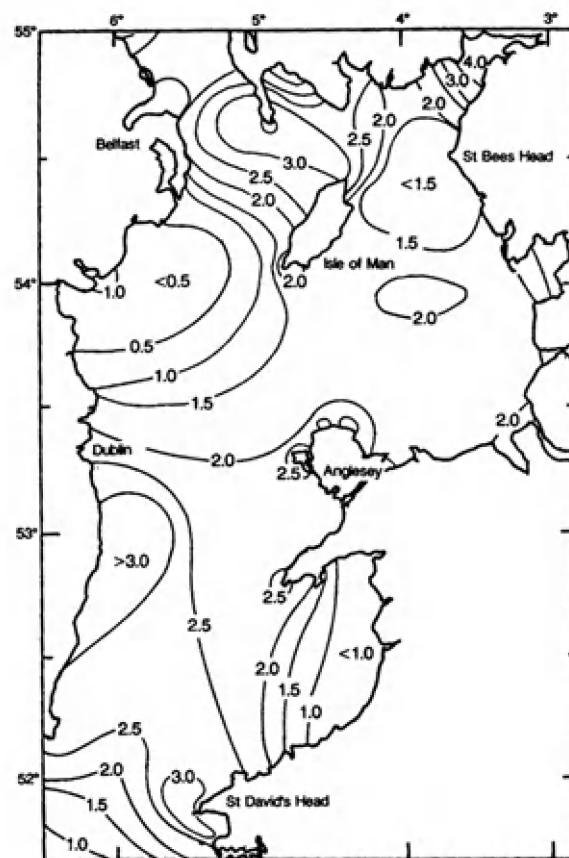


Figure 3.7.2. Maximum tidal stream amplitude and spring tide in knots (from Sager and Sammler, 1975).

Tides from the Atlantic Ocean propagate through St George's Channel and the North Channel (Robinson, 1979). The two branches meet to form a standing wave to the southwest of the Isle of Man which is, therefore, an area of weak tidal currents (Figure 3.7.2). This is reflected in the distribution of bottom sediments (Figure 3.7.3) with a large area of muddy deposits to the west and southwest of the Isle of Man. Surface waves depend on the duration and fetch of the wind. The Irish Sea is relatively sheltered so that the majority of waves are locally generated, steep and of fairly short period. Wave action during storms will have significant effects in the shallower areas to the east. Large surges in the Irish Sea can be generated by storms tracking between Inverness and the Shetlands. Surface currents in the Irish Sea are affected by wind stress, and transport of water through the North Channel can be, at least partly, correlated with the component of wind blowing along the Channel's axis (Young *et al.*, 2000, 2001).

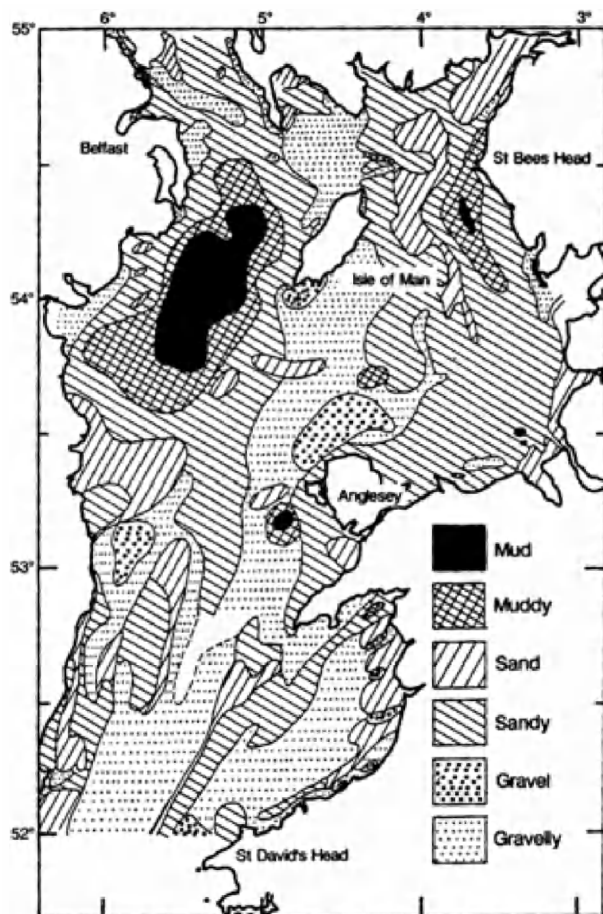


Figure 3.7.3. Simplified distribution of surficial sediment types. (from Dickson and Boelens, 1988).

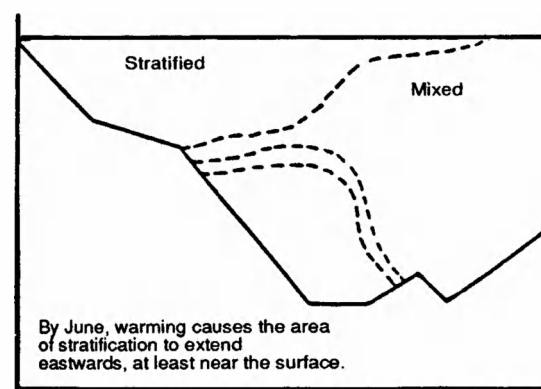
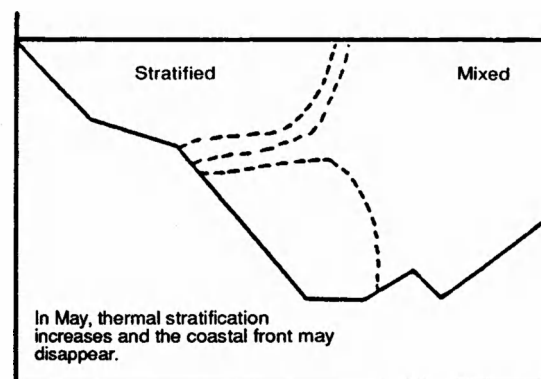
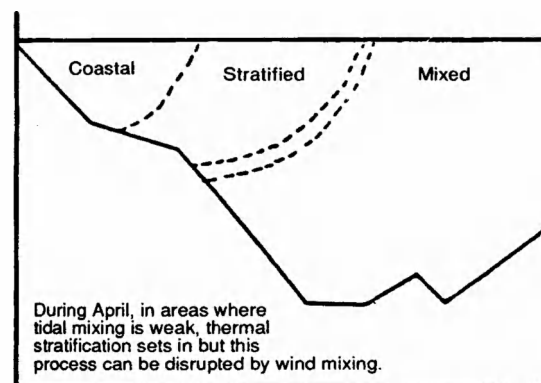
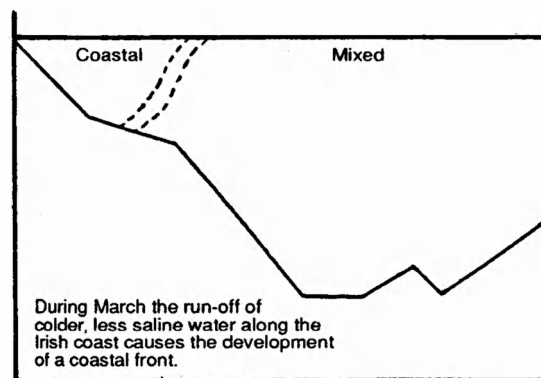


Figure 3.7.4. Schematic representation of the development of stratification in the western Irish Sea along an axis from Dundalk Bay to Anglesey. (Nichols *et al.*, 1993).

Circulation patterns in the Irish Sea have undergone re-evaluation based upon recent data and improvements in modelling (Davies, and Jones, 1992; Aldridge and Davies, 1993; Davies and Aldridge, 1993; Hill *et al.*, 1994a, 1994b, 1997; Horsburgh *et al.*, 2000; Brown *et al.*, 2003). The degree of tidal mixing and the depth of the water principally determine areas of the Irish Sea that are capable of becoming stratified. In most areas of the Irish Sea, tidal mixing is sufficiently strong to maintain a vertically homogeneous water column throughout the year. However, to the southwest of the Isle of Man, where the tidal flows are weak and the water is deep, seasonal stratification, to a depth of 20–30 m, is established between April and October. A generalised scheme for the development of stratification, along an axis from Dundalk Bay to Anglesey, is presented in Figure 3.7.4. Stratification early in the year is aided by the inflow of cold, low salinity water from the Irish mainland leading to the development of a coastal front. Later on, warming reinforces stratification, leading to a frontal region along the Dublin Bay/Isle of Man axis (Fogg *et al.*, 1985). Wind-induced mixing will disrupt the average pattern, especially early in the year.

Recent oceanographic work has shown the existence of a gyre-like circulation in the western Irish Sea around the area of low tidal mixing. This circulation is driven by bottom density fronts and develops seasonally as the overlying water becomes thermally stratified (Hill *et al.*, 1994a, 1997; Horsburgh *et al.*, 2000). The establishment of the stratified area and the associated gyre may be important for the growth and survival of juvenile cod (see section on location of spawning).

Seasonal stratification also occurs in the eastern Irish Sea, the haline contribution is of more importance than the thermal contribution due to the effect of the larger river flows on this side of the Irish Sea. Stratification is marked in winter and spring, especially near the main river inputs but thermal stratification may develop in the summer. Due to the shallow water depth, the Liverpool Bay front is prone to disruption by wind-induced mixing.

Several studies, based mainly in the western Irish Sea, have considered the links between hydrography and primary production (Mills *et al.*, 1997; Gowen *et al.*, 1995, 1998, 2000; Gowen and Bloomfield, 1996; Prestidge and Taylor, 1995).

The above section is up-dated from (Nichols *et al.*, 1993).

Stock and geographic distribution

Evidence of stock discreteness

Meristic evidence for stock structure in this area is limited. Brander (1979) derived a general relationship between vertebral number and water temperature for cod from around the North Atlantic. Samples from the Irish Sea did not conform to the relationship with observed

water temperatures at the time of spawning. Irish Sea cod had a lower average vertebral count than expected. Since vertebral count is influenced by water temperature during the early life stages, this led to the suggestion that there might be a significant level of immigration of cod into the region that had been spawned in warmer waters to the south.

Agnew (1988) examined length-at-age using market sampling data from Northern Irish ports. Landings in the first quarter (at time of spawning) showed evidence for two distinct populations of cod with differing growth rates. This bimodality was not apparent in samples from the other quarters of the year. The maintenance of two distinct populations would however require reproductive isolation for which there is limited evidence. Brander (1975) examined variability in otolith weight in Irish Sea cod but could find no regional differences within age classes.

Evidence for population structuring from genetic studies in this region is limited and equivocal. Glucose phosphate isomerase and lactate dehydrogenase allele frequencies gave evidence for separate populations based on samples of larvae collected in the eastern (Solway) and western Irish Sea (Child, 1988). Similar differences appeared to be present in samples from the same year class sampled in the following year but these differences had vanished one year further on. This was interpreted as evidence for movement away from nursery grounds and population mixing of the older fish. However, haemoglobin (Hbl) allele frequencies collected over a longer time period were for the most part similar all around the British Isles, except for a few unusual samples (Jamieson and Birley, 1989). More recent research by Hutchinson *et al.* (2001) using microsatellite markers did not find evidence for genetic sub-structuring within the Irish Sea and between the Irish and Celtic Seas.

Recaptures of cod tagged on the western and eastern Irish Sea spawning grounds in the 1970s showed that the majority of fish returned to the same spawning grounds each year. The pattern of recaptures suggested separation between cod in the eastern and western Irish Sea (Brander, 1975). Mature fish tagged on spawning grounds in the Bristol Channel were also recaptured from the same site in subsequent spawning seasons. Movement of fish from distinct spawning grounds to mixed feeding grounds may occur (Brander, 1975).

More recent studies on cod movements in this region by tagging (described below under time-series of spawning-stock biomass) did not provide evidence for large-scale movements of cod between the Celtic and Irish Seas. One problem with interpreting this evidence is that the overall stock sizes in both areas have declined significantly in recent years, and fishing patterns have also changed compared with the 1970s. There may therefore have been changes in geographic range and movement patterns, and in the likelihood of recapture in different

regions that make comparison of recent results with earlier studies problematic.

Assessment units, fishery and management

The main fleets targeting cod in Area VIIa include whitefish otter trawlers from UK and Irish ports. Midwater trawlers target spawning cod and haddock in spring and cod, haddock and hake in the summer and autumn. Due to the status of the cod stock, closures of the spawning grounds during spring have been in place since 2000. This resulted in some displacement of fishing effort to the North Channel and Firth of Clyde (Area VIa) in 2000, although the introduction of a cod closure off the Firth of Clyde since 2001 has further reduced cod fishing opportunities in spring. A number of midwater trawl vessels switched to twin-rig fishing for *Nephrops* since 2000 to take advantage of the derogation for the *Nephrops* fishery in Area VIIa.

Otter-trawl vessels in the Irish Sea operate mainly out of UK and Irish ports, although some French trawlers operating in the Celtic Sea extend their activities into the southern Irish Sea. Vessels from Northern Ireland concentrate their effort in the western Irish Sea but currently primarily target *Nephrops*. The UK whitefish fleet has declined substantially through the 1990s and now operates mainly in inshore waters of the eastern Irish Sea as a mixed demersal fishery.

Bycatches of cod are also taken by Belgian, Irish and UK beam trawlers targeting plaice and sole in the eastern Irish Sea and off the Isle of Man.

The status of the Irish Sea cod stock is assessed annually by the Northern Shelf Working Group on Demersal Stocks coordinated through ICES (ICES, 2003a). The assessment is undertaken using the sequential population analysis method, Extended Survivors Analysis (XSA); although the application of other methods including Integrated Catch-at-age Analysis (ICA) and ADAPT has also been investigated. The catch-at-age data are landings only although limited data on discards are available from UK and Irish sampling. The analysis is tuned using spring and/or autumn otter trawl surveys undertaken by the UK (Northern Ireland and Scotland) and Ireland, together with indices of abundance of 0-group cod from the UK (England and Wales) beam trawl survey of Irish Sea flatfish and the Northern Ireland Methot-Isaacs-Kidd (MIK) net surveys for juvenile cod in recent years. The fishing effort is managed by setting annual quotas for total allowable catch. In recent years the status of the stock has led to the development of recovery plans that include closed areas and technical measures (described below).

The management advice from ICES for 2002 was to implement a recovery plan to ensure a safe and rapid recovery of SSB to above 10 000 tonnes. Fishing mortality on cod should be reduced to the lowest possible level. The ICES advice for 2003 was for a closure of all fisheries

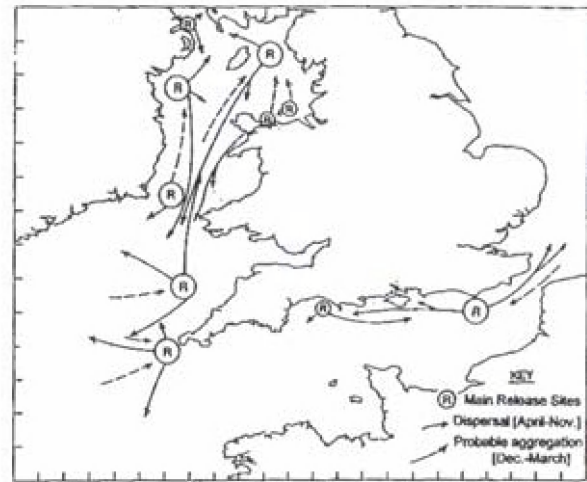


Figure 3.7.5. Movements of tagged cod in the Irish Sea, Celtic Sea, and English Channel (Pawson, 1995).

for cod as a targeted species or bycatch “until there is clear evidence of the recovery of the stock to a size associated with a reasonable probability of good recruitment and there is evidence that productivity has improved” (ICES, 2002). This advice was largely carried over for 2004.

The current precautionary reference points are:

$$B_{lim}=6,000 \text{ tonnes}; B_{pa}=10\,000 \text{ tonnes}; F_{lim}=1.0; F_{pa}=0.72$$

The recent state of the cod stock in Area VIIa is such that stock recovery plans have been in place since 2000. EC Council Regulation 304/2000 established measures for closure of the putative spawning grounds from 14 February to 30 April 2000. However, a number of derogations were provided for the *Nephrops* fishery. An additional measure (EC Council Regulation 2549/2000) established technical measures to aid stock recovery including an increase to 100 mm codends on towed gear.

The closed area and technical measures established in 2000 were extended to 2001, 2002, and 2003 by Council Regulations (EC) 300/2001 and 254/2002. In these latter years the closed area was applied only in the western Irish Sea. Some experimental fisheries were permitted in the closure to test inclined separator panels in *Nephrops* trawls and to examine the potential for a haddock fishery with a minimal cod bycatch. The use of separator panels appeared effective in releasing cod, so vessels employing these have been allowed to fish throughout the closure since 2002.

The ICES ACFM Report, 2003 (ICES, 2003b) notes that “Given the precision of the assessment and the tendency to under-estimate F in the final year, it is not yet possible to determine if the emergency and *ad hoc* measures from 2000 onwards have been successful in reducing fishing mortality and increasing SSB and recruitment”.

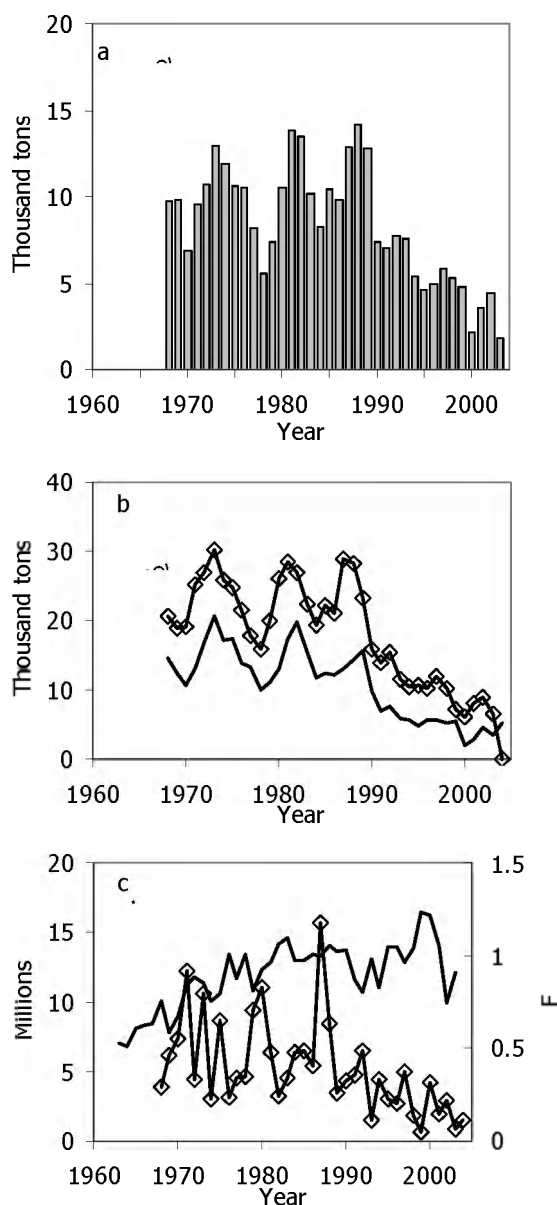


Figure 3.7.6. a: Landings; b: Total biomass (diamonds) and Spawning Stock Biomass (SSB); c: Recruitment at age 1 (diamonds) and Fishing Mortality (ICES, 2005).

Time-series of spawning-stock biomass and recruitment data

Trends in landings, fishing mortality, recruitment and spawning-stock biomass determined by XSA are shown in Figure 3.7.6.

Mis-reporting of cod landings in Area VIIa is known to have occurred since the 1990s due to restrictive catch quotas. Where it has been possible to estimate quantities mis-reported, these have been included in the stock assessment data, although there is still likely to be some underestimation where no information was available.

What is the geographical location of the stock and does it change seasonally?

A number of historical tagging programmes, together with data from surveys and commercial fisheries, were reviewed in 2000 as part of the development of the recovery plan for Irish Sea cod (Anon., 2000). Possible migration between the Irish Sea and surrounding areas was specifically addressed. It was concluded that cod that spawn in the western Irish Sea move predominantly southwards after spawning, and that their distribution extends into the St George's Channel and the Celtic Sea. Although movements in a north-south direction seem common, very few cod tagged to one side of the deep-water trough separating the eastern and western Irish Sea have been recaptured on the other side (Brander, 1975; Pawson, 1995) (Figure 3.7.5). A recent tagging programme run from 1997–2000, in which over 2200 cod were tagged using external and data storage tags showed that while there was some movement of cod between the Irish and Celtic Seas, the component of Irish Sea cod in the Celtic Sea was low (Connolly and Officer, 2001). Furthermore, few cod tagged in the Celtic Sea were recovered from the Irish Sea. High mortality levels in the Irish Sea have led to a reduction in abundance of cod in the 1990s, particularly the larger and older adults that may have a wider migration range. Together with a reduction in fishing effort in the St George's Channel, this may explain the relatively fewer tags returned from the Celtic Sea and St George's Channel in the recent study compared to the 1970s (Anon., 2000).

Extensive tagging off the west of Scotland between 1960 and 1978 produced only two recaptures in the Irish Sea of fish that had been tagged the previous year in the Firth of Clyde (Newton, 1999). For cod of the sizes tagged (mainly >50 cm), this indicated negligible interchange between the two areas.

Immature cod tagged by CEFAS (UK) in different areas of the Irish Sea in the 1960s and 1970s dispersed over a large area (Brander, 1975). Recaptures of 600 juveniles tagged in Belfast Lough were made in the same general area as well other parts of the Irish Sea, the Clyde and off northwest Ireland. Three of the fish were recaptured on the northwest Irish Sea spawning grounds when they would have been mature. Juvenile cod tagged in the NE Irish Sea and the Menai Straights (North Wales coast) tended to move southwards with recaptures extending into the Celtic Sea. Subsequent recaptures at maturity occurred on or near the northeast Irish Sea spawning grounds and off the Welsh Coast.

What is the depth range and temperature associated with the stock and does it change seasonally?

The Irish Sea is generally relatively shallow only becoming deeper than 50 m in restricted areas (see above). Results from data storage tags placed on four cod in the Irish Sea indicate however that the full depth range down to 154 m is utilised (Righton and Metcalfe, 2002). Irish Sea cod made continual depth changes throughout the

year in contrast to North Sea cod which were active only during the migration period. The minimum ambient temperature recorded was 7.9°C and the maximum 12.4°C. Based on inference from the hydrography of the region and the likely distribution of cod, the temperature range experienced may be around 6–8°C in the winter months to 11–13°C in the summer months, which is in accord with the above observations.

Time of spawning

Date of spawning and interannual variability or trend

Spawning begins in late January and is largely completed by the end of May (Fox *et al.*, 1997, 2000; Nichols *et al.*, 1993). According to Brander (1994), the peak of spawning probably occurs in early March in the western Irish Sea and late March in the northeast. More extensive surveys undertaken in 1995 showed that the peak of spawning occurred at the end of March – early April (Fox *et al.*, 2000). There is little information regarding interannual variability in the timing of spawning as egg surveys have not been conducted on a regular basis in this region.

Time of day when spawning occurs

Not known.

Timing of spawning in relation to planktonic production cycle

The timing and locations of spawning may be linked to the different production cycles in the eastern and western Irish Sea. In the western Irish Sea, the onset of primary production is earlier in the shallower waters close to the coast compared with in the deeper offshore waters, which must thermally stratify before a spring bloom can occur. Dickey-Collas *et al.* (1996, 1997) suggested that gadoid spawning in the west was constrained to the coastal region so that the hatching larvae could take advantage of the earlier food production in this region. In the eastern Irish Sea, which is shallower and more fully mixed, the spring bloom probably occurs a little later and is more widely spread. This may explain why cod spawning in the eastern Irish Sea appear to be more widely distributed. There are insufficient time-series of sampling of cod spawning or plankton in this region to fully investigate links between timing of spawning and the plankton production cycle and subsequent recruitment success.

Timing of spawning in relation to hydrographic events

The timing of spawning in the western and eastern Irish Sea may be related to the differing seasonal stratification patterns in the two areas (see above).

Timing of spawning in relation to other fish species spawning in the same location

The eggs and larvae of many other species have been recorded at the time when cod spawning is occurring (Fox *et al.*, 1997; Nichols *et al.*, 1993). The more abundant species include sprat (*Sprattus sprattus*), whiting (*Merlangius merlangus*), rocklings ('Onos' spp.) and gurnards (Triglidae), sandeels (Ammodytidae), gobies (Gobiidae), dragonets (Callionymidae), plaice (*Pleuronectes platessa*), dab (*Limanda limanda*) and sole (*Solea solea*). An approximate ordering of timing of peak spawning is given in Table 3.7.1.

Table 3.7.1. Approximate sequence of timing of peak spawning of various species in the Irish Sea based on data in Nichols *et al.* (1993) and Fox *et al.* (1997)

Species	Approximate peak spawning
Plaice (<i>P. platessa</i>)	March
Cod* (<i>G. morhua</i>)	late March – mid-April
Rocklings (Onos spp.)	early April
Whiting (<i>M. merlangus</i>)	larvae most abundant in mid-April
Sandeels (Ammodytidae)	April
Dragonets (Callionymidae)	April (but may also spawn beyond the end of the survey coverage)
Gurnards (Triglidae)	March, April and May depending on species
Dab (<i>L. limanda</i>)	April
Gobies (Gobiidae)	Late April – May (various species)
Sprat (<i>S. sprattus</i>)	mid-May
Sole (<i>S. solea</i>)	Late April – mid-May

*Strictly refers to 'cod-like' eggs as may contain haddock eggs and some whiting eggs.

Location of spawning

Geographic location and extent of spawning area

Several studies have produced maps of the spawning locations of cod in the Irish Sea (Nichols *et al.*, 1993; Fox *et al.*, 1997, 2000; Armstrong, 2002). However, these have been based on the assumption that the majority of eggs between 1.25 and 1.75 mm diameter and not possessing oil globules were those of cod. Eggs of other species, particularly haddock, overlap this size range and have a similar appearance (Figure 3.7.7). Although maps for the occurrence of late-stage cod eggs and cod larvae broadly match the assumed spawning locations, there is still concern that spawning area and duration may have been over-estimated because of egg misidentification. Currently, biochemical based methods for identifying gadoid eggs are being developed and applied to ichthyoplankton surveys in this region (Mork *et al.*, 1983; Taylor *et al.*, 2002; Armstrong, 2002).

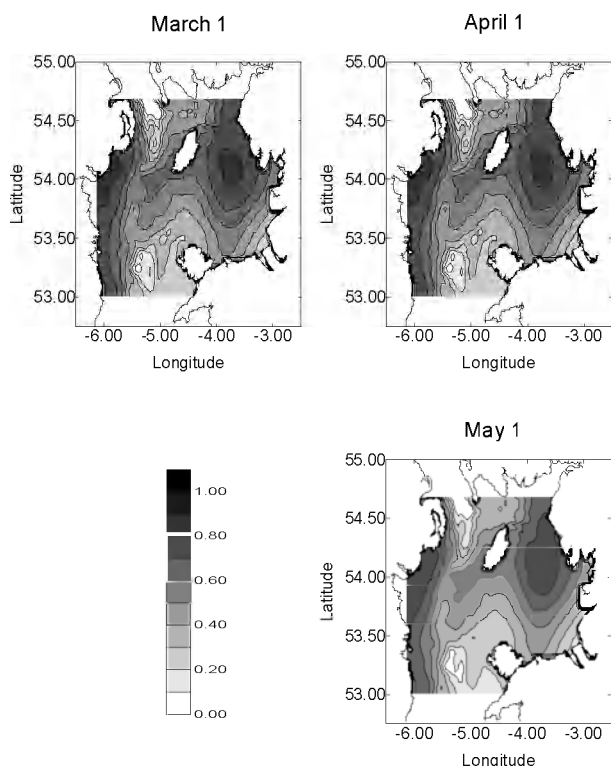


Figure 3.7.7. Probability of occurrence of stage IA 'cod-like' eggs in the Irish Sea modelled using generalised additive models from plankton survey data collected in 1995 (Fox *et al.*, 2000).

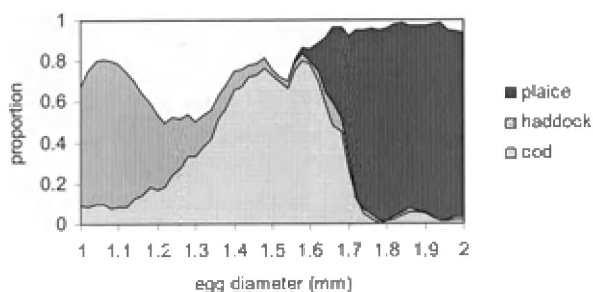


Figure 3.7.8. Proportions of eggs identified to species by isoelectric focusing against egg diameter from ichthyoplankton surveys in the Irish Sea in 2000 (Heffernan and Danilowicz, 2001; Armstrong, 2002).

Based on the above studies, and that of Brander (1975), spawning is concentrated in the western Irish Sea close to the coast between Carlingford Lough and Dublin, but also occurs in the eastern Irish Sea over a wider area. Estimation of the relative importance of the eastern and western spawning components is currently hindered by the inability to unambiguously identify cod, haddock and whiting eggs.

During the ichthyoplankton surveys conducted in 2000, supplementary sampling was conducted at water depths as shallow as 10 m (above chart datum) along two ex-

perimental transects off the North Wales and Northern Irish coasts. Cod-like eggs were most abundant off the western sides and very few were caught in water shallower than 20 m (Armstrong, 2002).

Does spawning regularly begin in one part of the spawning area and then move on to other parts?

The peak of spawning probably occurs earlier in the western Irish Sea and slightly later in the northeast (Brander, 1994). This pattern was not observed in the 1995 survey results although fitting a single GAM to the whole Irish Sea may have obscured this feature (Dickey-Collas *et al.*, 2003; Fox *et al.*, 2000).

Can the location be described in relation to hydrographic features?

In the western Irish Sea, spawning probably occurs before the development of a strong front related to the western Irish Sea gyre. Spawning in the eastern Irish Sea appears to be more widespread and it is not known if locations are related to specific hydrographic features such as haline fronts.

Can the location be described in relation to other species, including food organisms and predators?

In a general sense the location of spawning in the western Irish Sea may be related to spatial and temporal changes in the production of food organisms (Coombs *et al.*, 1994; Gowen *et al.*, 1995). In relation to gadoid larvae, this was presented as a general hypothesis by Dickey-Collas *et al.* (1996) and Dickey-Collas *et al.* (1997). A shift in distribution of late larval/juvenile gadoids from the coastal spawning areas to the offshore gyre region may be linked to an annual decline in abundance of zooplankton in the coastal region accompanied by increasing production over the stratified gyre. The decline in zooplankton in the coastal region may be caused (at least partially) by an increase in gelatinous predators as the season develops (M. Dickey-Collas, pers. comm.).

Specific data relating the occurrence of cod larvae/juveniles to food organisms and predators in the eastern Irish Sea are not available.

Can the location be described in relation to water mass circulation?

There is some evidence for the existence of a southward coastal flow along the east coast of Ireland. This may transport *Calanus finmarchicus* into the western Irish Sea. There is debate over whether *C. finmarchicus* breeds in the Irish Sea or whether the population is reliant on a seasonal influx (Gowen *et al.*, 1997). *C. finmarchicus* is known to be an important prey for cod larvae in other regions but whether there is any link between the abundance of *C. finmarchicus* and cod larval growth and survival in the Irish Sea is not known. The nauplii and copepodites of smaller copepod species may

form a more important component of the diet in this region (Thompson and Harrop, 1991).

In the western Irish Sea, the establishment thermal stratification overlying a cool-water pool leads to the creation of gyre-like flow patterns (Hill *et al.*, 1994a; Horsburgh *et al.*, 2000). This gyre circulation is usually well established by late May/June, a time when the cod larvae will be approaching metamorphosis. Based on shifts in the centres of abundance of the larval and juvenile stages, it is inferred that the gyre may play a role in small-scale transport processes in this region. However, this small-scale transport process has not been studied further.

Biological details

Fecundity

Fecundity of Irish Sea cod has been intensively studied using histological methods as part of the application of the Annual Egg Production Method to estimate spawning-stock biomass in 1995 and 2000 (Armstrong *et al.*, 2001; Armstrong, 2002). Fecundity-weight relationships were linear and parameters are given in Table 3.7.2. Spawning duration of individual cod in 1995 was around 40 d with low levels of atresia, mainly confined to spent fish towards the end of the spawning season. Estimated realised fecundity was 854 eggs g⁻¹ female⁻¹. Spawning duration of individual cod in 2000 was around 45 d. Levels of atresia were highest at the beginning of the spawning season (22% of samples, n=22) but then declined sharply. Over the whole spawning season, atresia resulted in an estimated loss of potential fecundity of only 2% resulting in a realised fecundity of 1046 eggs g⁻¹ female⁻¹.

Table 3.7.2. Parameter estimates for regression of potential fecundity (eggs female⁻¹) against gutted weight for female Irish Sea cod.

Year	Area	Wfs (g)	Slope	s.e. slope	Intercept	MS	N obs.
1995	Whole Irish Sea	4 367	961.9	50.52	-513 545	1.39x10 ¹²	84
2000	Western Irish Sea	3 540	1 068	57			63

Wfs=mean fish weight (gutted) in the regression in grams; MS= mean squared deviation from the regression.

Evidence for change in fecundity with time

The slopes of the relationships between fecundity and fish weight were significantly different in 1995 and 2000, possibly reflecting differences in fish condition. A longer time-series of data is not available.

Percentage mature-at-age

An analysis of proportions mature based on sampling in 1971 and 1972 were given by (Brander, 1975). There was evidence of differences in levels of maturity-at-age

with geographic area of capture. The current ICES assessment assumes that proportion mature-at-age is constant over the full time-series, and are as estimated from UK trawl surveys over the period 1992–1996. The Brander (1975) and current ICES values are given below:

	1-yr-old	2-yr-old	3-yr-old	4+ yr-old	source
Prop. mature	0.0	0.17	0.85	1.00	Brander, (1975)
	0.0	0.38	1.00	1.00	ICES, (2003)

Recent trends in maturity-at-age in Irish Sea cod have been investigated using samples collected during Northern Ireland groundfish surveys (NIGFS) carried out annually since March 1992 (Armstrong *et al.*, 2004). Maturity was defined by the presence of vitellogenic oocytes or production of milt. Proportion mature in the population was calculated from stratified mean estimates of abundance of mature and immature fish at each age. Almost all 1-year-old cod were immature, and all 3-year-olds mature. Proportions of 2-year-olds mature have increased over the sampling period (Table 3.7.3).

Table 3.7.3. Maturity of 2 year old Irish Sea cod as determined by (Armstrong *et al.*, 2004).

Year	Females	Males	Mean
1992	0.22	0.76	0.49
1993	0.48	0.81	0.65
1994	no data	0.93	-
1995	0.18	0.65	0.42
1996	0.38	0.88	0.63
1997	0.51	0.90	0.71
1998	0.42	0.81	0.62
1999	0.64	0.95	0.80
2000	0.79	0.98	0.89
2001	0.63	0.94	0.79
2002	0.47	0.91	0.69
Mean	0.47	0.87	0.67
SD	0.19	0.10	0.14

Sampling to determine the sex ratio in the Irish Sea cod stock has taken place during groundfish surveys as well as during the 1995 and 2000 Annual Egg Production Method (AEPM) exercises. Estimation of sex ratio during the spawning period is made difficult by skewed sex ratios for mature cod taken in trawl catches. (Armstrong *et al.*, 2004) showed that the mean proportion female (by number) in groundfish survey catches in March 1992–2002 declined from 0.48 at age 1 to 0.35 at age 2 and 0.28 at age 3, but increased again to 0.43 at ages 4 and above. They also recorded that on the spawning grounds males predominated in the bottom-trawl catches and the proportion of females was consistently higher in catches

by commercial midwater trawls. This suggested that males and females have different vertical migration behaviour on the spawning grounds. Non-random distribution in space of spawning male and female fish may also be related to lekking reproductive behaviour (Nordeide and Folstad, 2000). Using samples only from non-spawning areas, the proportion female in groundfish survey catches in March was not significantly different from the expected value of 0.5. Skewed sex ratios are also not apparent in groundfish survey catches in the Irish Sea in summer and autumn, at which time the proportion female by number is close to 0.5 in all size groups (Armstrong, 2002).

Sampling in the 1995 and 2000 AEPM surveys in the Irish Sea focused on estimating the proportion of spawning-stock biomass comprising females, as opposed to estimating numerical sex ratio at age. The population estimate for 1995 was 0.57 (CV=5%) and for 2000 was 0.46 (CV=11%), combining data from a variety of otter trawl and midwater trawl sampling exercises.

Data on fish size at 50% mature is not presented in the reports by Armstrong (2002) and Armstrong *et al.* (2001). Brander (1975) noted that proportion mature in Irish Sea cod was not a monotonic function of length. More detailed analysis of trawl survey data by Armstrong *et al.* (2004) showed that age was the predominant factor affecting maturity. Almost all 1-year-old cod were immature and all 3-year-olds mature, whilst the proportion mature at two years of age was independent of length over most of the length range at that age. The shape of the overall relationship between maturity and length is therefore a function of the age composition of the stock and is not a conservative feature. In a GLM analysis, age explained most of the variation in maturity in both males and females, followed by year, region and length (in that order) in males, and region, year and length in females (Armstrong *et al.*, 2004).

Comparing results in Brander (1975) with more recent results suggests that changes in proportions mature-at-age may have occurred over time, but given the pronounced effects of region and year on maturity within periods as short as a decade, it is difficult to evaluate the extent of any longer term changes without access to data on comparable space and time scales.

Egg size, specific gravity of eggs and larvae and changes in egg size with parental age or during the spawning season

According to Russell, cod eggs are in the size range 1.16 to 1.89 mm (Russell, 1976). Results from the application of iso-electric focusing during ichthyoplankton surveys in 2000 indicated that a proportion of eggs smaller than this limit were cod (Figure 3.7.8). Because of problems in reliably identifying cod eggs, analysis of changes in cod egg size through the spawning season have not yet been undertaken.

Although Conway *et al.* (1997) caught cod eggs and larvae during vertically resolved ichthyoplankton sampling in the Irish Sea, abundances were insufficient to allow analysis of depth distribution for this species.

Typical densities, i.e. number per m³ of eggs and larvae

Based on ichthyoplankton surveys in 1995, maximum density of stage I cod-like eggs recorded was 97 m⁻² of sea surface. Larvae were recorded at concentrations of up to 12 m⁻² sea surface (Fox *et al.*, 1997). In 2000, the maximum density of stage I cod-like eggs was 171 m⁻² of sea surface.

Incubation rate of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larva

Temperature dependent embryonic development rates have been examined using artificially fertilised eggs from cod broodstock of Irish Sea origin (Armstrong, 2002). Eggs from Irish Sea fish hatched earlier at a given temperature than predicted by the North Sea developmental model of Thompson and Riley (1981).

Larval development as a function of temperature

Not known.

Condition factor and nutritional status

No specific studies for this region published.

Egg and larval mortality rates

Egg mortality rates have been estimated by fitting exponential decay models to egg abundance estimates from the extensive egg surveys undertaken in 1995 and 2000 (Armstrong *et al.*, 2001; and Armstrong, 2002). Estimated mortalities were in the range of 0.21 to 0.36. However, in many cases the data indicated a relatively poor fit for a constant mortality model. It has been suggested that mortality may increase in later stages, possibly due to increased vulnerability to visual predators such as sprat and herring as embryonic pigmentation develops (Bunn *et al.*, 2000). It should be noted that egg mortality rate estimates might also be biased due to the current difficulty in unambiguously identifying early stage eggs of cod, haddock and whiting.

Results of studies into larval mortality rates have not been published from this region. Laboratory experiments indicate that the assumptions about daily deposition of otolith micro-increments for Irish Sea cod larvae are valid even under reduced growth rates, therefore such studies would be feasible (Geffen, 1995).

Time of first-feeding of larvae and food at first-feeding

The stomach contents of first-feeding larvae in the western Irish Sea were predominately copepod nauplii, with the occurrence of green-guts in some instances (Thompson and Harrop, 1991).

Food of larvae during development

Larval cod in the western Irish Sea were shown to feed almost exclusively on copepod nauplii and copepodites, the relative proportions shifting as larval size increased (Thompson and Harrop, 1991). Occasionally lamelli-branch larvae, gastropod larvae and cladocerans were found in larval gut contents.

Evidence of predation during the egg and larval stage

No specific studies in this region.

*Recruitment**Are there several spawning sites (sub-populations) which contribute to the same stock unit?*

As discussed in the section on stock and geographic distribution there may be separate reproductive stocks in the eastern and western Irish Sea (although genetic evidence is equivocal). There is also some north-south exchange of adult fish between the western Irish Sea and Celtic Sea. At present, the eastern and western Irish Sea cod are assessed as one unit with a separate assessment being made of the Celtic Sea. The relative contributions of recruitment from these different components are not known.

Earliest time in the life history when year-class strength can be predicted

The XSA stock assessment provides an index of recruitment as 0-group fish by back-calculation. Groundfish surveys in this region will begin to catch cod more reliably at age 1+. Over recent years a MIK net survey for pelagic juvenile cod has been run in the western Irish Sea but due to the poor state of the stock catches of pelagic 0-group fish have been low.

Hypotheses which have been put forward to account for year-to-year variability in year-class strength

Recruitment time-series are available from the XSA assessment, the estimates for recent years being driven heavily by survey indices (Figure 3.7.6). Statistical links have been drawn between interannual variability in Irish Sea cod recruitment and sea surface temperatures. Strong recruitments tend to be associated with years with colder winter sea temperatures (Planque and Fox, 1998). However, the mechanisms producing such patterns remain obscure.

Evidence for long-term trends in recruitment

Recruitment from 1968 to 1992 was variable but averaged around 8.2 million (at age 0) but since 1992 recruitment has declined to around half the previous value. This trend is likely related to the decline in spawning-stock biomass as well as possible environmental effects mentioned above. The period since 1992 has been characterised by the absence of very strong year classes, and the formation of some of the weakest year classes on record (e.g. 1992 and 1998). Trends in recruitment of cod in the different cod stocks around the British Isles show similarities in interannual variability, suggesting shelf-wide environmental effects on recruitment (Figure 3.7.9).

Evidence that variability in recruitment is linked to variability of other species in the same area; the same species in other areas or other species in other areas

A comparison of recruitment time-series derived from XSA suggests that recruitment of cod and whiting in this region may also be showing similar interannual patterns (Figure 3.7.9, Fox unpublished).

Evidence of inter- or intra-specific competition

Not known.

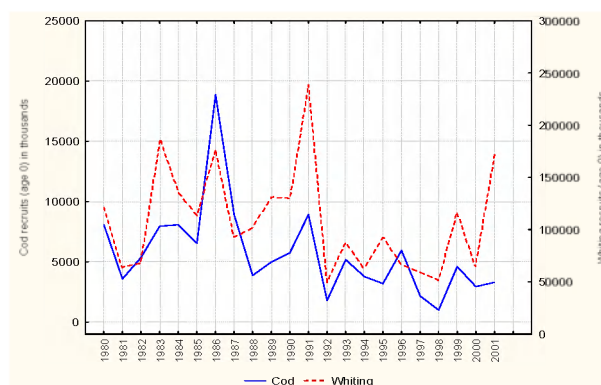
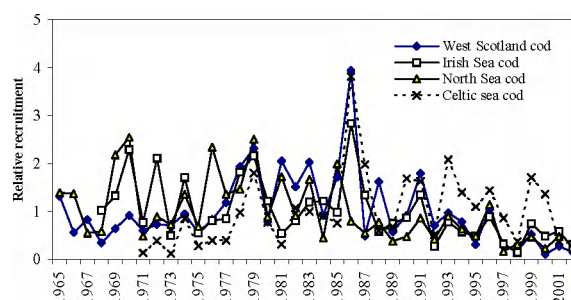


Figure 3.7.9. Time-series of recruitment. Upper panel shows several stocks relative to their long term mean. Lower panel shows cod and whiting in Area VIIa from XSA assessments (ICES, 2003).

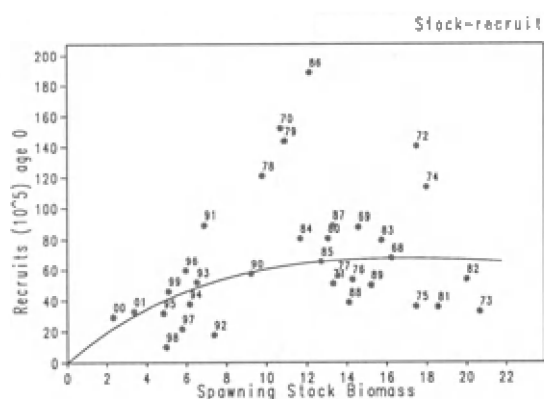


Figure 3.7.10. Stock recruit scatter for Irish Sea cod and fitted Ricker relationship (ICES, 2003).

Is recruitment related to SSB or any environmental factors?

Attempts have been made to fit a variety of stock-recruit curves to Irish Sea cod data but the variability in the data has precluded formal model selection (Figure 3.7.10). The Ricker S-R curve has been chosen on the *a priori* assumption that cannibalism in cod at high stock sizes would reduce recruitment (ICES, 2003). The estimated model parameters are given below:

$$\text{Recruitment} = a \times \text{SSB} \times \exp(-b \times \text{SSB})$$

$$a = 1.0941 \text{ and } b = 0.0595$$

The influence of environmental factors is discussed under biological details.

Survey and VPA estimates of abundance of Irish Sea cod were included in a meta-analysis examining the occurrence of juvenile density-dependent mortality in marine demersal fish (Myers and Cadigan, 1993).

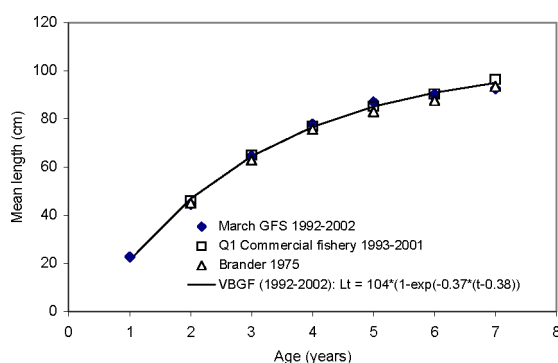


Figure 3.7.11. Mean length-at-age in Irish Sea cod: Data from Northern Ireland groundfish surveys (March 1992–2002) and quarter 1 commercial landings (1993–2001) (Armstrong *et al.*, 2004), plus Von Bertalanffy growth curve fitted to these data. Also shown are mean lengths from UK commercial fishery sampling in the 1970s (Brander, 1975).

Adults

What are the general growth characteristics? Have they changed over time?

Time-series of weights-at-age have shown fluctuations of up to 20% of the mean for each age group but without any obvious trend over time (ICES, 2003). Mean-lengths-at ages two and older in trawl surveys from March 1992 – 2002 were very similar to the estimates from first-quarter commercial landings samples in the same period, but one to two cm longer at age than given by Brander (1975) from sampling of the fishery in the 1970s (Armstrong *et al.*, 2004; (Figure 3.7.11)). Based on the combined survey and commercial catch data from 1992 onwards given in (Armstrong *et al.*, 2004), the lengths-at-age are described by the following Von Bertalanffy growth parameters:

Asymptotic length:	104 cm
K:	0.37
t ₀ :	0.38 years

Interannual changes in growth since the 1990s are discussed in the following section.

Evidence for density-dependent growth

Survey data since the 1990s show clear and consistent variations in length-at-age between year classes of Irish Sea cod (Figure 3.7.12). These have occurred against a backdrop of increasing sea surface temperature and the formation of some of the weakest year classes on record (Armstrong *et al.*, 2004). The data series are too short to disentangle the potentially linked effects of year-class strength, growth rate and temperature. Annual growth increments from ages one to two and two to three have been positively correlated with mean sea surface temperature (SST), whilst the fastest observed growth was for fish of the 1998 year class which was extremely weak but was also formed during a year with the warmest SST in the 1990s.

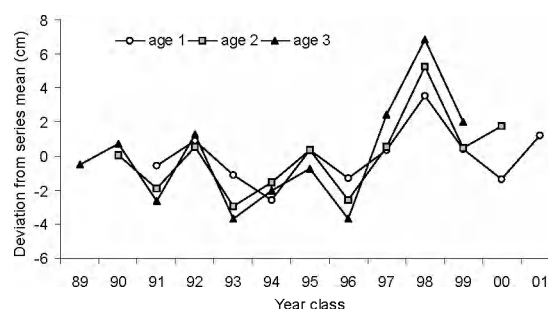


Figure 3.7.12. Deviations in mean length-at-age of Irish Sea cod from the mean values given in Figure 3.7.11, by year class and age. Data from 1992–2002 Northern Ireland groundfish surveys (Armstrong *et al.*, 2004).

Evidence of temperature-dependent growth

See above.

Feeding and predator-prey relationships of adults

General studies on the diet of cod in the Irish Sea have been reported by Nagabhushanam (1965), Armstrong (1982), Patterson (1983) and Symonds and Elson (1983) and more recently by Newton (2000). The study by Newton is the most comprehensive in terms of spatial coverage, using samples from groundfish surveys in the 1990s. Because the western Irish Sea *Nephrops* fishery is economically valuable, other studies have concentrated specifically on the impact of cod on *Nephrops* (Hillis and Fannon, 1981; Boyd, 1983; Armstrong *et al.*, 1991). Several models for cod-*Nephrops* interactions have been developed principally with the aim of providing management advice on relative fishing effort on these two species (Brander, 1983; Bennett and Lawler, 1994).

All studies have shown the diet of Irish Sea cod to be dominated by various species of epibenthic and burrowing crustacea including *Nephrops*, and various species of fish (Table 3.7.4, adapted from Armstrong *et al.* (1991)). The composition of the diet varies spatially in the Irish Sea, and cod appear to be opportunistic. The main commercial species eaten by cod include *Nephrops* and whiting, which together formed 43% of the stomach contents of cod sampled throughout the northern Irish Sea during spring, summer, and autumn 1994 and 1995 (Newton, 2000). The latter study showed a much lower contribution of crustacea to the weight of stomach contents (47%) than recorded in the more localized studies from the 1960s to the 1980s (mostly >70%; Table 3.7.4). Newton (Newton, 2000) considered this to reflect the abundance of juvenile whiting, which made up 29% of the stomach contents on average. Pelagic species such as herring have been relatively uncommon in cod stomachs in the Irish Sea.

Table 3.7.4. Percentage composition (by weight) of the stomach contents of cod caught in the Irish Sea, as reported by different authors. Data from all length classes and months of capture are lumped in each case. NB: (Nagabhushanam, 1965); SE: (Symonds, and Elson, 1983); AR(82): (Armstrong, 1982), AR(91): (Armstrong *et al.*, 1991) and (Boyd, 1983), FH: (Fannon and Hillis, 1982), KP: (Patterson, 1983) NE: (Newton, 2000). All studies are in the western Irish Sea with exception of Newton (2000) which covers the whole northern Irish Sea.

	% composition by weight						
	NB	SE	AR(82)	AR(91)	FH	KP	NE
<i>Nephrops</i>	30	58	60	30	16	20	14
Other crustacea	41	24	18	27 incl above	55	53	33
Other items	12	1	4		7	17	6
Fish (all spp)	16	16	17		22	6	47
Whiting	No data	5	1	10	9	No data	29

Armstrong (1982) showed a linear relationship between the log of fish length and the log of mean fresh weight of items in the diet of cod sampled off the southwest of the Isle of Man. His estimates of daily rations calculated using data on digestion rates given by Jones (1974) indicated a daily food intake of around 1.0% – 1.5% of wet body weight for a diet comprising roughly one third fish and two thirds crustacea. A similar study carried out closer inshore to the Isle of Man by Patterson (1983), gave daily rates of food intake that were 30–50% less than those estimated by Armstrong (1982) although the diet was principally crustacea which digest more slowly than fish.

As cod are known to undergo regular vertical migrations in the Irish Sea (Righton *et al.*, 2001), the use of bottom trawls may give biased data on diet. Armstrong *et al.* (1991) showed a greater incidence of Norway pout, sprat and herring in the stomachs of cod taken using large commercial midwater trawls compared with samples collected from otter trawls in the same areas. A high proportion of the stomach contents comprised *Nephrops* irrespective of where the cod were caught in the water column. This possibly reflects the slow digestion rate of the large crustacea consumed when the cod were on the seabed. A recent study employing electronic data storage tags demonstrated differences in the summer foraging behaviour of individual cod in the Irish and North Seas. Such differences may be related to the energetic costs of foraging in both areas (Righton and Metcalfe, 2002; Righton *et al.*, 2001).

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3.8 North Sea (ICES Divisions IVa-c and VIIId)

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Environment

The North Sea is a relatively shallow basin, ranging in depth from 30–200 m. It is shallowest in the southern North Sea and gradually deepens towards the Atlantic Ocean and the edge of the continental shelf to the north (Figure 3.8.1). The Norwegian Trench, which has a sill depth (saddle point) of 270 m off the west coast of Norway and a maximum depth of 700 m in the Skagerrak, plays a major role in steering large inflows of Atlantic water into the North Sea. The surface area of the North Sea is 575 300 km² including the Skagerrak, its volume 42 294 km³ (ICES, 1983). The North Sea is influenced by the Atlantic, mainly by input from the northern North Sea and to a lesser extent via the Channel. To the north-west of the British Isles a strong Atlantic current flows north along the edge of the continental shelf. Via different currents Atlantic water enters the northern North Sea (see e.g. Svendsen and Sætre (1988). One of these currents enters the Norwegian Deeps (Booth and Meldrum, 1987).

The North Sea can be divided into seven geographical boxes (Figure 3.8.2), for which hydrographic and biological conditions vary spatially (ICES, 1983). Strong seasonal differences in the vertical structure of the water column also exist. Most areas are vertically mixed or only slightly stratified throughout the winter. From spring to autumn, however, the North Sea is divided into areas which remain mixed and others which become stratified. In large parts of the central and northern North Sea a strong seasonal thermocline develops by May–June which deepens throughout the summer, breaking down by November. The boundaries between these different regimes may be characterised by large gradients in temperature and/or salinity (Reid *et al.*, 1988). The density contrasts (fronts) between these areas generate strong along-frontal circulations (order 15 km/day), inhibit cross frontal movement and support high levels of primary and secondary production. In the central and southern North Sea fronts are near bed with temperature contrasts of typically 8°C over a horizontal distance of 10 km. The locations of these fronts are stable, being determined by the strength of the tides and gradient of bathymetry. In the case of the Dogger Bank, they represent a site where primary production is guaranteed.



Figure 3.8.1. Depth contours (in metres) of the North Sea.

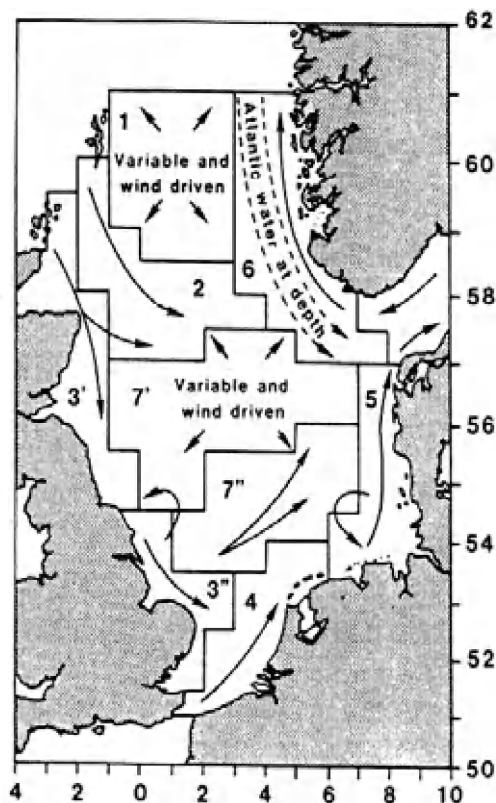


Figure 3.8.2. Hydrographic subdivisions of the North Sea (after Anon., 1983).

A recent major review and synthesis of physical and biological processes of many aspects of the North Sea ecosystem has been carried out as a part of the German Federal Ministry funded project called: "Synthesis and New Conception for North Sea Research" (SYKON). The project reports are available on the website: <http://www.rz.uni-hamburg.de/SYKON>. Another general overview of the physical and biological characteristics of the North Sea is available from OSPAR (2000).

Stock and geographic distribution

Evidence for stock discreteness

The North Sea cod stock does not necessarily comprise one distinct population. ICES (1994, citing Jamieson and Birley, 1989) concluded that, although North Sea cod is not one homogeneous stock, sub-stocks with clear boundaries could not be discriminated on the basis of genetic studies. More recent analysis using microsatellites has however detected some sub-stock structure within North Sea cod. Hutchinson *et al.* (2001) have identified several genetically distinct populations within the southern and northern North Sea at Bergen Bank, Moray Firth, Flamborough Head and the Southern Bight. These populations appear to form units that are reproductively isolated from each other and which are, presumably, spatially distinct at least during the spawning season.

Assessment units, fishery and management

For management purposes, ICES currently defines the North Sea cod stock as cod in three separate areas: Divisions IIIa (Skagerrak), VIIId (English Channel) and Sub-Area IV (southern and northern North Sea). The basis for treating these as one 'management unit' is conventional tagging data, which have demonstrated intermingling of cod between these three areas but little intermingling of cod between the North Sea and other areas such as West of Scotland.

The assessment has grouped the cod stock in the Skagerrak (Division IIIa), the North Sea (Subarea IV), and the eastern Channel (Division VIIId) since 1996. Prior to 1996 cod in these areas were assessed as separate stocks. Since 1971 the spawning-stock size has declined and averaged around 43 000 tonnes since 2000, which is well below what is considered a safe biological limit (B_{pa}) of approximately 150 000 t (ICES, 2003b). The SSB has been in the region of B_{lim} (70 000 t) or below for a number of years. Furthermore, F has been at or above F_{lim} (0.86) for nearly 30 years. Over the past decade, approximately 99% of the stock in number consists of fish aged 1–4 and approximately 90% of the spawning-stock in number has comprised 1 to 3 year old cod (ICES, 2003b).

Historic landings data collected by ICES showed that landings fluctuated between about 60 000 t. and 160 000 t. with a marked fall during the two war periods (Daan *et al.* 1994; Pope, and Macer, 1996). Landings

peaked immediately after each war. In the 1960s there was a remarkable increase and a peak of about 340 000 t was reached in 1972. A recent assessment (ICES, 2005), which includes an estimate of discarded fish shows catches peaking at over 550 000 t in 1980 (Figure 3.8.3a). There have been wide fluctuations subsequently, but since 1981 landings have steadily decreased and have almost reached the same level as before 1960. Whether the reasons for lower landings were in fact due to lower cod abundance or are also a result of increased effort from the 1960s onward or other factors (Beaugrand *et al.*, 2003; Brander and Mohn, 2004) is not entirely clear. However, it has been hypothesised that one of the main reasons Dutch fishermen sailed to Iceland to fish for cod (Beaujon, 1885) from the end of the 16th until the end of the 19th century may have been because cod was not an abundant species in the North Sea historically.

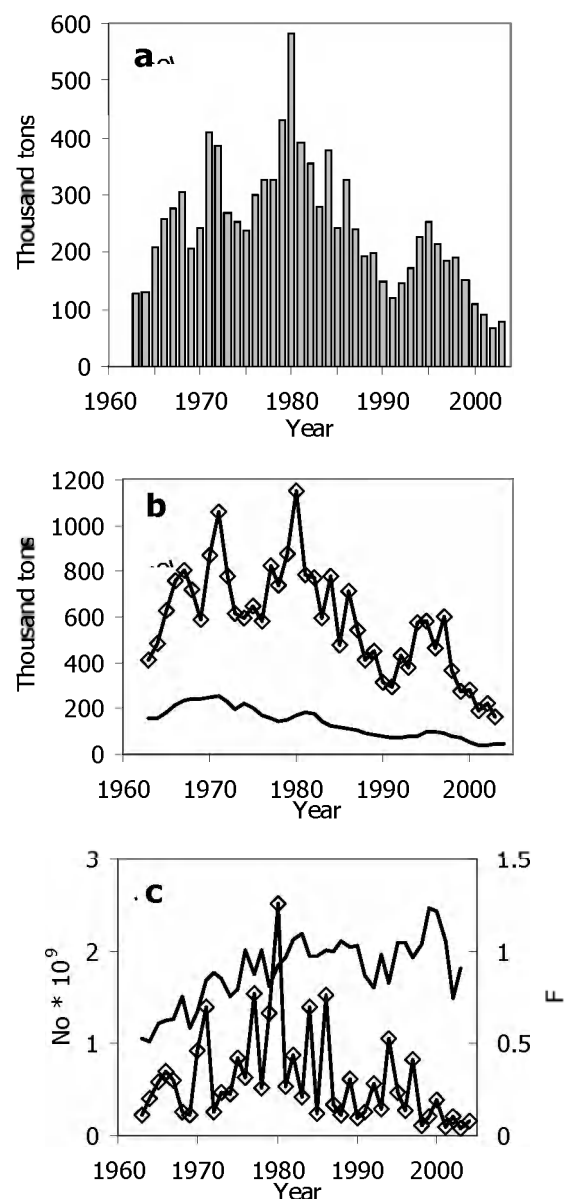


Figure 3.8.3. a: Landings; b: Total biomass (diamonds) and Spawning-Stock Biomass (SSB); c: Recruitment at age 1 (diamonds) and Fishing Mortality (ICES, 2005).

Average estimated fishing mortality (based on ages 2–8 from VPA) has apparently increased at a rate of just over 0.1 per decade since the VPA time-series started in 1963.

Time-series of spawning-stock biomass and recruitment data

The recruitment time-series (VPA, based on age 1, Figure 3.8.3c) for North Sea cod exhibits large fluctuations, with the occurrence of several very large year classes from 1963 until the late 1980s. Since the most recent large year class in 1996, recruitment has been weak. Estimates from Virtual Population Analysis (VPA) of the size of the spawning-stock are available since 1963 (Figure 3.8.3b). Spawning-stock biomass increased steadily up to 1971 when a maximum of approximately 277 000 t was reached.

Geographical location of the stock

Analysis of data from the International Young Fish Survey in February over the period 1972–1992 showed that cod had a widespread distribution throughout the North Sea (Brander, 1994). In comparison, more recent data covering the three periods (1971–1981, 1982–1992, and 1993–2002) suggest a decline in the importance of the German Bight for age 1 and 2 cod (Figure 3.8.4). Age 1 and 2 fish now appear to occur predominantly in the north-eastern North Sea (north of the 50 m contour line from Flamborough Head to the Jutland Bank) although cod still occur in the Southern Bight. Relatively few fish of 4 years and older were caught in the surveys reflecting high fishing pressure on this stock during the period considered. In addition, maps produced on an annual basis show large interannual variability reflecting changes in year-class strength (CEFAS, Lowestoft, UK, http://www.cefass.co.uk/fishinfo/cod_summary.htm).

On the basis of extensive tagging data, reviewed by the ICES North Sea Roundfish Working Group (ICES, 1970 and ICES, 1971), it was concluded that cod do not disperse uniformly throughout the North Sea, but remain more or less within one region. As an approximation the following regional grouping was suggested:

- the Norwegian side of the Skagerrak,
- the Danish side of the Skagerrak,
- one or possibly several coastal regions, from Flamborough to the Scottish east and north coasts,
- the central North Sea,
- the Southern Bight, from the Straits of Dover to latitude 54°N, the English Channel, south and west of the Straits of Dover.

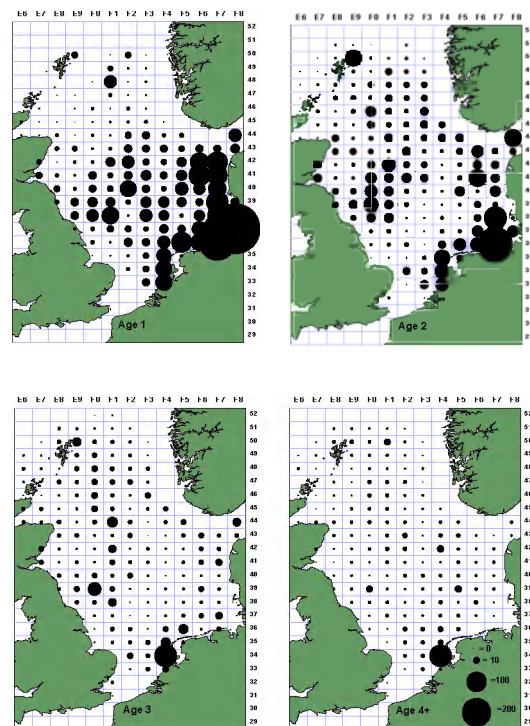


Figure 3.8.4. Numbers of 1, 2, 3 and 4+ cod (caught per hour) by rectangle in the North Sea 1971–1981. Data from 1st Quarter IBTS.

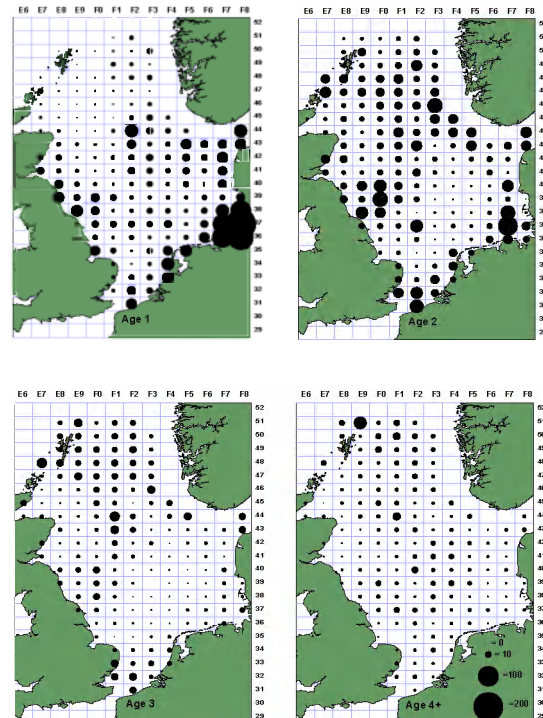


Figure 3.8.4 Continued. 1982–1992.

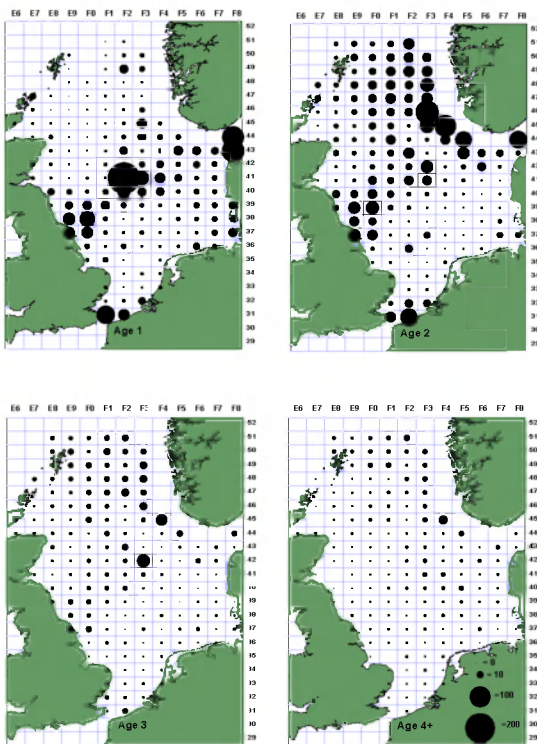


Figure 3.8.4 Continued. 1993–2002.

Evidence of migration

The relationship between cod in discrete areas within the North Sea is not entirely clear, with intermingling of cod between some regions and a degree of genetic isolation of at least a few distinct populations. Migration of adult cod is restricted to limited areas; they generally do not disperse throughout the North Sea (ICES, 1970 and ICES, 1971). The distance between summer feeding grounds and winter spawning grounds usually varies between 20 and 120 miles but cod tagged in the North Sea have migrated for up to 200 miles from the release site. In general, cod in the North Sea undertake southward migrations to spawn and migrate northward post-spawning to feeding grounds. Results from tagging studies suggest that while some cod populations in the North Sea are relatively resident, remaining within a confined region from one spawning season to the next, others may undertake long-distance migrations, most likely between feeding areas and spawning localities. However, there is much variation between individuals within spawning populations. A large-scale research programme is currently being conducted on cod behaviour and migration in the northeast Atlantic using electronic data storage tags (CODYSSEY, <http://www.codyssey.co.uk/>). Results from tag recaptures over the next two years should provide a greater understanding of the patterns of migration within the North Sea and the extent of individual variation within populations and sub-stocks.

Depth and temperature range

Heessen and Daan (1994) analysed survey data on the distribution of individual age groups of cod in the North Sea. There were marked annual differences in the ambi-

ent temperature, but no indication that these differences are related to a certain preferred temperature, 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.

Righton and Metcalfe (2002) analysed the depth and temperature records of 32 cod electronically tagged in the North Sea in 1999. Their analyses showed that the mean temperature experienced by the fish while at liberty (a period between 85 and 475 days) was $10.7 \pm 0.42^\circ\text{C}$, with a maximum of 18.35°C and a minimum of 5.1°C . Turner Welsby *et al.* (2003) reported from analyses of data storage tag records that cod in the southern North Sea ($6.4\text{--}16.2^\circ\text{C}$) experience a much wider mean temperature range than cod in the northern North Sea ($7.0\text{--}12.9^\circ\text{C}$) throughout the year. Cod in the southern North Sea also experience higher mean temperatures on average, particularly during the summer months (16.0°C compared to 12.7°C). The daily mean temperature experienced by cod in the southern North Sea is more consistent throughout the year and does not show the same cyclical seasonal pattern experienced by cod in the northern North Sea.

Righton and Metcalfe (2002) reported that cod at liberty in the North Sea between March 1999 and October 2000 reached an average mean depth of 26.41 ± 1.27 m. The maximum depth reached was 84.3 m. Mean depth varied on a monthly basis throughout the year. These cod were tagged and released in the southern North Sea. Cod north of 59°N in the North Sea have been observed in deeper waters (David Righton, CEFAS, pers. comm). There are several deep (140 m) troughs known in the area around Shetland where cod are caught. North Sea cod are likely to experience the greatest depth range in the Norwegian deeps, which reach 600 m in places. To date, there are no electronic tagging data from cod in this region.

Spawning

Timing of spawning

Although some autumn spawning has been recorded from the northern North Sea (in the period between 1900 and 1930), the majority of spawning takes place from the beginning of January through to April (Brander, 1994). In the Southern Bight, peak spawning occurs in February but in the southern North Sea varies from the last week of January to mid-February (Daan *et al.*, 1980; Heessen and Rijnsdorp, 1989). For example, peak spawning of cod occurs in the eastern English Channel in mid-February (Brander, 1994; Pawson, 1995) but is thought to occur slightly earlier, in January, on the French side of the eastern English Channel (Pawson, 1995). In more northerly regions maximum spawning activity occurs later in the year. In the west-central North Sea and German Bight peak spawning occurs in late February–March (Brander, 1994). In the northern North Sea, Raitt (1967) recorded that eggs were abundant in April, but by May the occurrence of cod eggs and larvae was much reduced.

Mean dates of spawning ($\pm$ standard deviation) from results reported in Brander (1994) are shown in Figure 3.8.5.

Time of day when spawning occurs.

The time of day when spawning occurs is unknown for North Sea cod.

Timing of spawning season in relation to planktonic production cycle

Cod spawn at the southern edge of the Dogger Bank in late February-March and cod larvae remain within this area as the season progresses (Brander, 1994). The region is characterised by a strong seasonal thermocline that develops towards the end of spring (May-June) and deepens as the summer progresses. The thermal front supports high levels of primary and secondary production, providing a favourable food resource for developing larvae. Similarly, spawning in the English Channel

occurs mainly in February (Brander, 1994), where production occurs much earlier than in other areas at the same latitude (Pingree *et al.* 1986).

Timing of spawning season in relation to hydrographic events

Spawning occurs offshore in waters of salinity 34–35 (Riley and Parnell, 1984). In the more northern areas spawning may be associated with subterranean banks on which the spawning fish may aggregate. Little appears to be known about the spawning behaviour of North Sea cod. In the Southern Bight, the abundance of early stage cod eggs has been reported to be significantly correlated with water transparency, with few cod eggs found in waters of lower than 50% transparency (Brander, 1994). Cod spawning in Southern Bight during this period (1967–1968) was also concentrated in areas of higher than average salinity. As discussed above (under “timing of spawning season in relation to planktonic production cycle”) there is some evidence of the timing of spawning occurring just prior to the development of thermal stratification in the central North Sea.

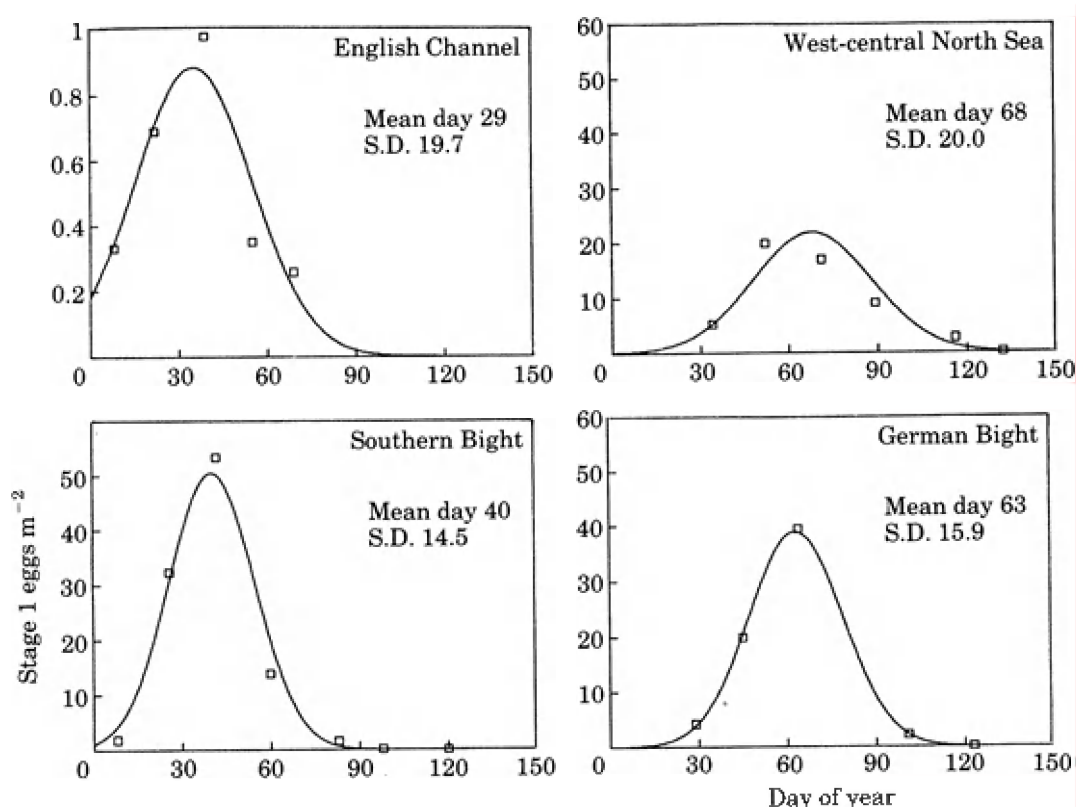


Figure 3.8.5. Abundance of stage I cod eggs and fitted normal distributions with mean dates of spawning and standard deviations. For the English Channel cod eggs of all stages are amalgamated because abundance of stage I eggs was too low to give an estimate (Brander, 1994b).

Timing of spawning season in relation to other fish species that spawn in the same location

Cod and haddock are known to spawn in the same areas during similar periods in the northern North Sea (Heath *et al.*, 1994). In parts of the central and southern North Sea cod and plaice spawning areas appear to overlap both spatially and temporally (Harding and Nichols, 1987; ICES, 1994; Simpson, 1959; Harding *et al.* 1978; Cushing, 1990). Egg and larvae distributions of several other fish species (including plaice, dab, whiting and sandeel) overlap spatially and temporally with those of cod in the North Sea (Harding, and Nichols, 1987; Munk *et al.*, 2002).

Location of spawning

Geographic location and extent of spawning area

Several attempts have been made to define the spawning areas of cod in the North Sea (Daan, 1978; Brander, 1994). No fully comprehensive ichthyoplankton surveys have ever been conducted in this region, and knowledge of spawning areas has been based upon compilations of existing small-scale survey data and distributions of maturing adults (fisheries surveys and commercial catches). Daan (1978) showed spawning areas based on a compilation of surveys from 1945. Large parts of the North Sea were not surveyed during that period but have been since then (ICES, 2003a). Based on surveys conducted by Harding and Nichols (1987) mainly directed towards plaice, cod spawning occurs off the NE coast of England. Ichthyoplankton surveys around the coast of Scotland have been undertaken by Saville (1959) in the 1950s. The Saville surveys were principally concerned with haddock, but Raitt (1967) re-analysed the data and presented maps for cod. Since they were unable to distinguish cod and haddock eggs the results are based upon the occurrence of late-stage eggs. The 1950s surveys in March showed some cod eggs off Butt of Lewis, west of Orkney and Shetland and off the Moray Firth and east Scottish coast. In 1992 the area was re-surveyed by Heath *et al.* (1994). It should be noted that based upon the proportions of late-stage eggs and larvae, the majority of the eggs sampled by Heath appeared to be those of haddock. Application of biochemical methods for identifying gadoid eggs should overcome this problem in future surveys (Mork *et al.*, 1983; Heffernan and Danilowicz, 2001; Taylor *et al.*, 2001). Since spawning occurs off the north and north-west coasts of Scotland it is likely that a proportion of the eggs and larvae are transported into the northern North Sea (Heath and Gallego, 1998). It might be expected that this one-way drift of eggs and larvae into the North Sea would be counterbalanced by a return migration of adolescent or mature fish to the westerly spawning grounds (Daan *et al.*, 1990). Spawning is also known to occur in the Norwegian Deep off the coast of Norway but ichthyoplankton survey results are lacking for this area. In the southern North Sea there is an interchange of spawning fish and spawning products (Daan *et al.*, 1990). Conventional tagging studies suggest that a proportion of immature

cod migrate from the eastern English Channel to the North Sea and, once mature, return to the Channel to spawn. Tag recaptures of 30–49 cm cod in the area have shown a general eastward migration into the southern North Sea (Trevor Boon, CEFAS, pers. comm.) The eastern Channel population is thus considered as part of the North Sea cod stock. Ichthyoplankton surveys of the southern part of the North Sea have been more frequent and much of the work was directed towards plaice (see Harding and Talbot, 1973; Harding *et al.*, 1974; Daan, 1981; Van der Land *et al.*, 1990). A survey during March 1997 covering the central and southern North Sea compared distributions of cod, plaice and lesser sandeel with hydrographic conditions, specifically frontal systems (Munk, 1997). In the southern North Sea cod are known to spawn in the German Bight, the Southern Bight, Dogger Bank and the English Channel. The latter are considered to be the most southerly cod spawning grounds in the Northeast Atlantic.

Comprehensive, internationally coordinated, ichthyoplankton surveys of the spawning areas for cod and plaice in the North Sea are to take place during 2004 (ICES, 2003a).

Does spawning in one region regularly precede other regions?

Peak spawning consistently occurs earlier in the southern North Sea than in the northern North Sea. Brander (1994) reanalysed data collected by Harding and Nichols (1987) and showed that the earliest spawning of cod in 1976 in the west-central North Sea took place in late January to early February along the southern edge of the Dogger Bank and spread NW-SE from the Dogger Bank from late February until the end of April. Cod in the English Channel spawned inshore in January and moved offshore later in the season in February (Brander, 1994). The spatial distribution of spawning throughout the season for spawning within the North Sea is otherwise unreported, due to the lack of comprehensive ichthyoplankton surveys in the region.

Is location of spawning related to specific hydrographic features?

The location of spawning can be related to the formation of frontal systems in the North Sea (Munk *et al.*, 1995; Nielsen and Munk, 1998; Munk *et al.*, 2002). These areas are characterised by salinity gradients in the winter and intense thermal stratification from late spring to summer. Cod spawn in early spring and the larvae are subsequently entrained within stratified regions during the summer where they feed. Little is known about the vertical distribution of cod in the water column during spawning in the North Sea. Survey results from the west central North Sea in 1976 show that vertical distribution of cod larvae is similar to that of plaice, and whiting larvae, with peak densities occurring at approximately 20 m in winter/early spring (February) and at approximately 25–30 m (below the thermocline) in late spring (May)

when they were at a later stage of development (Harding and Nichols, 1987).

Can location be described in relation to other species, including food organisms and predators?

The timing and location of cod spawning in the North Sea can be related to the onset of primary production in a general sense (see section on time of spawning). Specific data on the co-occurrence of predators and cod early life stages are not well understood although Harding and Nichols (1987) present some data on the predators and prey of fish larvae for several species including cod.

Can location be described in relation to water mass circulation?

There is some evidence from 1967 and 1968 survey data (Brander, 1994) that the location of cod spawning in the Southern Bight is related to water mass circulation. Eggs were concentrated in a specific area offshore, from which the larvae were subsequently advected in a NNE direction.

Biological details

Fecundity

Fecundity data exist for prior to 1891: (Fulton, 1891), 1969: (Schopka and Hempel, 1973), 1970–1972: (Oosthuizen and Daan, 1974) and 1987–1988: (Heessen, unpublished, reported in Rijnsdorp *et al.*, 1991).

Evidence of changes in fecundity with time.

The relative fecundity appeared to be higher in the late 1980s (by approximately 20%) compared to the early 1970s (Rijnsdorp *et al.*, 1991). This increase coincided with a marked decrease in the spawning-stock from 265 000 t to about 90 000 t. Current and near-future data collection has been planned as part of an EU funded project called 'Reproductive and stock evaluation for recovery' (RASER, <http://raser.imr.no/index.php>).

Percentage mature-at-age

Age and size of maturity of North Sea cod has been reported in several studies at various periods throughout the stock's history. In general, North Sea cod become mature in their second year of life, but it is not before they are 6 years old that they are all mature (Oosthuizen and Daan, 1974; Rijnsdorp *et al.*, 1991). A historical comparison of the changes of length-maturity ogives is given in Oosthuizen and Daan (1974) from the 1890s (Holt, 1893), the 1920s (Graham, 1924) and the 1970s. The comparison demonstrated a shift in length at maturity (L_{50}) from approximately 75 cm to just above 50 cm over this period. However, this difference could be explained by geographical differences in the origin of the samples and analyses have demonstrated that age and size and maturity varies a great deal in both time and

space in the North Sea (Rochet, 2000). The data given in ICES (1994) indicated that the values of L_{50} obtained for both of the earlier periods fall within the range of inter-annual differences in L_{50} observed between 1980 and 1989. Therefore there appears to be a large degree of variation from year-to-year and spatially. There is a tendency for cod in the southern North Sea to become mature at a slightly younger age than those in the northern North Sea (ICES, 1994). This could be influenced by patterns and processes that affect growth (Cook *et al.*, 1999; Rochet, 2000). Although cod maturity data from the IBTS for 1980–1995 are also given in Cook *et al.* (1999) for males and females combined, both recent and historical data show that males mature at a slightly younger age and at a smaller size than females. Maturity ogives separated by sex are reported in Rijnsdorp *et al.* (1991) for the 1985–1989 period.

Egg size, specific gravity of eggs and larvae and changes in egg size with parental age or during the spawning season

Russell (1976) described the cod egg as 1.16–1.89 mm in diameter, but noted that Ehrenbaum (1905) recorded the size of cod eggs in the North Sea as between 1.16 and 1.60 mm in diameter. There is a lack of more recent data on cod egg size distributions from the North Sea owing to the absence of dedicated plankton surveys in the region.

Typical densities, i.e. number per m² of eggs and larvae

Densities (number per m²) of stage 1 eggs at peak spawning are shown in Figure 3.8.5 (taken from Brander, 1994). Maximum densities ranged from approximately 1 eggs m⁻² in the eastern Channel (in 1971), 20 eggs m⁻² in the west central North Sea (in 1976), 40 in the German Bight to 50 in the Southern Bight (both in 1967 and 1968).

Maximum densities of cod larvae reported from a survey carried out in the central and southern North Sea during March of 1997 was 4 larvae m⁻².

Incubation rate of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larvae

Embryonic development is described for the temperature range of 1.7 to 11.6°C (Thompson and Riley, 1981). Abnormal development was observed at temperatures above 12°C and below 1.5°C; death occurred in the early stages of cleavage (Thompson and Riley, 1981). The time from fertilisation to hatching is approx. 8.5 days at 13°C and 27 days at 2°C (Thompson and Riley, 1981). Russell (1976) documented the size of cod larvae at hatching as 4.0 mm in length. Thompson and Riley (1981) describe the yolk sac as extending beyond the fin margin when complete in the first larval stages. The yolk is fully absorbed at lengths of 4.5–5.1 mm (Ehrenbaum, 1905 in Russell, 1976).

Larval development rate as a function of temperature.

Laboratory experiments by Thompson, and Riley (1981) suggest that cod larvae take 6 days to reach the end of the yolk sac stage when reared at a temperature of 6.5°C

Condition factor and nutritional status

St John and Lund (1996) reported that North Sea juvenile cod using a diatom-based food web (found in proximity to regions of frontal mixing) were in significantly better condition than juvenile cod utilising a flagellate-based food web (found in stratified regions of the North Sea).

Adult condition is thought to vary from year to year although individual body weights have not strictly been collected on an annual basis. The limited data that have been collected suggest that interannual fluctuations do occur (ICES, 2002).

Egg and larval mortality rates.

Cameron, and Westernhagen, (1997) monitored rates of malformation of embryos in pelagic egg samples taken in the southeastern North Sea between 1991–1992. Rates of malformation of eggs identified as those of cod varied from 20–38% for stage I eggs declining to 4–5% in stage IV eggs. Malformation rates appeared to be highest close to the major rivers and estuaries such as the Elbe/Weser, Rhine, Thames and Forth. The precise causes for such malformations are not clear but the impact of pollutants is a possibility

Time of first-feeding of larvae and food at first-feeding.

Little is known about the ecology of cod larvae in the North Sea although temperature-dependent development rates are available (Thompson and Riley, 1981). Munk *et al.* (2002) conducted plankton surveys in the southern North Sea in March 1997. Cod larvae were found predominantly in the southeastern sector of the survey area. Some of the highest estimates of abundance of larvae were found in the vicinity of frontal regions which may relate to enhanced feeding conditions in these hydrographic structures.

Based on extensive studies in other areas and on experience from aquaculture it seems that first-feeding larvae consume diatoms, dinoflagellates and tintinnids before moving onto the nauplii and copepodites of calanoid copepods, particularly those of *Pseudocalanus*. (Last, 1980; Economou, 1991; Meeren, 1991; Fossum and Ellertsen, 1994; McLaren and Avendaño, 1995; McLaren *et al.*, 1997). It has been suggested that first-feeding larvae may require phytoplankton as a source of essential polyunsaturated fatty acids (Meeren, 1991).

Food during early development

Based on sampling in 1992 in the deeper offshore water north of the Fisher Bank, Nielsen and Munk (1998) re-

ported that the main prey items for smaller cod larvae were *Paracalanus*/*Pseudocalanus* and for larger larvae/juveniles were the larger species such as *Calanus* spp. and *Temora* spp. The concentration of cod larvae/juveniles in this region may also be linked to physical convergence and enhanced primary and secondary production in the shelf break front (Munk *et al.*, 1995; Munk, 1997; Nielsen and Munk, 1998). In demersal juvenile cod the food is dominated by crustaceans (Daan, 1973, 1989).

Robb and Hislop (1980) analysed the diet of pelagic 0-group cod in material collected in July 1973 in the northern North Sea. The food was dominated by copepods: *Paracalanus* and *Pseudocalanus* spp. and the most common fish species in the diet was Norway pout (*Trisopterus esmarki*). The food composition for different size classes of predators was reported. The diet of 20–29 mm juveniles consisted almost exclusively of copepods by percent weight. From 30–39 mm onwards juveniles begin feeding on fish and euphausiids were important prey species for the 40–49 mm length classes. From 50 mm onwards more than 80% of the diet in weight consisted of fish. It was suggested that the degree of competition between pelagic 0-group gadoids was not due to differences in the diet of five gadoid species.

Significant diurnal changes in the amount and composition of food in the stomachs of pelagic 0-group cod have been reported (Robb, 1981; Bromley *et al.*, 1997). Robb (1981) observed a steady increase in stomach content weight commencing late afternoon or early evening. A maximum was found at midnight and the lowest values around midday. The diet did not vary significantly with depth but changes were found in the course of the feeding period. Around 18:00 hours BST and again at 06:00 hours, copepods were found to be the main prey group but at midnight the stomach samples contained an abundance of euphausiids. Bromley *et al.* (1997) also found that depth did not greatly influence the range of prey consumed but size-dependent and species-specific diel feeding patterns were found and the timing of peak feeding (maximum mean numbers of prey in stomachs) varied for different size groups of juvenile pelagic cod.

Evidence of predation during the egg and larval stage

Predation mortality at age has been estimated from Multispecies VPA (MSVPA) (ICES, 2003b). In the MSVPA, 11 commercial fish species are taken into account. The estimates rely heavily on stomach contents data collected in two years, 1981 and 1991 (Anon., 1991; ICES, 1997). The natural mortality due to causes such as diseases, spawning stress, physiological characteristics and so on is estimated to be 0.2 for all age groups. Important predators of juvenile cod are cod themselves, whiting (*Merlangius merlangus*) and saithe (*Pollachius virens*) (Daan, 1989).

Recruitment

Are there several spawning sites that contribute to the same stock unit?

There are several spawning locations within the North Sea that appear to influence the genetic structure of the stock.

Earliest time in the life history when year class strength can be predicted

Year class strength is usually estimated using 1-year-olds (ICES, 2003b).

Hypotheses that have been put forward to account for year-to-year variability in year class strength

Links have been made between reduced sea temperatures and improved recruitment for North Sea cod (Dickson and Brander, 1993; Planque and Fredou, 1999; O'Brien *et al.*, 2000). However, this still remains an intriguing statistical observation and research into mechanisms is required before such information can be utilised in management (Sundby, 2000). Based upon the critical timing for the temperature effect it is likely that early life history events are crucial. Fluctuation in plankton (through match-mismatch) has recently been suggested as a mechanism for long-term changes in cod recruitment. Favourable plankton conditions have been suggested as an explanation for the "Gadoid Outburst" of the 1963–1983 period and unfavourable conditions for the recent reduced survivorship of the stock. Survival of cod was shown to be dependent on three key biological parameters of their planktonic prey: mean size, seasonal timing and abundance (Beaugrand *et al.*, 2003; Brander and Mohn, 2004).

Evidence of long-term trends in recruitment

No increasing or decreasing long-term trend was evident in Myers *et al.* (1995) for the recruitment series up to 1990. The addition of more recent data, however, show that a long-term decreasing trend in recruitment from 1980 to the present has occurred (Figure 3.8.3c).

Evidence that variability in recruitment is linked to variability of other species in the same area; the same species in other areas or other species in other areas?

Year to year variability in the recruitment of North Sea cod has been significantly correlated with the short term variability in the recruitment of nearby cod stocks to the west of Scotland and Skagerrak (Myers *et al.*, 1995; Brander, 2003).

Evidence of inter- or intraspecific competition

See section on adult growth.

Is recruitment related to SSB or any environmental factors?

Recruitment has been linked to SSB, temperature (Myers *et al.*, 1995; O'Brien *et al.*, 2000; see section on recruitment) to plankton production timing and mean prey size (Beaugrand *et al.*, 2003) and to the NAO, (Brander and Mohn, 2004).

Adult growth

What are the general growth characteristics, e.g. typical size at age? Has it undergone changes over time?

Typical sizes-at-age based on estimated mean weights reported in the assessment (ICES, 2003b) are shown in Figure 3.8.6. According to these data, size-at-age is more variable over time for older fish (Figure 3.8.7) but there is no apparent decline in weight-at-age of North Sea cod across the entire time-series.

Is there evidence for density-dependent growth?

Houghton and Flatman (1981), Macer (1983) and Alphen and Heessen (1984) found evidence for density-dependent growth, although, as concluded by Rijnsdorp *et al.* (1991), they point to rather different mechanisms. The results obtained by Macer (1983) would imply that juvenile cod compete strongly with adult cod, whereas the data of Alphen and Heessen (1984) suggest strong within-year-class competition during the first three years of life. Cook *et al.* (1999) related variability in growth to stock biomass (density dependence), but Brander (in Andersen *et al.*, 2002) pointed out that this conclusion was very sensitive to recent, uncertain, estimates of stock biomass.

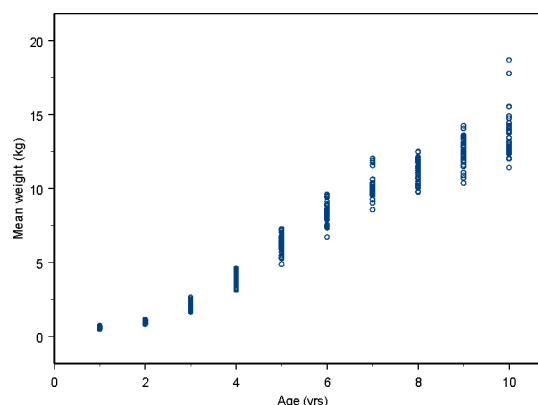


Figure 3.8.6. Mean estimated weights at age from 1963–2001 for North Sea cod as used in the assessment (ICES, 2003b).

Is there evidence of temperature-dependent growth?

The spatial and temporal differences in growth of North Sea cod have been discussed in relation to temperature. Growth parameters of North Sea cod given in ICES (1994) demonstrated that cod in the southern North Sea grow faster than those in the north but reach a smaller maximum length (Oosthuizen and Daan, 1974) and considerable spatial differences in size-at-age have been reported (Alphen and Heessen, 1984).

Differences in the mean length by age and by sex of immature versus mature fish have also been found. Within an age group the mature individuals of each sex are on average larger than the immatures (Hislop, 1984).

By the time the fish reach 3 years old they have moved off into deeper water and appear to be in a more constant thermal regime (Heessen and Daan, 1994). Such observations accord with recent work on temperature experience of cod as determined using oxygen isotopes (Weidman and Millner, 2000). There also appears to have been a shift in the distribution of fish in recent years. However, the relative importance of environmental, density-dependent and fishing effort effects on these apparent changes is not yet known.

Adult feeding

Cod is a predatory species with a very diverse diet. In the central North Sea cod have been reported to feed on ocean quahog (*Cyprina islandica*), crustaceans, sandeels (*Ammodytes* sp.), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*) and several flatfish species (Adlerstein and Welleman, 2000). Cod are potentially responsible for significant mortality on commercial stocks of clupeid, gadoid and flatfish species (Daan, 1973). Adlerstein and Welleman (2000) showed from analysis of stomach contents that cod feeding peaks in the morning and evening. Righton *et al.* (2001), using evidence from seasonal activity levels determined from electronic tag data, argued that North Sea cod reduce their foraging activity during summer months. In coastal banks off southwestern Norway in the northern North Sea (Hoines and Bergstad, 1999), the spatial distribution of cod has been related to food availability. During the herring spawning season in spring (March–April), cod are found almost exclusively on herring spawning grounds where they feed extensively on herring and herring eggs. When herring are absent from the banks, cod eat epibenthic prey such as decapod crustaceans. In autumn, cod in this area feed on the sandeel (*Ammodytes marinus*). Predation of cod on various species of sandeels has also been observed in the central North Sea (Olive A. Heffernan, CEFAS, pers. observation).

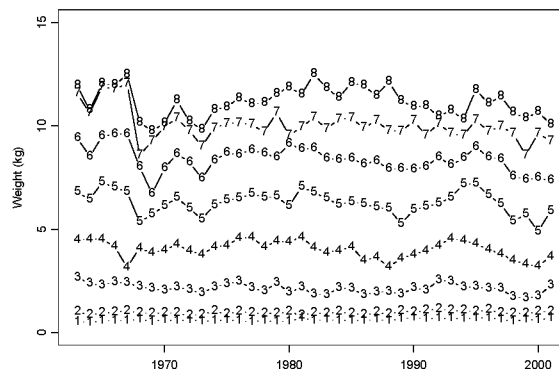


Figure 3.8.7. Time-series of weights at age from 1963–2001 for North Sea cod as used in the assessment (ICES, 2003b).

The most comprehensive data on feeding of North Sea cod were collected during the ICES Stomach Sampling Project 1981 (Daan, 1989). In juvenile cod crustaceans are the dominant prey items but in larger/older cod, fish comprise an increasingly important part of the diet. Most of the fish species consumed are of commercial importance. Cannibalism is frequently observed. There are large individual, regional and seasonal variations in food composition, which are partly caused by changes in the availability of the different food items. The total amount of food eaten in 1981 is estimated to be 507 000 t. of which 331 000 t (65.3%) consisted of commercial fish species.

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3.9 West of Scotland (ICES Division VIa)

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Stock and geographic distribution

Evidence of stock discreteness

Work into stock structuring is currently underway as part of the METACOD project (Q5RS-2001-00953). There is no genetic evidence for structuring to date. Historic and conventional tagging data from this project is being used to study movements between spawning areas.

Units for which assessment of spawning-stock biomass and recruitment are available

ICES area VIa.

Time-series of spawning-stock biomass and recruitment data

ICES area VIa time-series data are available from the ICES Working Group on the Assessment of Northern Shelf Demersal Stocks.

Time of spawning

Date of spawning and interannual variability or trend

Peak spawning appears to be in March, based on egg surveys (Raitt, 1967). Recent sampling for METACOD suggests that this is still the case.

Location of spawning

Geographic location and extent of spawning area

Spawning has occurred throughout much of the region in depths < 200 m. However, a number of spawning concentrations can be identified from egg surveys in the 1950s, 1992 and from recent surveys of spawning adult distribution. Based on recent evidence there are no longer any significant spawning areas in the Minch.

Biological details

Fecundity

Fecundity data are available from West (1970) and Yoneda and Wright (2004). Potential fecundity for a given length is higher than in the northern North Sea but lower than off the Scottish east coast (see Yoneda and Wright, 2004).

Evidence of changes in fecundity with time

There was no significant difference in the potential fecundity – length relationship for cod between 1970 (West, 1970) and 2002–2003 (Yoneda and Wright, 2004).

Percentage mature-at-age

Length at 50% maturity has always tended to be lower than that found in the North Sea. Length at 50% maturity was reported to be 49 cm in the period 1967–1970 (West, 1970) compared to 42 cm TL in recent years (Yoneda and Wright, 2004). Most females mature-at-age 2 or 3 and some males mature-at-age 1.

Recruitment

Are there several spawning sites which contribute to the same stock unit?

There are several main spawning areas, the most commercially important of which range from the Butt of Lewis to Papa Bank. There are also important spawning areas in the Clyde and off Mull. The relative contribution of these areas is not known, but will be investigated within the METACOD project. The main concentrations of juveniles are now found in coastal waters.

Migration

No information.

Adult growth

No information.

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3.10 Flemish Cap (NAFO Division 3M)

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Stock and geographical distribution

The Flemish Cap (Figure 3.10.1) is a relatively deep bank east of the northern Grand Bank of Newfoundland at about 47°N, 45°W. The minimum depth is about 150 m. It has a diameter at the 500 m isobath of about 200 km and a total area of about 3.0×10^4 km². The Cap is separated from the Grand Bank by the Flemish Channel or Flemish Pass, which has a depth of 1000–1100 m.

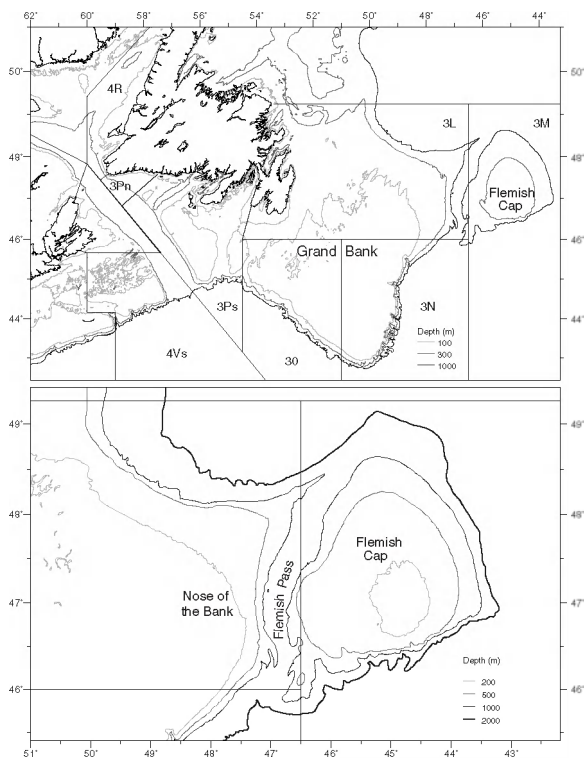


Figure 3.10.1. Flemish Cap and adjacent areas.

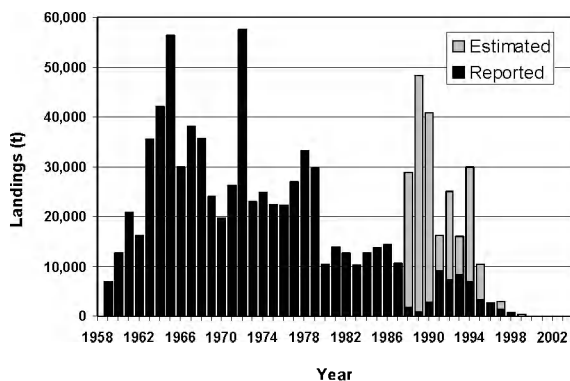


Figure 3.10.2. Cod in Division 3M. Reported and estimated landings (t). Catches in 1999–2003 (16–55 t annually) were too small to be distinguishable on the axis (Data from Cerviño and Vázquez, 2004).

The water mass characteristics of the Flemish Cap area are a mixture of Labrador Current Slope Water and North Atlantic Current Water. This water mass is generally warmer and saltier than the sub-polar shelf waters with a temperature range of 3° to 4°C and salinities in the range of 34 to 34.75. The general circulation in the vicinity of the Cap consists of the offshore branch of the Labrador Current which flows through the Flemish Pass on the Grand Bank side and a jet that flows to the east, north of the Cap, which then flows southward. To the south, the Gulf Stream flows to the northeast merging with the Labrador Current to form the North Atlantic Current, which influences waters around the southern areas of the Cap. In the absence of strong wind forcing, the circulation over the central Flemish Cap is dominated by a topographically induced anticyclonic gyre. The stability of this circulation pattern may influence the retention of ichthyoplankton on the bank and is probably a factor in determining the year-class strength of various fish and invertebrate species, such as cod, redfish and shrimp. Recent trends in temperature on the Flemish Cap indicate cold periods during the 1970s, mid-1980s and from the late 1980s to the mid-1990s. By 1995 temperatures moderated and were above normal at most depths from 1997 to 2002. The time-series of salinity anomalies show fresher than normal conditions from 1970 to 1975. Negative salinity anomalies also occurred during the mid-1980s and mid-1990s, however, the amplitude was much smaller than the great salinity anomaly of the early 1970s. The trend in salinity values during the latter half of the 1990s ranged from slightly above normal at the surface to near normal at deeper depths. [This description of oceanography was taken directly from NAFO (2004). For additional information regarding the Cap and its oceanography, see Templeman (1976) and Colbourne and Foote (2000).]

The Flemish Cap had long been considered a good cod fishing ground (Templeman, 1976). Almost the entire catch reported since the mid-1950s (Figure 3.10.2) was taken by European nations (Cerviño and Vázquez, 2004). Under-reporting of catches has been a serious concern for scientific assessment and management (Vázquez *et al.*, 1995). The stock is currently considered to be collapsed, and has been closed to directed fishing since 1999.

The Flemish Cap was the site of an international programme of research into the causes of variation in year-class strength of cod and redfish (Grosslein and Lilly, 1987; Lilly, 1987). The program was initiated by the International Commission for the Northwest Atlantic Fisheries (ICNAF) in the mid-1970s and was continued under its successor, the Northwest Atlantic Fisheries Or-

ganization (NAFO), until the mid-1980s. Although much was learned about the biology of adult cod and juvenile redfish, the programme met only limited success in achieving its goals, in part because the research effort was less than originally expected. In particular, a survey directed at juveniles was not conducted. In addition, inadequate biological sampling of commercial catches and inadequate reporting of catch and fishing effort made it difficult to measure recruitment and spawning-stock size. It is also interesting to note that very little was learned about the biology of cod eggs and larvae because both were caught in extremely low numbers.

Evidence of stock discreteness

The Flemish Cap cod stock is isolated and discrete. Support for this viewpoint comes from tagging studies and the study of meristics and parasite burdens (Templeman, 1976; Lear *et al.*, 1981). Two recent series of genetic studies indicate that the Flemish Cap stock is the most distinct of all offshore populations in the Labrador – Newfoundland area (Ruzzante *et al.*, 1998, 2001; Beacham *et al.*, 2002).

Units for which assessment of spawning-stock biomass and recruitment are available

Flemish Cap cod is considered a unit stock within NAFO Division 3M.

Time-series of spawning-stock biomass and recruitment data

The most recent assessment indicates peaks in total (1+) biomass in 1976 and 1989 (Figure 3.10.3). Peaks follow the production of good year classes by 3–4 years (Figure 3.10.4), but they are very short-lived because of intensive fishing. Spawning-stock biomass (Figure 3.10.3) tended to fluctuate between 10 000 t and 30 000 t from the mid-1970s to the mid-1990s, but has been very low since 1996. Year classes have been very small since 1992.

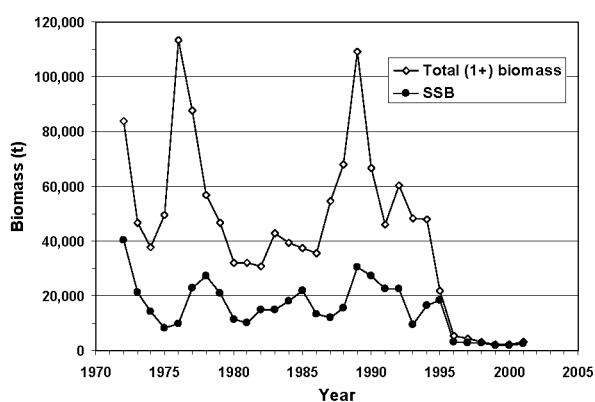


Figure 3.10.3. Cod in Division 3M. Total (1+) biomass and spawning-stock biomass (SSB) (from Vázquez and Cerviño, 2002).

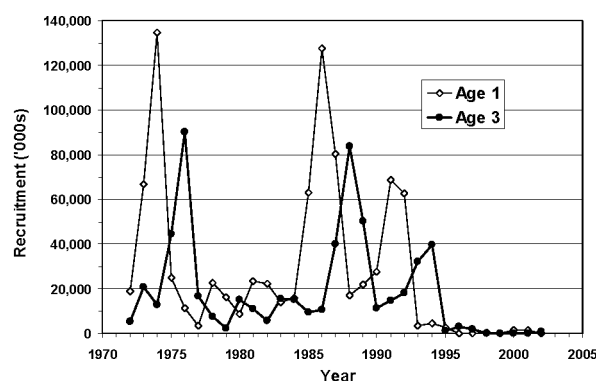


Figure 3.10.4. Cod in Subdivision 3M. Recruitment (numbers at ages 1 and 3) (from Vázquez and Cerviño, 2002).

There is considerable uncertainty in the population estimates because of under-reporting of catches and inadequate biological sampling (Vázquez *et al.*, 1995).

What is the geographical location of the stock and does it change seasonally?

Flemish Cap cod do not leave the bank. There are short-distance migrations to deep water in the southwest associated with spawning.

What is the depth range and temperature associated with the stock and does it change seasonally?

There has been no study of either the average depth occupied by the stock as a whole on an annual basis, or of the average temperature experienced by the stock.

Cod may be found from the shallowest part of the bank (150 m) to depths of 500 m or more (Templeman, 1976; Wells and Baird, 1989). The temperature in this depth range tends to be 3.5–4.5°C.

Time of spawning

Date of spawning and interannual variability or trend

As summarized by Templeman (1976), several authors have noted that cod on Flemish Cap spawn from late February to early April, with peak spawning in March. From an analysis of samples from Canadian surveys, Myers *et al.* (1993) determined that the date on which 50% of mature females were in a spent state was Julian day 77 ± 11 (March 18). The authors thought that their method would over-estimate the mean spawning date by about 2 weeks.

Flemish Cap cod tend to spawn earlier than other cod populations in the Newfoundland – Labrador area (Myers *et al.*, 1993). They also have a relatively short spawning season.

Time of day when spawning occurs

No information.

Timing of spawning season in relation to planktonic production cycle

No information.

Timing of spawning season in relation to hydrographic events

No information.

Timing of spawning season in relation to other fish species that spawn in the same location

No information.

Location of spawning

Geographic location and extent of spawning area

As summarized by Templeman (1976), several authors have noted that cod on Flemish Cap spawn at a considerable depth (> 350 m) on the slopes of the bank. Spawning is concentrated on the southwestern slope, but may occur on the other slopes.

Does spawning regularly begin in one part of the spawning area and then move on to other parts?

No information.

Can the location be described in relation to hydrographic features?

No information.

Can location be described in relation to other species, including food organisms and predators?

No information.

Can location be described in relation to water mass circulation?

The prevailing water movement on the plateau of the bank is anticyclonic. There has been no modelling to test the concept that spawning on the slope of the bank, particularly the southwestern slope, confers an advantage with respect to entraining eggs into the anticyclonic circulation. It may be noted that all six drogued buoys deployed on Flemish Cap in 1979–1980 left the bank from the southeastern corner (Ross, 1981).

Biological details

Fecundity

Wells (1986) provided raw data for length, age, and fecundity of 36 cod collected on Flemish Cap in 1979 and 1982–1984, and regression parameters for log-log regressions of fecundity vs. length and fecundity vs. age. The fecundity-length relationship was updated with a total of 61 samples by Wells and Baird (1989).

<i>Fecundity - length</i>		
Area	Slope	Intercept
Flemish Cap	3.16	0.069

Evidence of changes in fecundity with time

No information.

Percentage mature-at-age

The proportion of female cod mature-at-age has increased among younger cod. For example, the proportion of four-year-old females that are mature has increased from less than 10% in the 1978–1985 to 87% in 1998–2001 (Vázquez and Cerviño, 2002).

The trend in female age at 50% maturity (A_{50}), estimated from the annual sampling during Russian surveys, varied from 5 to 7 during the 1980s, but declined to about 4 during the mid-1990s. Saborido-Rey and Junquera (1998) reported a dramatic decline in age at maturity during 1992–1995.

The trend in female length at 50% maturity (L_{50}), estimated from the annual sampling during Russian surveys, varied from 50 to 70 cm during the 1980s, but declined to about 40 cm during the mid-1990s. Saborido-Rey and Junquera (1998) reported a dramatic decline in length at maturity during 1992–1995.

The period of rapid reduction in age and size at maturity was a period of very high fishing mortality (Vázquez and Cerviño, 2002). See the section on the cod of Southern Labrador and Eastern Newfoundland (2J+3KL) for discussion regarding a similar situation.

Egg size and evidence of changes with age and with time during the spawning season. Specific gravity of eggs and larvae

No information.

Typical densities, i.e. number per m^3 of eggs and larvae

No information.

Incubation rate of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larvae

No information.

Larval development rate as a function of temperature

No information.

Condition factor and nutritional status

No information.

Egg and larval mortality rates

No information.

Time of first-feeding of larvae and food at first-feeding

No information.

Food of larvae during development

No information.

Evidence of predation during the egg and larval stages

No information.

Recruitment

Are there several spawning sites (sub-populations) that contribute to the same stock unit?

As noted above, spawning occurs around the bank, and at spawning time the largest concentrations of cod are found in the southwest. There is no indication that there are two or more populations, each with its own spawning site.

Earliest time in the life history when year-class strength can be predicted

No information.

Hypotheses that have been put forward to account for year-to-year variability in year-class strength

At the start of the Flemish Cap project, twelve hypotheses were proposed to explain variation in year-class strength (Akenhead, 1978; Lilly, 1987). None of these hypotheses received adequate study during the period of the project. There was mild support for the hypothesis that year-class strength was related to the persistence of the anticyclonic circulation on the bank (Lilly, 1987). In addition, cannibalism by larger cod was documented (Templeman, 1976; Lilly, 1987), but there was insufficient information to assess whether such predation was an important factor in modifying year-class strength.

Evidence of long-term trends in recruitment

The SPA output indicates that recruitment has been very poor since 1992.

Evidence that variability in recruitment is linked to variability of other species in the same area, the same species in other areas, or other species in other areas

No information.

Evidence of inter- or intraspecific competition

No information.

Is recruitment related to SSB or any environmental factors?

Analyses during the Flemish Cap project found no relationship between recruitment and SSB (Lilly, 1987). However, it was felt at the time that both recruitment and stock size were poorly estimated from commercial catch data because of inadequate sampling. The time-series of information from surveys was very short at the time.

More recent analyses (Vázquez and Cerviño, 2002; Marshall *et al.*, 2003) do find support for an influence of SSB on recruitment, particularly since recruitment has been very small during the period of very low SSB (mid-1990s to present). (It may be noted, however, that there is great variability in year-class strength at intermediate stock sizes.)

Migration

See section on stock and geographic distribution above.

Adult growth

What are the general growth characteristics, e.g. typical length and size at age? Has it undergone changes over time?

Wells (1983) presented mean lengths-at-age from Canadian surveys, and demonstrated an increase from the period 1949–1951 to the 1960s, and a further increase by the early 1980s. Kiseleva (1999) presented mean length-at-age and weight-at-age from sampling during Russian surveys, and demonstrated an increase from the early 1980s to the late 1980s and early 1990s with a subsequent decline.

Is there evidence for density-dependent growth?

See P.-Gandaras and Zamarro (1990) and the references above for differing thoughts on this question.

Is there evidence of temperature-dependent growth?

See P.-Gandaras and Zamarro (1990) and the references above for differing thoughts on this question.

In addition to the possible influence of stock (or cohort) size and temperature, there has also been a suggestion that growth is dependent on the availability of prey of an appropriate size, specifically intermediate-sized redfish (Lilly, 1980).

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3.11 Gulf of Maine and Georges Bank (NAFO Subareas 5 and 6)

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Species, stock and area of distribution

In the waters off the coast of the USA, Atlantic cod (*Gadus morhua*) can be found in both the inshore and offshore waters of the Gulf of Maine, on Georges Bank, and south along the continental shelf. Based on tagging studies, three stocks are considered to exist in the waters off New England (Figure 3.11.1): 1. Gulf of Maine; 2. Georges Bank; and 3. Southern New England, which also includes the New Jersey coastal cod that, historically, moved into Southern New England waters in the summer (Wise, 1963).

The Gulf of Maine cod stock appears to be relatively distinct from other nearby cod stocks inhabiting the offshore Banks on the Scotian Shelf and Georges Bank, and there are several indications that cod in the Gulf of Maine are relatively isolated from those in other regions. Tagging studies (Schroeder, 1930; Wise, 1963; Hunt *et al.*, 1999; McKenzie, 1956) and infestation of parasitic copepods (Sherman and Wise, 1961) all suggest a very low rate of exchange of cod in to and out of the Gulf of Maine.

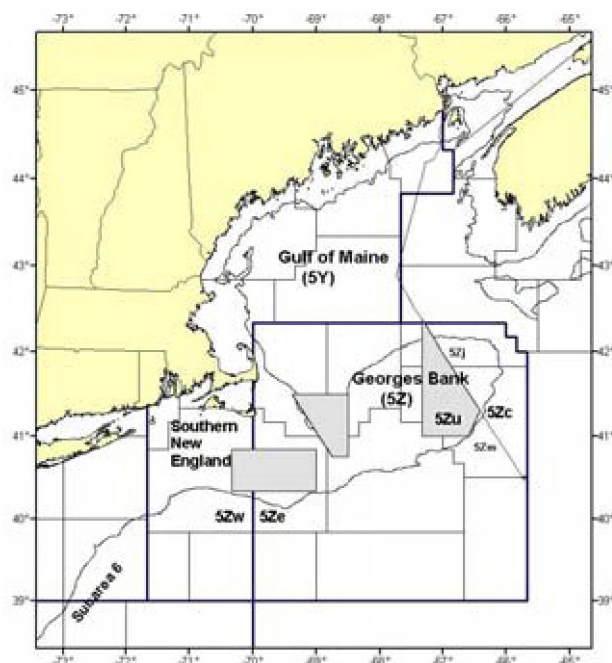


Figure 3.11.1. Geographical areas of distribution of the Gulf of Maine (NAFO Division 5Z and Subarea 6) Atlantic cod stocks off the coast of the United States. 5Z is further subdivided at 70 degrees W longitude into 5Ze and 5Zw. 5Ze is divided by the International Boundary Line into 5Zc and 5Zu. 5Zc is subdivided into 5Zj (north) and 5Zm (south) and these areas extend into 5Zu. Shaded polygons are year-round closed areas.

Cod on Georges Bank are primarily resident, however, tagging results indicate some movement of Georges Bank cod north onto the Scotian Shelf and east (Wise, 1963; Hunt *et al.*, 1999). Although some mixing occurs between the Gulf of Maine and Georges Bank cod stocks (Hunt *et al.*, 1999; Wise, 1963) their relative isolation is reflected in different otolith patterns (Penttilä, 1988) and different rates of growth (Penttilä and Gifford, 1976) and maturity (O'Brien, 1999). Differences in life history parameters between Gulf of Maine and Georges Bank cod stocks have persisted over time (O'Brien *et al.*, 1993; O'Brien, 1999) despite large scale changes in exploitation rates (Begg *et al.*, 1999). Processes that may account for these differences may be both biological (e.g. isolation of spawning locations and times) and physical (opposing gyral circulation patterns in the Gulf of Maine and on Georges Bank). These studies support the characterization of cod in the Gulf of Maine as a unit stock and cod on Georges Bank as a unit stock according to the criteria of Marr (1957).

Cod in the Southern New England area appears to be the most mobile of the three groups and moves to the southwest in the autumn and northeast in the spring and summer with favourable hydrographic conditions (Schroeder, 1930; Wise, 1963). Recent analyses suggest that cod from Nantucket Shoals are genetically distinct from the cod on Georges Bank (Lage *et al.*, 2004). Historically, cod were resident on Nantucket Shoals year round, with some movement of fish to the southwest in the early winter. These fish migrated as far south as Rhode Island to North Carolina, and would return to Nantucket Shoals in the spring. Some larger fish would continue east to deeper water near Georges Bank (Schroeder, 1930). The northeast movement in the spring was attributed to a return to spawning grounds; however, Wise (1958) postulated that the autumn migration was actually a return to winter spawning grounds. The presence of spawning fish off the New Jersey coast (Smith, 1902) and the occurrence of cod eggs and larvae south to North Carolina suggest the Middle Atlantic cod may be a genetically distinct population from those to the north (Smith, 1902; Berrien and Sibunka, 1999; Wise, 1963). Unfortunately, in more recent times, cod eggs and larvae are not found in any quantity south of Long Island (Berrien and Sibunka, 1999; Serchuk and Wood, 1979).

Seasonal movements and range contraction of these stocks can be seen in the distribution plots of the Northeast Fisheries Science Center's (NEFSC) spring and autumn research survey indices of abundance (Figure 3.11.2). The cod are generally more dispersed in the spring than in the autumn, when the fish tend to

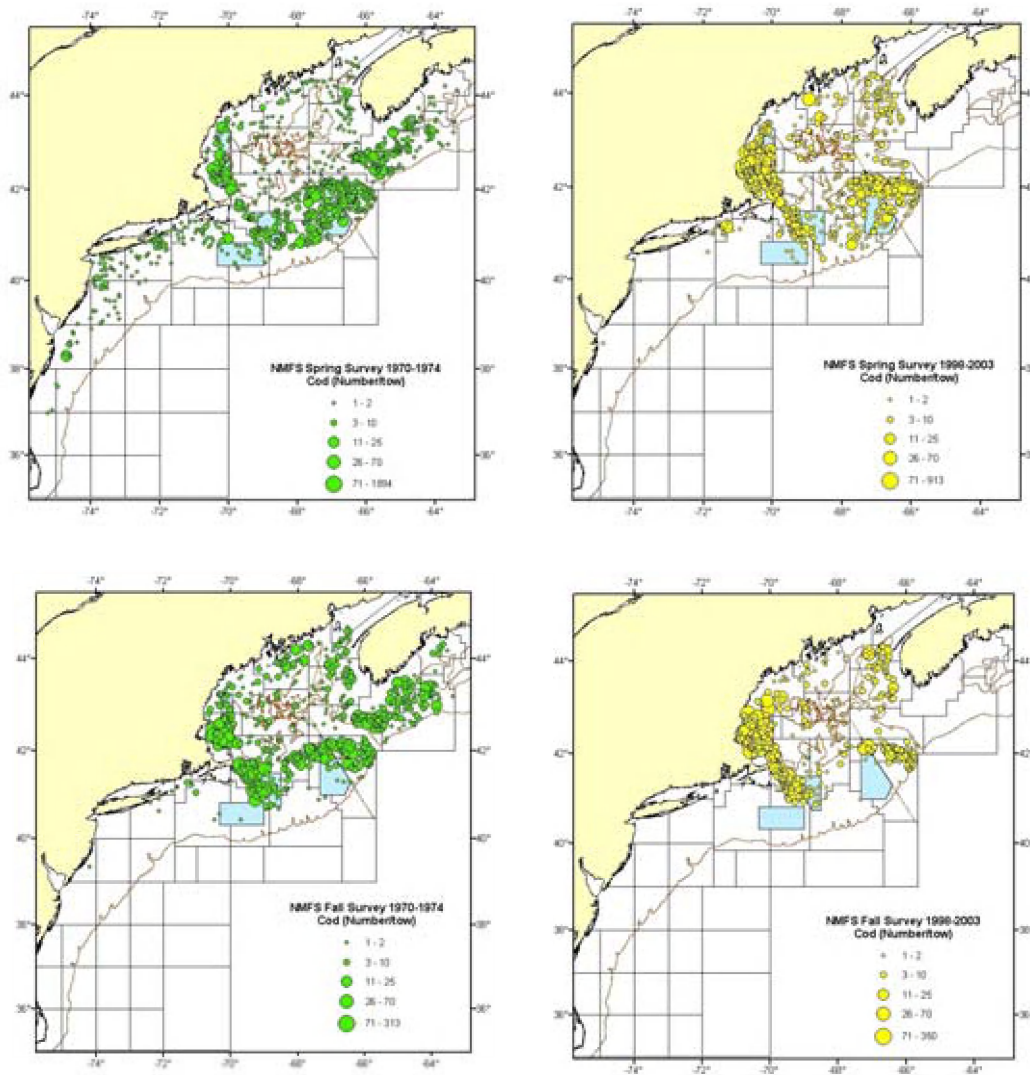


Figure 3.11.2. Indices of abundance (mean number/tow) of Atlantic cod from NEFSC research bottom trawl spring (1970–1974, 1998–2003) and autumn (1970–1974, 1998–2002) surveys, thin line is the 100 m isobath.

Table 3.11.1. Measurements of depth (m) and temperature (°C) of cod from NEFSC spring and autumn research surveys.

DEPTH (m)		Spring			Autumn		
	Min.	Number/Biomass Weighted	Max	Min.	Number/Biomass Weighted	Max	
GM	49	114 / 136	290	46	99 / 124	269	
GB	32	74 / 81	226	32	83 / 92	226	
MA	27	43 / 45	73	29	42 / 42	56	
TEMPERATURE		Spring			Autumn		
(° C)	Min.	Number/Biomass Weighted	Max	Min.	Number/Biomass Weighted	Max	
GM	3.5	4.9 / 5.2	8.3	5.8	8.1 / 7.7	10.2	
GB	3.9	5.3 / 5.4	8.8	5.6	8.9 / 8.9	14.7	
MA	3.6	4.7 / 4.7	6.1	29	12.0 / 12.0	13.1	

aggregate near the 100 m isobath. The southerly movement of the Southern New England stock is apparent early in the time-series during 1970–1974 but is barely discernable in the later period, during 1998–2002. Although not as marked a change, a similar decline in cod along the northern Maine coast is also evident. The apparent lack of fish on the Scotian Shelf in the latter part of the time-series is due to a discontinuation of survey coverage in this area.

Measurements of depth (m) and temperature (°C) from NEFSC spring and autumn research surveys, weighted by both number and biomass, indicate that Gulf of Maine cod occupy cold, deep water in the spring and warmer, shallower water in the autumn (see Table 3.11.1). Georges Bank cod occupy cold, shallower water in the spring and warmer, deep water in the autumn. In the Southern New England area cod occupy relatively shallow water in both seasons, which is cool in the spring and warmer in the autumn.

The Georges Bank and Southern New England cod stocks are currently considered together as a single stock because the demographics, i.e. growth, recruitment patterns, abundance indices, and size and age of commercial catches, are so similar (Serchuk and Wood, 1979).

Commercial landings of Gulf of Maine cod have ranged as high as about 18 000 tonnes since the early 1890s (Serchuk *et al.*, 1994). During the most recent 4 decades, total commercial landings increased during the 1960s and 1970s from about 3500 tons per year to 17 800 tonnes in 1991. Landings declined steadily, thereafter, reaching a low of 1600 t in 1999 as a result of low trip limits and reduced fishing effort across the region. Additional catches by the recreational fishing sector have averaged about 1800 t since 1981, and more recently, discards of cod by the commercial sector have ranged from about 1000 to 2500 t since 1999 (Figure 3.11.3). Instantaneous fully recruited fishing mortality (F) on this stock, obtained from Virtual Population Analysis (VPA), averaged about 1.0 between 1983 and 1997. During the past 4 years, however, F declined from 0.9 in 1997 to about 0.5 in 2001 (Figure 3.11.3).

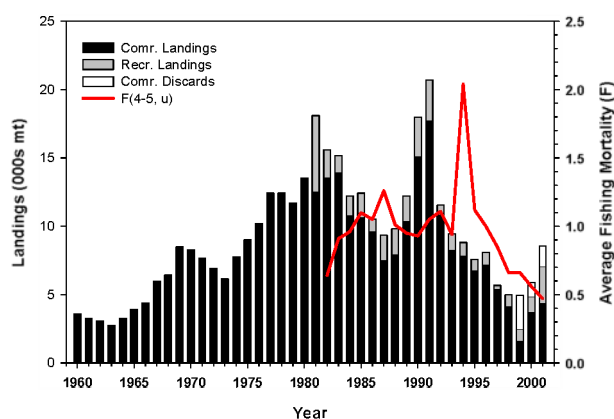


Figure 3.11.3. Trends in landings and fishing mortality for the Gulf of Maine Atlantic cod stock (NAFO Division 5Y), 1961–2001.

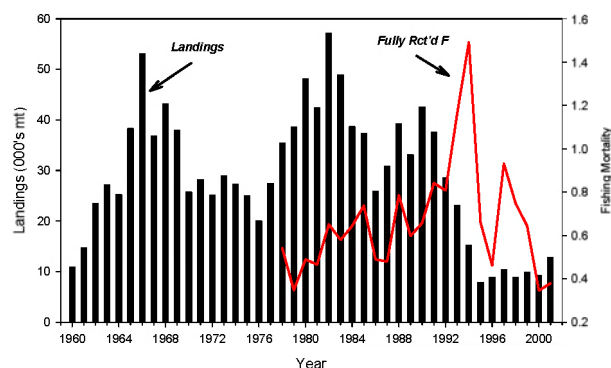


Figure 3.11.4. Trends in total commercial landings and fishing mortality for the Georges Bank Atlantic cod stock (NAFO Division 5Z + Subarea 6), 1960–2001.

Georges Bank cod is a transboundary resource shared between the USA and Canada. The USA assesses Georges Bank cod as a unit stock consisting of cod from NAFO Division 5Z+Subarea 6 (Serchuk *et al.*, 1994) (Figure 3.11.1). Canada assesses cod on eastern Georges Bank as a management unit consisting of cod from areas 5Zj and 5Zm (Hunt, 1989; Halliday and Pinhorn, 1996). Total commercial landings of Georges Bank cod peaked in the early 1900s at about 44 000 t, then declined and remained relatively stable through 1940 (Serchuk *et al.*, 1994). Landings began to increase in 1960 from the effort of distant water fleets and again in 1977 from increased domestic effort. In 1982, landings peaked at a record high of 57 000 t. Landings remained relatively high until year-round closures were invoked, in addition to other management measures, in December 1994 (Figure 3.11.4). Population estimates for the 5Zj and 5Zm management unit show similar trends to those of the larger Division 5Z+Subarea 6 unit with some inter-annual variation (Hunt and Hatt, 2002). Prior to the year round closure of a large portion of eastern Georges Bank in December 1994, about 46% of the total commercial landings of Georges Bank cod were from the 5Zj and 5Zm areas. Since 1995, only about 28% of the landings were from the 5Zj and 5Zm areas. Fully recruited fishing mortality (ages 4–8) generally increased from 1978 and reached a record high of 1.5 in 1994. Between 1995 and 1997 F averaged at about 0.7, and has since declined to 0.4 in 2001 (Figure 3.11.4).

Within the Gulf of Maine, cod have traditionally been found aggregated along the 100 m isobath off the coast of Maine, and in greatest concentrations between Cape Cod, Massachusetts and Cape Elizabeth, Maine. During the past two decades, the extent of cod distribution in the Gulf of Maine has been substantially reduced to this core region, primarily within the confines of Massachusetts Bay, although some expansion to former grounds has occurred most recently. On Georges Bank, cod are dispersed over the Bank during the spring and summer, and become more aggregated to the north near the 100 m isobath during the autumn (Serchuk *et al.*, 1994). Similarly, juveniles are generally dispersed over the Bank ex-

cept during the last half of the year (June–December) when aggregations occur along the 100 m isobath eastward of Cape Cod (Wigley and Serchuk, 1992).

Recruitment to the Gulf of Maine stock, as indicated by research vessel survey indices, became more variable during the 1980s and 1990s compared to previous decades. The largest year class, estimated by VPA during 1982–2001 (Mayo and Col, 2002), was produced in 1987 (Figure 3.11.5), although survey data suggest that this year class was within the range of several moderate to strong year classes (Figure 3.11.6) produced during the 1970s.

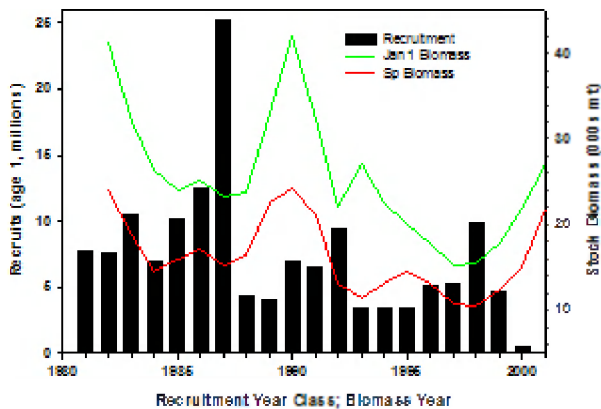


Figure 3.11.5. Trends in recruitment, biomass, and spawning-stock biomass for the Gulf of Maine Atlantic cod stock (NAFO Div. 5Y), 1980–2000.

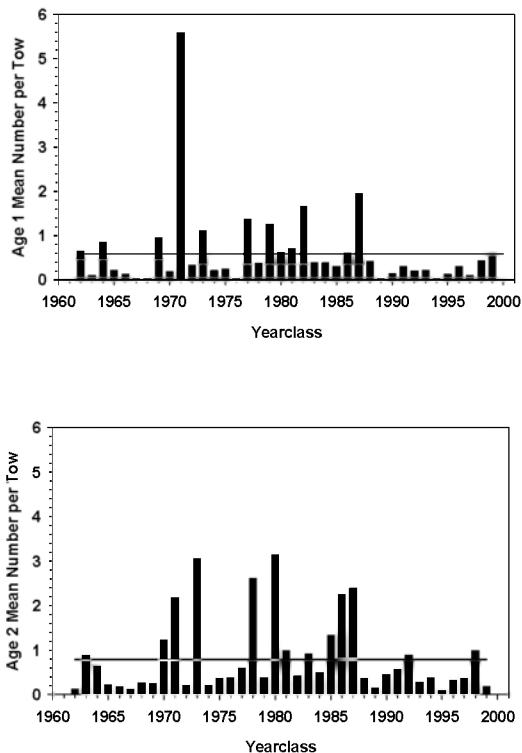


Figure 3.11.6. Relative year-class strength of age 1 and 2 Gulf of Maine cod, based on standardized catch (number) per tow indices from NEFSC autumn research vessel bottom trawl surveys, 1963–2002. Horizontal line represents the time-series average.

Historically, Georges Bank cod recruitment was characterized by large recruitment pulses every three to five years (Figure 3.11.7 and Figure 3.11.8) (O'Brien *et al.*, 2002; Hunt and Hatt, 2002). NEFSC research vessel survey indices suggest that the largest year classes appeared in the late 1960s and early 1970s (Figure 3.11.8). In the last decade, recruitment has been below the long term average in both USA and Canadian research vessel surveys, except for the 1993 year class measured as age 2 fish. During 1978–2001 the largest year class was produced in 1985 and the most recent above average year class as estimated by VPA (Figure 3.11.7) occurred in 1990.

Since the early 1960s, there has been a steady decline in the total biomass of Gulf of Maine cod as indicated by research vessel surveys (Mayo and Col, 2002). VPA suggests a sharp decline in spawning biomass during the early 1990s (Figure 3.11.5) followed by a substantial increase during the past 3 years, due in large part to growth and maturation of a moderate 1998 year class. This increase is reflected in the most recent research survey biomass indices.

Research vessel surveys indicate declines in total biomass of Georges Bank cod since the early 1960s (O'Brien *et al.*, 2002). Based on VPA, SSB generally declined between 1980 and 1994 and has since increased slightly through 2001 (Figure 3.11.7). The gradual increase in SSB is due to accumulated growth, particularly by the below average 1996 and 1998 year classes, rather than any large recruitment event.

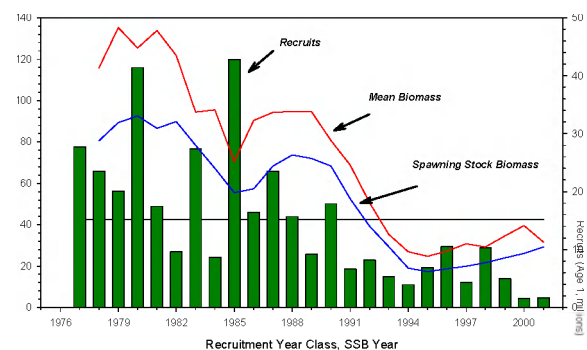


Figure 3.11.7. Trends in stock biomass and recruitment for the Georges Bank Atlantic cod stock (NAFO Divisions 5Z+SA6). Horizontal line is the average recruitment for the time-series.

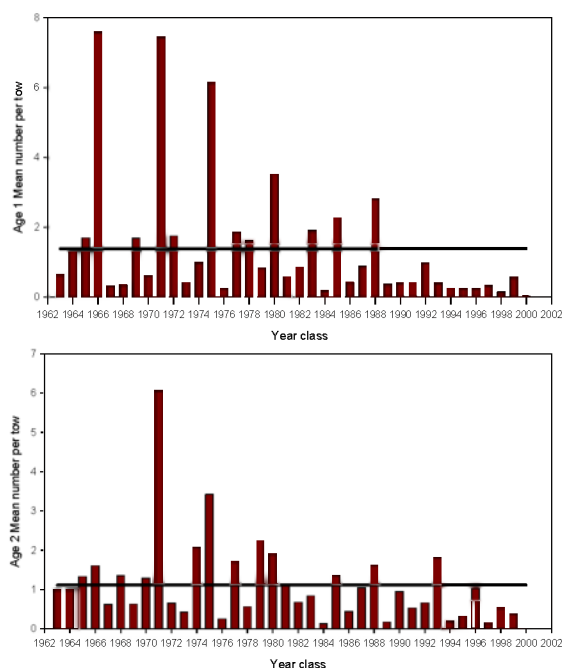


Figure 3.11.8. Relative year-class strength of age 1 and age 2 Georges Bank cod based on standardized catch (number) per tow indices from NEFSC autumn research vessel bottom trawl surveys, 1963–2002. Horizontal line represents the time-series average.

Time of spawning

Within the Gulf of Maine, cod generally spawn throughout the winter and early spring in most locations, but the period of peak spawning varies depending on location (Schroeder, 1930). In general, spawning occurs later in the year in the more northerly regions. Within Massachusetts Bay, Fish (1928) reported peak spawning activity during January and February. Bigelow and Welsh (1924) noted that north of Cape Ann, Massachusetts, most spawning occurred between February and April and further north, between Cape Elizabeth and Mt. Desert Island, Maine, the peak spawning period was between March and May. It has also been noted that cod spawning occurs mostly at night and may be crepuscular (Klein-MacPhee, 2002).

On Georges Bank, the spawning season extends from November to May with peak spawning occurring during February and March (Berrien and Sibunka, 1999; Colton *et al.*, 1979; Smith, 1985). Peak spawning coincides with the months of peak retention of water on the Bank (Page *et al.*, 1999). Historical data indicate that bottom temperature during the spawning season ranges from 1.4–12.7°C, however, based on laboratory experiments by Laurence and Rogers (1976) the highest percentage of viable hatching occurs in the range of 2–10°C. Years of high or low recruitment could originate from either side of peak spawning or hatching (Lough *et al.*, 2002).

Atlantic cod have a protracted spawning season that overlaps that of several other species in the Gulf of Maine and on Georges Bank. These include haddock *Melanogrammus aeglefinus*, pollock *Pollachius virens*, white hake *Urophycis tenuis*, winter flounder *Pseudopleuronectes americanus*, American plaice *Hippoglossoides platessoides*, and witch flounder *Glyptocephalus cynoglossus*. Only the peak spawning time of haddock (March–April) overlaps that of cod in both areas (Smith, 1985).

Location of spawning

The principal cod spawning areas in the Gulf of Maine are along the western side, with the most productive grounds centered in Massachusetts Bay and just north of Cape Ann (Bigelow and Schroeder, 1953). Additional spawning grounds have traditionally been located off the coast of Maine as far north and east as Mt. Desert Island (Figure 3.11.9). As noted in the previous section, there is a seasonal progression in spawning with spawning occurring in southerly areas earlier in the season, than in the north.

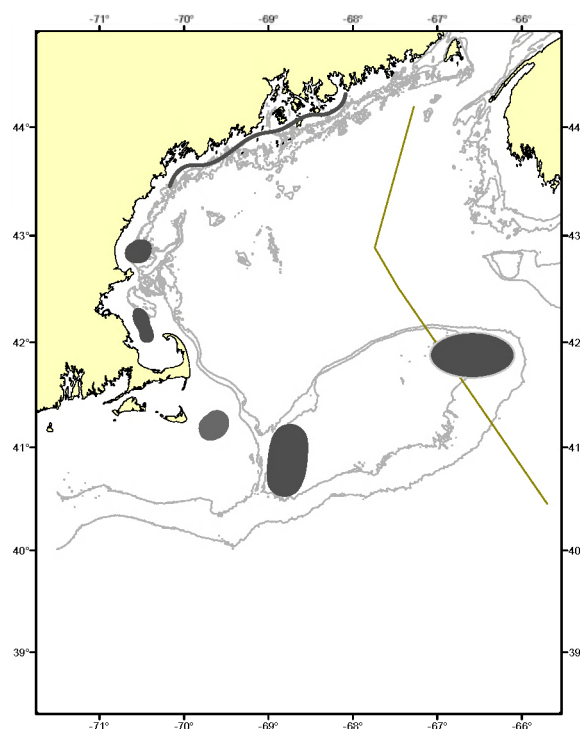


Figure 3.11.9. General spawning areas (dark line and polygons) for Atlantic cod in the Gulf of Maine and Georges Bank area as described in the literature (Bigelow, and Schroeder, 1953; Berrien, and Sibunka, 1999; Lough *et al.*, 2002; Heyerdahl and Livingstone, 1982). Light grey lines are the 70 m and 100 m isobaths.

The distribution and abundance of cod eggs in the Gulf of Maine were summarized by Berrien and Sibunka (1999) based on Marine Resource Monitoring Assessment and Prediction (MARMAP) cruises from 1978–1987. Cod eggs were found along coastal Gulf of Maine mostly in waters shallower than 100 m. Highest concentrations generally occurred in the western part from Penobscot Bay to Cape Cod in the vicinity of Massachusetts Bay and Jeffrey's Ledge.

Eggs spawned in the Gulf of Maine and developing larvae tend to drift south and eastward towards Georges Bank owing to the counter-clockwise Gulf of Maine gyre. The extent of exchange of cod offspring between the Gulf of Maine and Georges Bank region, however, is unknown.

Historically, cod have spawned on both eastern and western Georges Bank. Patterns of egg distributions indicate that cod spawn predominantly on the Northeast Peak or western Georges Bank (Berrien and Sibunka, 1999; Lough *et al.*, 2002). Spawning also occurs on Nantucket Shoals (Subdivision 5Zw) (Heyerdahl and Livingstone, 1982) south of Cape Cod (Figure 3.11.9). During 1995–1999, the period of the GLOBEC cruises, spawning occurred mostly on the Northeast Peak (P. Berrien, unpublished data).

Eggs spawned on the northeastern portion of Georges Bank generally drift southwesterly. At typical early spring temperatures, the eggs hatch in about two to three weeks (Laurence and Rogers, 1976). In their experiments, Laurence and Rogers (1976) found that time to mean hatch was inversely related to temperature and salinity. 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 and Morse, 1985; Lough and Bolz, 1989). A variable fraction of the eggs and larvae reaching the western part of Georges Bank near the Great South Channel are caught up in the gyre (as are the eggs and larvae spawned in the Channel area) and are recirculated around the Bank. Some fraction, however, is advected westward to 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 may be transported northeastward from Georges Bank to the Scotian Shelf.

Model simulations (Lough *et al.*, 2002) show how variable spawning within a bank gyre system can have different consequences for transport and survival of eggs and larvae. Particles released from the Northeast Peak usually had higher retention than releases from western Georges Bank; however, the western Georges Bank releases could contribute significantly to retention, espe-

cially during the winter period when there is wind loss of particles from the Northeast Peak.

Biological details

Fecundity of Gulf of Maine cod was estimated to be 2.7 million to 9.1 million eggs for females ranging in size from 100 cm to 130 cm (Earll, 1880). On average, female cod in the Gulf of Maine produce about 1 million eggs per season (Bigelow and Schroeder, 1953). Fecundity of Georges Bank cod was estimated to increase from about 0.3 million eggs at 50 cm to about 4.1 million eggs at 100 cm, and up to 11.6 million eggs for 120 cm females (McIntyre and Hutchings, 2003).

Atlantic cod cease feeding prior to spawning in both the Gulf of Maine and on Georges Bank. A significantly higher amount of food was found in cod stomachs after spawning than before spawning (Link and Burnett, 2001). This strategy is hypothesized to balance the energetic constraints of growth, metabolism, and reproductive development during the overwintering period.

Gulf of Maine cod attain sexual maturity at a later age than Georges Bank cod. In the early 1970s median maturity-at-age occurred at about age 4 in the Gulf of Maine and at about age 3 on Georges Bank (O'Brien, 1999). Differences in sexual maturity can be attributed to the differences in growth rate between the two stocks (Penttila and Gifford, 1976; Penttila, 1988). In the more recent years, not only has age at maturity appeared to have declined in both stocks but the difference between the stocks has also decreased to about a year or less in some instances. In the Gulf of Maine, median age and length at maturity declined over a 25 year time period beginning in the early 1970s, and a less pronounced decline was also observed during this same period for Georges Bank cod (O'Brien, 1999; Hunt, 1996). The decline in maturation occurred during the time period when exploitation increased on both stocks with a subsequent stock biomass decline and truncated age structure (Mayo and Col, 2002; O'Brien *et al.*, 2002). The decline in biomass and the effect of temperature both appear to influence the rate of maturation in these stocks (O'Brien, 1999).

Estimates of median maturity-at-age (A_{50}) and length (L_{50}) derived from 2000–2002 pooled data from the NEFSC spring research bottom trawl survey were as follows:

	A_{50} (years)	L_{50} (cm)
Gulf of Maine		
Females	2.6	43.3
Males	2.9	44.0
Georges Bank		
Females	2.1	43.3
Males	2.1	42.2

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; Lough *et al.*, 1996). 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.

Growth in standard length of larval cod on Georges Bank has been described by Gompertz-type curves (Bolz and Lough, 1988) and linear and exponential curves (Stein and Borokov, 2004) based on daily growth increments of otoliths. Growth rate increases from 0.13 mm/day after hatching (3–5 mm) to about 1.0 mm/day at 100 days of age. The highest growth rates of larval cod, made from field measurements during May 1992–1994, were observed when the mean water temperature was around 7°C (Buckley *et al.*, 2004). Comparison of field growth rates and the temperature optima with laboratory rearings suggest that growth in the sea may be food limited at higher temperatures. In June, pelagic juveniles range from 20–50 mm in length, and most juveniles are between 50 and 80 mm in size by end of July (Lough *et al.*, 1989). By the end of first year of life, Georges Bank cod reach an average length of 26 cm (Penttila and Gifford, 1976).

The mortality rates of cod eggs and larvae on Georges Bank have been estimated from the bimonthly MARMAP surveys, 1978–1987, and the monthly U.S. GLOBEC broadscale surveys, 1995–1999. Monthly GLOBEC broadscale surveys of Georges Bank were conducted from January to July, and the fish eggs were identified, staged, and counted from quantitative Bongo-net hauls. Spawned and hatched densities were averaged (delta-mean) by survey and accumulated over the season to estimate total eggs spawned and hatched. Instantaneous daily mortality rates for cod eggs ranged from 0.094 to 0.195 (Berrien, unpublished data). Percent survival ranged from 1.5 to 10.6. Numbers of eggs spawned have increased to the highest level observed since the early 1980s; however, the number of eggs hatched has not exhibited a similar increase. The cause of mortality is not known. There was no direct correlation between mortality rates and percent of first-time spawner biomass. Abundance of spawned eggs during 1995–1999 was in the range of $11\text{--}35 \times 10^{12}$. The highest abundance of eggs spawned in 1997 had the lowest number of eggs hatched.

Daily egg mortality rates from the 1995 and 1996 GLOBEC field seasons ranged from 2–20% and averaged 12–14%/day (Mountain *et al.*, 2003) over a 20-day incubation period. The mortality rates for the two years, were considerably higher than rates calculated for the MARMAP time-series, 1978–1987. A seasonal average

mortality rate of cod larvae from the MARMAP period was estimated at 4%/day during the approximate 100-day period between hatching (4 mm) and 20 mm size (Morse, 1989). Larval mortality rates from the 1995 and 1996 GLOBEC field seasons were estimated between 3–9%/day, based on the decrease in larval abundance between surveys (Mountain *et al.*, 2003). Direct estimates of post larval mortality rates were estimated to be in the range of 6–7%/day, based on the >20mm cod abundance collected during 1986 and 1987 Georges Bank surveys (Serchuk *et al.*, 1994).

Yolk sac and first-feeding larvae prey primarily on small plankton such as protozoans and copepod eggs and nauplii. Older larvae feed on the nauplii and copepodites of the common species *Pseudocalanus*, *Calanus*, *Centropages*, *Oithona* (Kane, 1984; Lough and Mountain, 1996). Pelagic and recently-settled juveniles shift to epibenthic prey and swarming species such as mysids, amphipods, chaetognaths, and euphausiids (Auditore *et al.*, 1994; Lough *et al.*, 1989).

Predation is considered to be an important source of pre-recruit mortality despite limited direct evidence. Mackerel and herring are likely predators of pelagic cod larvae and juveniles when their distributions overlap in the spring (Garrison *et al.*, 2000). Various invertebrate predators (e.g., amphipods, jellyfish, chaetognaths, crustacean, and squid) can have a potential impact and the quantification of these potential mortality rates will be made in the U.S. GLOBEC Georges Bank Study. Many piscivorous fish, such as dogfish, silver hake, larger cod, and sculpin, prey on juvenile cod (Edwards and Bowman, 1979).

Seasonal stratification of the water column along the southern flank of Georges Bank has been shown to aggregate larvae and their prey near surface pycnoclines (Lough, 1984; Lough and Potter, 1993) which can result in increased feeding (Lough and Mountain, 1996) and growth (Buckley and Lough, 1987; Buckley *et al.*, 2004). Bisagni (2000), in an 11-year study (1985–1995) of stratification on the southern flank noted that the maximum abundance of early cod larvae as well as copepod nauplii generally coincided with the first date of transient stratification in mid-April.

Recruitment

Spawning concentrations along the coast of the Gulf of Maine as well as those on Jeffrey's Ledge and Stellwagen Bank all contribute to the recruitment of the Gulf of Maine stock.

Recruitment to the Georges Bank stock includes all fish spawned on the Northeast Peak, on western Georges near the Great South Channel, on Nantucket Shoals, and south. Stock sizes of age 1 fish, as estimated by VPA, are typically considered as an index of year-class strength for both stocks.

Cod on Georges Bank are generally considered to reside at the upper range of temperatures, 10–14°C annual mean at 100 m, although there is a compression of the isotherms on the western side of the Atlantic. Therefore, strong cod recruitment might be related to colder temperatures as a result of the more southerly transport of the Labrador Current along the Scotian Shelf. Zooplankton abundance estimates were made by Kane (1993), specifically *Calanus finmarchius* and *Pseudocalanus minutus*, from the MARMAP time-series, 1977–1986 winter, early-spring, and late-spring periods. In spring 1977, both species of calanoids were exceptionally abundant in the time-series. The following year, only *C. finmarchicus* reached high abundance by late spring. All other years had spring periods of similarly low abundance of both species.

Lough and Bolz, 1989) found evidence for continuous retention of both cod and haddock onto the central shoal area (<60m) of Georges Bank. At depths less than 70 m, retention of larvae appears to be enhanced via interactions with cross-isobath tidal currents (Lough and Manning, 2001). 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), however, by late summer settled juveniles are mostly found on gravel bottom.

Two contrasting spawning seasons of cod were studied by Lough *et al.* (1994) to examine the influence of wind-driven advection of eggs and larvae. During April 1982, there was an apparent offshore loss of eggs and larvae but in 1985, there was little evidence of offshore loss of eggs and larvae. There was poor recruitment of the 1982 year class and relatively good recruitment at age 1 for the 1985 year class. A 3-D numerical circulation model was used to track particles in monthly-mean flow fields from February through May. Passive, Lagrangian descriptions of the particles were used to examine the effects of variable advection and spawning date on larval distributions for the two years. Results were consistent with the greater loss of eggs/larvae in April 1982 associated with a strong northeast wind stress. Whether a particular wind stress and resultant flow field was good or bad for retention on the Bank depended on the location of eggs/larvae on the Bank at the time of the event. Cross-bank winds (SE, NW) generally have little influence on along-shelf flow.

There is also considerable variability in cod egg survival as shown in Figure 3.11.10 based on a 20-year time-series of Georges Bank ichthyoplankton surveys (1979–1999). Large year classes, such as those of 1980 and 1985 (Figure 3.11.7) can arise from high or low egg mortality (Figure 3.11.10). However, there is a strong positive correlation between the abundance of both small and large cod larvae and year-class strength at age 1 (Lough *et al.*, 2002). Given the relatively low levels of spawn-

ing-stock biomass on Georges Bank, any additional survival of larvae is reflected in recruits. The proportion of egg mortality that can be attributed to egg quality, transport loss, or predation has not been quantified, but probably is variable from year to year. Variability in egg survival can be explained partially by the age diversity of repeat spawners, bottom temperature, and the spatial distribution of the eggs (O'Brien *et al.*, 2003). Survival during the pelagic larval and juvenile period also needs to be considered. There is a positive correlation between abundance of the recently settled O-group juveniles and VPA age 1 recruits, based on limited survey data (Lough *et al.*, 2002). While Brodziak *et al.* (2001) showed strong evidence that SSB influences recruitment of Gulf of Maine and Georges Bank cod, model uncertainty was substantial and environmental forcing may explain a significant portion of the variability in the stock recruit models. On Georges Bank, age 1 cod and haddock exhibit moderate recruitment synchrony, probably related to the general productivity of the system (Fogarty *et al.*, 2001).

Migration

An intensive migration is not apparent for either the Gulf of Maine or Georges Bank cod stock. Although some cod appear to remain resident in certain areas, there is a general seasonal movement related to spawning. In the Gulf of Maine, cod will move inshore in the autumn to the spawning grounds and offshore in the summer into the central part of the Gulf of Maine. On Georges Bank, cod will form spawning aggregations in the late autumn and early spring and become more dispersed after spawning with movement to the northeast (Hunt *et al.*, 1999) as well as to the southwest (Wise, 1963). Historically, the Southern New England stock exhibited the most movement between areas even though large numbers of fish remained resident in the area. Under favourable hydrographic conditions, fish would move to the southwest in the autumn and northeast in the spring and summer (Schroeder, 1930; Wise, 1963). New Jersey coastal cod that intermingled with the Southern New

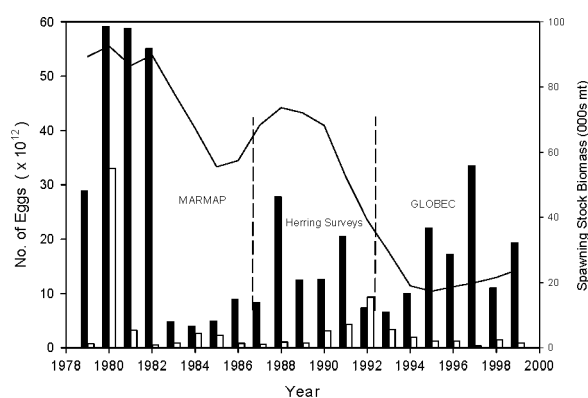


Figure 3.11.10. Estimates of cod eggs spawned and hatched (number $\times 10^{12}$) on Georges Bank from MARMAP, Herring, and GLOBEC surveys conducted during 1979–1999, and Georges Bank spawning-stock biomass (000s t). There is a significant linear relationship between egg abundance and SSB for Georges Bank cod (O'Brien *et al.*, 2003).

England cod in the summer would migrate south in the autumn to the winter spawning grounds (Wise, 1958).

Adult growth

Gulf of Maine and Georges Bank cod commonly grow to lengths above 130 cm and are estimated to weigh as much as 25–30 kg (O'Brien and Munroe, 2001). A record cod of 183 cm, weighting 96 kg was landed by longline in 1895 (Klein-MacPhee, 2002). The maximum recorded age of cod from research survey data is 18 years (Penttila and Gifford, 1976). Georges Bank cod grow faster than Gulf of Maine cod, generally by about 10 cm at each age (Penttila *et al.*, 1989).

Mean lengths at age for cod from the NEFSC spring research survey, averaged over the five year period 1995–1999, are as follows:

Age	2	3	4	5	6
GM	33.8	48.9	57.2	66.3	74.6
GB	43.6	54.8	66.5	73.0	77.6

Commercial length- and weight-at-age data are variable but indicate no trend for either Gulf of Maine or Georges Bank cod (O'Brien, 1999; Mayo and Col, 2002; O'Brien *et al.*, 2002).

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3.12 Northern Gulf of St. Lawrence (NAFO 3Pn and 4RS)

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The northern portion of the Gulf of St. Lawrence used to support a large standing stock biomass of cod which has been exploited from as early as in the 16th century. This biomass has now largely declined as a result of high fishing mortalities combined with low productivity on a per capita basis (Dutil *et al.*, 1999; Dutil and Brander, 2003). Surplus production is only $218 \text{ g} \times \text{fish}^{-1} \times \text{year}^{-1}$, first to last among 15 stocks examined in the North Atlantic. This results from low growth production ($287 \text{ g} \times \text{fish}^{-1} \times \text{year}^{-1}$ over the period 1974–2001) and low recruitment to the fishery as late as age 3 ($156 \text{ g} \times \text{fish}^{-1} \times \text{year}^{-1}$). Yield to fisheries has averaged $155 \text{ g} \times \text{fish}^{-1} \times \text{year}^{-1}$ over the same period (Dutil and Brander, 2003). The Northern Gulf cod has been under a fishing moratorium since the mid-1990s. Low fishing mortalities in the late 1990s and early 2000s exceeded surplus production and forced a second moratorium that started in 2003. Low productivity in a cold and changing environment and increased natural mortality has been hypothesized to explain why the Northern Gulf cod have failed to recover (Dutil *et al.*, 1998a; 2003a; Lambert and Dutil, 2000). Hypotheses for the failure of the Northern Gulf and other Canadian cod stocks to rebuild after the mid-1990s have been reviewed by Rice *et al.* (2003) in an effort to draw lessons from the present status and recent history of the Northern Gulf fishery and other Canadian fisheries.

Stock and area of distribution

The cod of the Northern Gulf of St. Lawrence (Divisions 3Pn and 4RS) undertake extensive annual migrations (Figure 3.12.1). In winter they gather off southwestern and southern Newfoundland at depths of more than 400 m (200 fathoms). In April and May they move towards the Port au Port Peninsula, on the west coast of Newfoundland (Division 4R), where spawning starts. In 2002, a new zone was established in 4R to protect the spawning stock. It is a sector where any groundfish capture is prohibited between 1 April and 15 June. During the summer the fish continue their migration and disperse towards the coastal zones: along the west coast of Newfoundland (Division 4R) and towards the middle and lower north shore of Quebec (Division 4S). This migration towards the coasts is associated with warmer water and the presence of capelin, the principal prey consumed by cod. Capelin is the dominant fish species consumed by cod less than 65 cm (DFO, 2003b).

The results of the many tagging experiments that have been carried out indicate that generally this stock is isolated from adjacent stocks (those of Divisions 4TVn, 2J+3KL and 3Ps). The stock can sometimes mix in the northwest Gulf, (with stock of Division 4TVn), in the Strait of Belle Isle, (with the 2J+3KL stock), and especially in the area of the Burgeo Bank with the 3Ps stock.

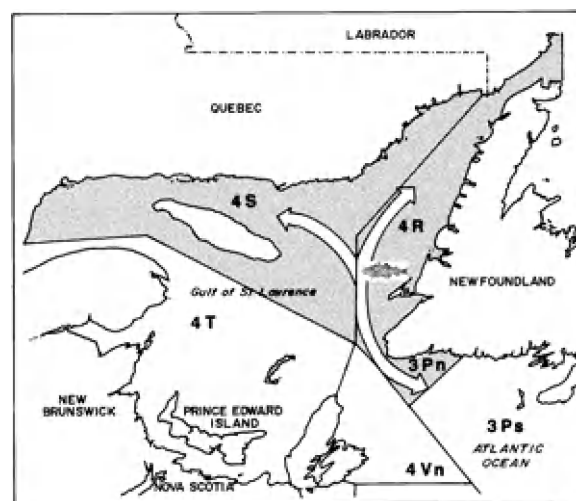


Figure 3.12.1. Cod stock management area in the Northern Gulf of St. Lawrence (4R, 4S and 3Pn). The arrows indicate the general direction of seasonal migrations (winter in southern Newfoundland). The image of the cod indicates the location of major spawning aggregations observed in spring in the late 1990s.

A recent study estimated that 75% of cod present on the Burgeo Bank (3Psa and 3Psd) in winter would have come from the Northern Gulf (Campana *et al.*, 1999).

Evidence of stock discreteness

Historical studies on stock delineation have been available for a while, based on meristics and tagging (Templeman, 1962; 1974; Gascon *et al.*, 1990)

More recently there has been increasing concern about and research into mixing with the adjacent stock in 3Ps during the winter. This has warranted a specific workshop (Chouinard, 2000) and led to many publications on associated research (Campana *et al.*, 1998; 1999; 2000; Bérubé and Fréchet, 2001). Stock management units have not been redefined but closures have been in effect to reduce the impact of fishing on the rebuilding of the Northern Gulf cod stock. Scenarios on the impact of stock mixing on stock assessment have also been conducted recently (DFO, 2003b)

Units for which assessment of spawning-stock biomass and recruitment are available

Stock size is estimated by VPA and the use of a standard assessment package ADAPT (Gavaris, 1988; 1999). Population estimates are expressed in thousands of fish. These are converted to total biomass expressed in thousand tons by using average weights from the commercial fishery. The mature biomass is calculated using annual

maturity ogives (available for only 14 years out of the 29 years included in the VPA).

Time-series of spawning-stock biomass and recruitment data

Adequate commercial sampling is available since 1974 in order to calculate a catch-at-age matrix (Fréchet and Gascon, 1986). Indices of abundance from research vessels are available for the DFO survey since 1990. Industry sentinel surveys, gillnet and longline CPUE series are available since 1995. The most recent VPA estimated beginning of year population numbers at age from 1974 to 2003 (DFO, 2003b; Fréchet *et al.*, 2003).

What is the geographical location of the stock and does it change seasonally?

Summer and winter surveys conducted in the 1980s as well as data from the fishery show that Northern Gulf cod perform seasonal migrations between the overwintering area outside the Gulf in Cabot Strait, and the spawning and feeding areas in the Northern Gulf (Figure 3.12.1). Before the late 1980s, adult cod overwintered in southern 4R and 3Pn, on the northern side of Cabot Strait. They entered the Northern Gulf in spring for spawning and remained there during the feeding period, where they could be found inshore. (Templeman, 1974; Chouinard and Fréchet, 1994; Castonguay *et al.*, 1999). They migrated back to Cabot Strait in late autumn/early winter.

The Northern Gulf of St. Lawrence represents both the spawning and feeding areas for this stock although fish are found more inshore during the feeding season. The Northern Gulf can be thought of as a “large bay” and thus it may represent a suitable region for egg and larval retention. The migration to the outside the Gulf in the autumn could be in response to the cooling of the waters at mid-depth (Castonguay *et al.*, 1999). The migration could also have evolved to avoid the ice-covered waters of the Northern Gulf in winter (Fréchet, 1990).

Recent sentinel mobile surveys conducted in January and March 2002 indicate that in winter the whole stock now seems to be found outside 3Pn+4RS, specifically off Newfoundland's south coast in Division 3Ps. In the summer cod are found throughout the Northern Gulf, although in the current depressed stock state, their distribution is concentrated along the west coast of Newfoundland in Division 4R. This contrasts with the 1980s, where summer surveys showed that a higher proportion of the abundance occurred along the Québec north shore in Division 4S.

What is the depth range and temperature associated with the stock and does it change seasonally?

Since the late 1980s and early 1990s cod have been found deeper in winter, as shown by annual research vessel surveys conducted annually between 1978 and 1994 (Castonguay *et al.*, 1999). While the proportion of traw-

lable biomass deeper than 350 m was always less than 20% before 1989, it increased to over 90% in the early 1990s (Fréchet and Gagnon, 1993; Chouinard and Fréchet, 1994). The median depth where Northern Gulf cod are found in summer and winter is around 150 m and 450 m, respectively (Castonguay *et al.*, 1999). However, summer surveys do not adequately sample fish in shallow waters because depths shallower than 37 m are not sampled. According to the same surveys, cod occupy waters with temperatures around 2°C in summer and 5°C in winter (Castonguay *et al.*, 1999).

Time of spawning

Date of spawning and interannual variability or trend

Spawning takes place from April to June. Peak spawning occurs in May (Ouellet *et al.*, 1997; Méthot, 2002). Spawning seems to begin when fish first enter the Gulf and aggregate in large shoals. Spawning continues as the fish then disperse in smaller groups on their way up north into the Northern Gulf (Ouellet *et al.*, 1997; Méthot, 2002). There is no reliable information on interannual variability or trend.

Time of day when spawning occurs

No information.

Timing of spawning season in relation to planktonic production cycle

The spring phytoplankton bloom typically occurs from April to June as one moves from south to north in the Gulf (considering both Southern and Northern Gulf of St. Lawrence) (Starr *et al.*, 2002). This suggests that spawning may coincide with the spring bloom. There is no information on cycles of secondary production in the Northern Gulf.

Timing of spawning in relation to hydrographic events

No information.

Timing of spawning season in relation to other fish species which spawn in the same location

A spring-spawning-stock of Atlantic herring spawns in the same general area (DFO, 2003a).

Factors affecting reproduction

Temperature and food availability in the fall and winter may explain variations in reproduction in the spring period. In the spring the size of the maturing gonads of more emaciated fish was similar to that of other fish, but poor-condition fish had a larger gonad-to-liver dry weight ratio. This suggests that poor-condition fish might be in a difficult position to meet the energy demand of maturation and spawning once committed to reproduc-

tion (Dutil and Lambert, 2000). Feeding level has been shown to affect the size of the gonads early in the process of maturation (Lambert *et al.*, 1994). Lower gonad-somatic indices and smaller proportions of maturing to non-maturing fish were observed at higher temperatures suggesting that food deprivation may be more detrimental to maturation at higher temperatures (Dutil *et al.*, 2003b). Temperature selection by individual cod during the winter may thus be critical in terms of both survival and reproduction in situations of food shortage and it may also have an influence on the variations observed in the spawning patterns of individuals in the spring in the Northern Gulf (Ouellet *et al.*, 1997).

Location of spawning

Geographic location and extent of spawning area

In the current depressed stock situation the only regions where Northern Gulf cod are known to spawn are Subdivision 3Pn and NAFO Division 4R (Ouellet *et al.*, 1997; Méthot, 2002). In 4R spawning takes place primarily off Newfoundland's west coast in the Esquiman Channel and at a depth of 200–250 m (Figure 3.12.1) (Ouellet *et al.*, 1997). However, mature cod are known to occur elsewhere later in summer (Méthot, 2002). There is also evidence from ichthyoplankton surveys conducted in the mid-1980s that spawning used to occur off Québec's lower north shore (NAFO Division 4S in the Northern Gulf of St. Lawrence) (Ouellet *et al.*, 1994). Furthermore, anecdotal reports from trawlers indicate that cod used to spawn around Anticosti Island (4S).

Does spawning regularly begin in one part of the spawning area and then move on to other parts?

Cod overwinter outside the Gulf (Chouinard and Fréchet, 1994; Castonguay *et al.*, 1999). Spawning begins in 3Pn as cod re-enter the Gulf in spring. Fish keep spawning as they enter 4R on their way north. Fish in spawning condition have been sampled as far north as around 50°N (Méthot, 2002).

Can the location be described in relation to hydrographic features?

Most spawning occurs under the cold intermediate layer, deeper than 150 m (Ouellet *et al.*, 1997).

Can the location be described in relation to other species, including food organisms and predators?

Between 1 and 2 million harp seals leave the Gulf in spring after reproduction. The seals, as they proceed on their way out of the Gulf, may coincide with aggregations of spawning cod.

Can location be described in relation to water mass circulation?

No information.

Biological details

Fecundity

The relationship between potential fecundity and length of female cod captured in May 1995 and 1998 in the Northern Gulf of St. Lawrence indicate that potential fecundity varies from 0.86×10^5 eggs to 12.52×10^5 eggs per female for the size range between 35–62 cm (Lambert and Dutil, 2000; Lambert *et al.*, 2000).

Laboratory experiments conducted in 1995 and 1996 revealed that realised fecundity related positively to female size and condition (Lambert and Dutil, 2000). Length and postspawning condition factor explained 72% of the variability in realised fecundity. Realised fecundity of females in poor condition for different size classes ($K \sim 0.5$) was 2.5–7 times lower than realised fecundity of females in better condition ($K \sim 0.8$ – 0.9).

Evidence of changes in fecundity with time

Significant differences in the relationship between potential fecundity and length were observed between the spring of 1995 and 1998 (Lambert *et al.*, 2000). The higher condition factors observed for prespawning females in 1998 were associated with higher potential fecundities in 1998 than in 1995. The potential fecundity estimate for a 50 cm female was 355 700 eggs in 1995 compared to 545 800 eggs in 1998.

Percentage mature-at-age

Mean length at 50% maturity in 1973 was 46 cm for males and 52 cm for females. Corresponding ages at 50% maturity for males and females were 5.5 and 6.6 years, respectively (Minet, 1977). From 1983–1990, female age at maturity increased from 5.4–6.0 years, after which it declined to 5.3 years by 1994 (Trippel *et al.*, 1997). Female age at maturity further decreased to 4.5 years in 1998 when it reached its lowest value of the series, and increased again to 5.4 years in 2002 (Figure 3.12.2) (Fréchet *et al.*, 2003). Male age at 50% maturity, from 1983–1988, increased from 4.8–5.5 years and then declined to 4.6 years by 1994 (Trippel *et al.*, 1997). Female length at 50% maturity remained between 45–49 cm from 1983–1990 after which it declined to 41 cm by 1994 (Trippel *et al.*, 1997; Ouellet *et al.*, 1997) and to its lowest value (39 cm) in 1998. Female length at 50% maturity increased to 47 cm in 2002. This value would be comparable to the observations for the early eighties (Figure 3.12.2) (Fréchet *et al.*, 2003). Male length at 50% maturity was 44–45 cm from 1983–1985, around 41 cm from 1986–1991 and declined further to 34–36 cm from 1992–1995 (Trippel *et al.*, 1997; Ouellet *et al.*, 1997).

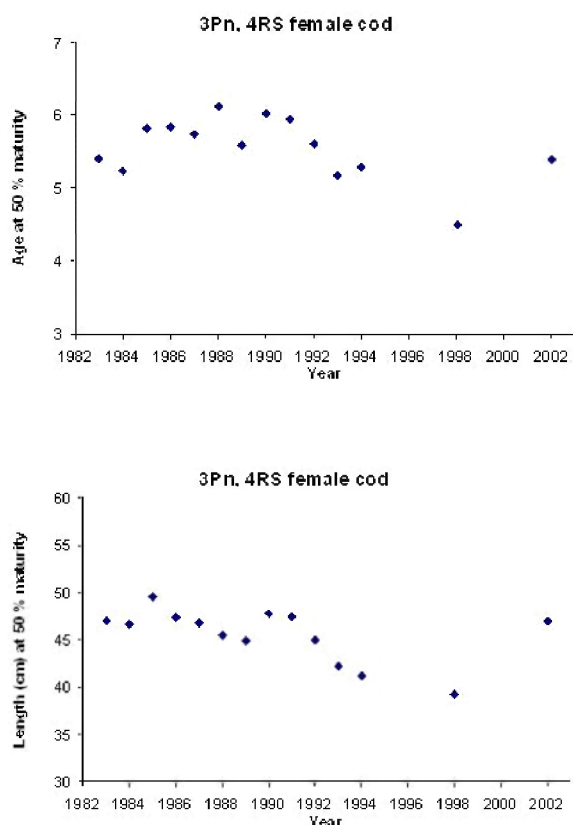


Figure 3.12.2. Changes in age and length at 50% maturity over time for female cod.

Egg size and evidence of changes with age and with time during the spawning season

Cod eggs were sampled over the entire water column in the area of spawning cod in the northeast Gulf of St. Lawrence (3Pn+4RS cod) in the spring (early May and June) from 1993 to 1995 (Ouellet, 1997; Ouellet *et al.*, 1997). In 1993, cod eggs spawned in June (diameter: ~1.37 mm) were smaller than eggs spawned in May (~1.44 mm). In May 1994 cod eggs were more abundant above 100 m and mean diameters ranged from 1.36 mm to 1.46 mm. The analysis of vertical distribution of eggs in relation to the vertical structure of the water column revealed two modes: one between 25–25.5 kg m⁻³ and a second mode between 25.6–26 kg m⁻³ (Ouellet, 1997). The median of the (stage I) egg distribution was at 25.4 kg m⁻³ but there was a slight trend toward a deeper distribution as eggs develop.

Cod spawning activity was monitored under laboratory conditions in 1995 and 1996. Each year, mean egg diameters declined from the first batch to the last batch for each female (Ouellet *et al.*, 2001).

Typical densities, i.e. number per m³ of eggs and larvae

The density of cod eggs reached 338.2 ± 560.4 eggs $\times$ 100 m⁻³ between 50–100 m off the west coast of Newfoundland in May 1993 (Ouellet *et al.*, 1997). However,

over the shoal of spawning cod in May 1994, maximum density of cod eggs never exceeded 30 eggs $\times$ 100 m⁻³.

Incubation rate of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larva

In the laboratory cod eggs incubated at 4°C took on average 21 days to hatch whereas ~45 days were needed for eggs incubated at 0°C (Ouellet *et al.*, 2001).

Larval development rate as a function of temperature

No information.

Condition factor and nutritional status

The condition of cod in the Northern Gulf of St. Lawrence varied significantly with the reproductive status of the fish. Significant changes in the condition factor were observed between prespawning, spawning and spent females between 1994 and 1998, with spent females showing the lowest condition factors (Lambert and Dutil, 2000; Lambert *et al.*, 2000). Female cod captured in the spring of 1994 had significantly lower condition factors than in the other years. The mean condition factor was at the level from which mortality risks are found to increase rapidly in the laboratory (Lambert and Dutil, 1997a).

In the laboratory, potential fecundity was significantly lower in poor-condition females (Lambert and Dutil, 2000). The loss in somatic mass and energy during reproduction in these poor-condition females was nevertheless higher, in relative terms, than the losses experienced by females in good condition. Consequently, energy reserves invested in reproduction by poor-condition females increase their risk of mortality.

Egg and larval mortality rates

Low (1.6 to 2.9%) hatching success (high mortality) was recorded in eggs incubated at 0°C (temperature expected for eggs between ~30 and 100 m in the field in 1993 and 1994), but at 4°C hatching success ranged from 26.3 to 34.8% (Ouellet *et al.*, 2001).

Time of first-feeding of larvae and food at first-feeding

No information.

Food of larvae during development

No information.

Evidence of predation during the egg and larval stage

No information.

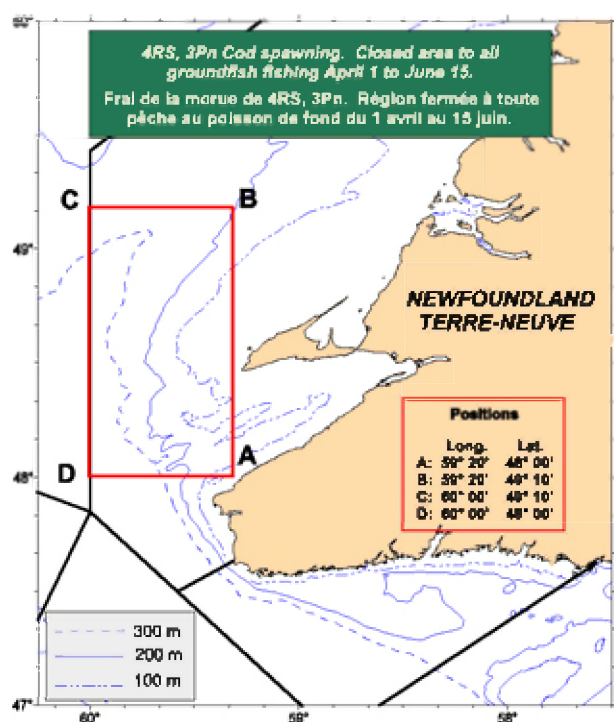


Figure 3.12.3. 3Pn+4RS Cod spawning area closed to all groundfish fishing 1 April to 15 June.

Recruitment

Are there several spawning sites (sub-populations) which contribute to the same stock unit?

The best documented spawning site has been sampled by four distinct surveys since the mid-1980s. Spawning activities have been observed at the same location in April-May, at 250 meters depth off Bay St. George (southern part of 4R along the west coast of Newfoundland). This area was identified in 2002 as a spawning box and closed to all groundfish fishing activities from 1 April to mid-June (Figure 3.12.3).

Fishermen have reported spawning activities in the Blanc Sablon area (eastern portion of 4S), off Anticosti (4S) as well as in the southwestern portion of Newfoundland (3Pn).

Earliest time in life history when year-class strength can be predicted

Although the regular annual stratified random surveys catch fish of age one, it is only by age two and three that the actual strength can be reliably assessed. These annual surveys are conducted in July, August and October. For the August survey, a 44 mm URI shrimp trawl with a 19 mm liner is used. For the other surveys a Rockerhopper 300 trawl with a mesh size of 145 mm and a 40 mm liner is used.

In 2003 the population estimates from these three groundfish surveys for fish at age 2 in 2002 were used

for the first time to estimate year-class strength in a VPA for fish of age 3 (DFO, 2003b; Fréchet *et al.*, 2003).

Hypotheses which have been put forward to account for year-to-year variability in year-class strength

The stock-recruitment relationship for this stock shows a good span (Figure 3.12.4), with high population estimates in the 1980s followed by a precipitous decline to very low values (less than 100 000 t) in the early 1990s. This decline led to a moratorium from 1994 to 1997. The failure of the stock to rebuild led to a second moratorium starting in 2003. While the mature biomass (3+) increased from 1974 and reached a peak close to 400 000 t in 1983, recruitment in the following 6 years (1984–1989) was lower than expected (Figures 3.12.4 and 3.12.5). During the collapse in the late 1980s and early 1990s the stock-recruitment curve did not follow a Ricker style stock-recruitment relationship. Several factors may have played a role in shaping this relationship (Dutil *et al.*, 2003a; Rice *et al.*, 2003), but it has also been speculated that misreporting during this period may have contributed to this lack of fit.

Evidence of long-term trends in recruitment

As seen in the previous section, there is a considerable amount of auto-correlation in the recruitment time-series (Figure 3.12.5) (Fréchet *et al.*, 2003). Recruitment generally closely follows the spawning-stock biomass.

Evidence that variability in recruitment is linked to variability of other species in the same area; the same species in other areas or other species in other areas

Recent recruitment values are very low. Seals have been shown to consume large amounts of small cod (Hammill and Stenson, 2000), which is considered to seriously hamper the rebuilding process.

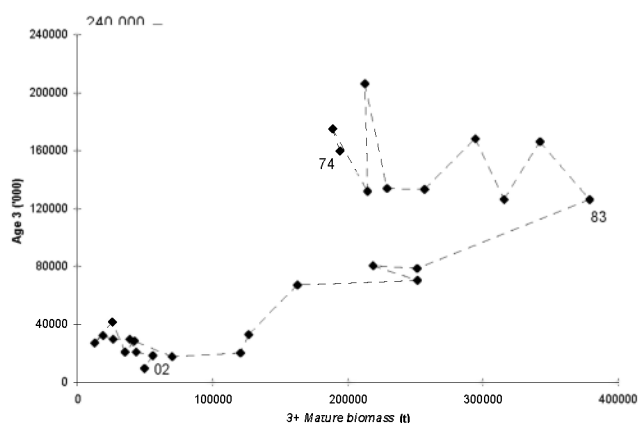


Figure 3.12.4. The stock-recruitment relationship for 3Pn and 4RS cod for the period 1974 to 2002.

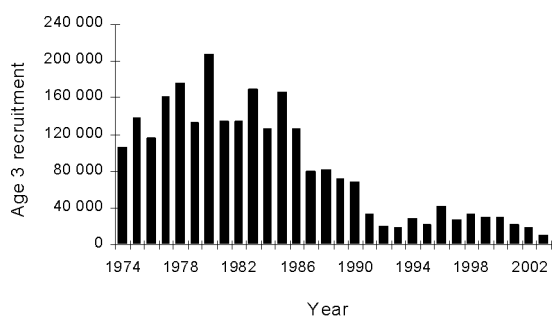


Figure 3.12.5. Estimated recruitment at age 3.

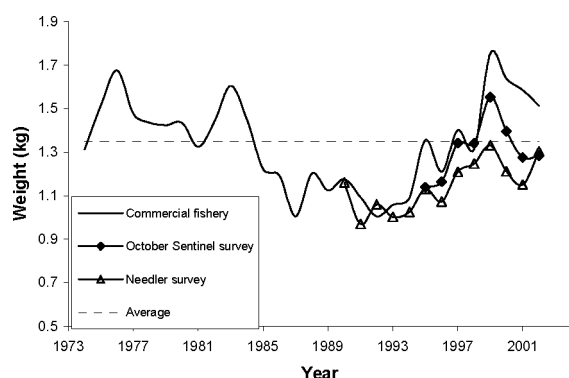


Figure 3.12.6. Weight of Northern Gulf cod at age 6, based on different surveys. The long-term average for the commercial fishery is also shown.

Evidence of inter- or intraspecific competition

Studies show that large cod cannibalize small cod. Based on a large number of samples collected between 1993 and 2002, cod were grouped into four functional length classes. Gadoids, and in particular cod, represented a significant proportion of the diet in larger cod (>50 cm, and particularly those above 70 cm) (Fréchet *et al.*, 2003).

Adult growth

General growth characteristics

Growth production of Northern Gulf cod is very low, 271 g/fish for age groups 3–5 and 287 g/fish for all age-groups combined, second to last among 15 cod stocks examined by Dutil and Brander (2003). Lengths-at-age in the commercial catch averaged 34 cm at age 3, 42 cm at age 4, 50 cm at age 5, 54 cm at age 6, and 64 cm at age 10 in 2002 (Fréchet *et al.*, 2003). This represents the situation for an exclusive fixed gear fishery (longline and gillnet) conducted mainly in summer of 2002.

Von Bertalanffy parameters were estimated by cohort for the 1989 to 1998 cohorts with data collected during the August scientific survey in the period 1990–2002.

Growth coefficient K varies between 0.06 and 0.25 (mean: 0.13) with values of L_{∞} between 68 cm and 153 cm (mean: 100). The low L_{∞} value may be due to low catches of fish older than 10 years in the scientific survey. Moreover, since 1990 the stock is depleted, with very few fish above age 10.

Commercial and research survey data indicate that length-at-age and weight-at-age declined in the 1980s and early 1990s, particularly in older fish (Figure 3.12.6) (Chouinard and Fréchet, 1994; Dutil *et al.*, 1999). This would suggest slower growth rates during that period. Size-at-age has increased in the late 1990s. Growth production varies from year-to-year and this has an influence on surplus production (Figure 5 in Dutil and Brander, 2003). Growth does not take place year round (refer to section on condition factor below); metabolic correlates of growth suggest that Northern Gulf cod experience a period of negative growth in late winter and early summer (Dutil and Lambert, 2000) and a period of fast growth in late summer and early fall (Guderley *et al.*, 1996).

Salinity and dissolved oxygen may have an impact on cod growth in the Northern Gulf. Surface waters are brackish in coastal areas and in the St. Lawrence Estuary whereas the bottom waters in the deep Esquiman and Laurentian Channels are low in oxygen. Deep waters of the Gulf become progressively depleted in oxygen as they flow from the Atlantic upstream towards the estuary and Northern Gulf. In many areas, water is less than 65% saturated with oxygen (>200 m) and in the estuary percentage saturation is down to less than 35% (D'Amours, 1993; Gilbert *et al.*, 1997), even as low as 20% in some areas.

Salinity effects on cod in the wild in the Northern Gulf are undocumented. The effect of low salinity has been studied in the laboratory on adult cod from the St. Lawrence Estuary. Survival was jeopardized below 7 psu (Dutil *et al.*, 1992; Provencher *et al.*, 1993) whereas intermediate salinities promoted faster growth (Lambert *et al.*, 1994; Dutil *et al.*, 1997).

Oxygen saturation levels that killed 50% and 5% of adult cod over 96 h averaged 21% and 28% respectively (Plante *et al.*, 1998). No fish survived at 10% and only a few fish survived at 16% saturation. No mortality occurred between 34–40%. Temperature (2°C and 6°C) had no measurable effect on tolerance. At 10°C hypoxia decreased food consumption. Food consumption in turn explained 97% of the variation in growth (Chabot and Dutil, 1999). Based on oxygen profiles and cod distribution, the loss in growth production due to low oxygen in the Northern Gulf has been estimated to range between 10–20% (Chabot and Couturier, 2002). Northern Gulf cod avoid waters below 35% saturation (D'Amours, 1993).

Evidence for density-dependent growth

Density effects have not been tested for this stock, but it can be observed that larger sizes-at-age were observed in the early 1980s when landings and stock abundance peaked. Sizes-at-age were lowest when the stock was depleted at the time of the first moratorium. They increased again in the post-moratorium period in the absence of any significant change in abundance.

Evidence of temperature-dependent growth

Temperature in 3 layers that have been examined (30–100 m, 100–200 m and 200–300 m) has varied over time with the early 1980s being exceptionally warm and the early 1990s exceptionally cold (Dutil *et al.*, 1999). The composite index of temperature for the range 30–300 m showed a major decline (2°C) in temperature in the period 1980–1991. The slope of the regressions between size-at-age (3 age groups) and four temperature indices were all positive, suggesting slower growth at lower temperatures, but these relations were not significant for the period 1974–1994 (Figure 3.12.7) (Dutil *et al.*, 1999). Northern Gulf cod avoid cold water below 1.5 °C (D'Amours, 1993).

Condition

The condition factor (somatic weight-at-length) is a convenient tool for monitoring levels of energy reserves in Northern Gulf cod (Lambert and Dutil, 1997b). Stocks with fast growth rates and large sizes at age 6 have on average higher condition factors than stocks living in cold water (Figure 9 in Dutil *et al.*, 1999). Northern Gulf cod have on average a low condition factor (range 0.84 to 1.03 in August–September 1972–1996). The condition factor peaks in the fall period and reaches a low in the spring at the onset of spawning (Figure 3.12.8) (Fréchet *et al.*, 2003). Liver fat reserves follow a similar pattern (Lambert and Dutil, 1997a; Dutil *et al.*, 2003a). This suggests that feeding activity is reduced in winter.

Fish condition also declined during the late 1980s and early 1990s. The condition factor observed in spring averaged 0.70. Thus a large proportion of fish had values in the range 0.60–0.70, with some individuals below 0.60 in the Northern Gulf. Low condition factors have far reaching effects. They have been shown to result in natural mortality due to energy exhaustion (Dutil and Lambert, 2000) and increased vulnerability to diseases (Dutil *et al.*, 2001). Mortality is thought to occur in the spring, but some of the survivors may also die off in the following winter as suggested by the proportion of cod with condition factors below 0.75 in late summer (Dutil and Lambert, 2000). Total lack of food during the period January–April would have caused condition to decline to a level at which very high mortality takes place. Actual changes in condition in wild cod were less than predicted from the laboratory experiments, except in the period April–May at the onset of spawning. Thus wild cod were able to meet part of the metabolic costs during winter through

occasional feeding, as confirmed by stomach content data (Dutil *et al.*, 2003b).

Low condition factors also correlate with decreased metabolic capacities in several tissues including muscle, pyloric caeca and intestine (Dutil *et al.*, 1998b; Bélanger *et al.*, 2003; Martínez *et al.*, 2003). As a result, their swimming capacity is reduced (Martínez *et al.*, 2002; 2003) with potential consequences for their ability to feed on mobile prey and to escape predators and fishing gears. They must also increase the size of their pyloric caeca and intestine and enhance the metabolic capacity of those tissues before compensatory growth can take place (Bélanger *et al.*, 2003).

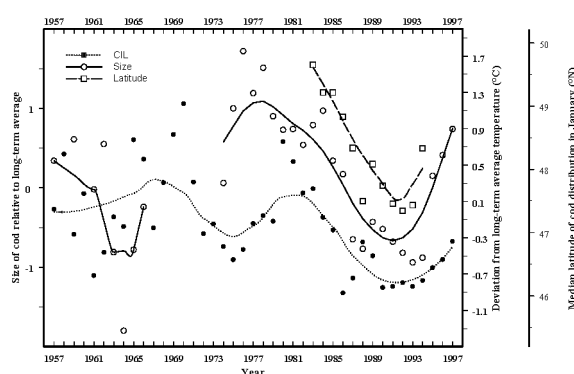


Figure 3.12.7. Size of 4-, 6-, and 8-year-old cod (standardized data), median latitude of cod distribution in January, and deviations from the 1948–1994 mean temperature of the cold intermediate water layer in the Gulf of St. Lawrence for the period from 1957 to 1997. Both commercial data (Helser *et al.*, 1996; Pinhorn, 1969; Chouinard and Fréchet, 1994) and research survey data are used to describe variations in length-at-age. Symbols represent actual observations and lines were smoothed using locally weighted least-squares.

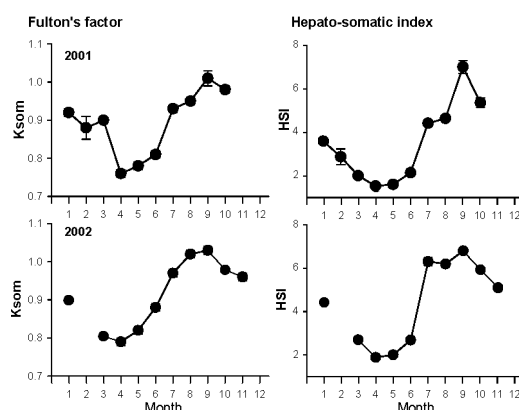


Figure 3.12.8. Seasonal changes in the somatic condition factor and liver-somatic index of Northern Gulf cod for 2001 and 2002.

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prespawning and other aggregations, times and places of spawning, and ancillary information such as growth patterns and relative year-class strength, to determine stock structure within Atlantic Canada. Cod of the southern Grand Bank overwinter on the slopes of the bank and migrate onto the plateau of the bank during summer. Some of these cod may cross into 3L in the area of the Virgin Rocks, and some may even approach the southeastern shores of Newfoundland. Some of the cod that overwinter within 3Ps at the southern end of the Halibut Channel and Green Bank may move onto the Grand Bank during summer.

The distinctiveness of 3NO cod has received support from genetic studies employing analysis of microsatellite loci (Ruzzante *et al.*, 2001; Beacham *et al.*, 2002).

Units for which assessment of spawning-stock biomass and recruitment are available

For the purpose of assessment of the status of the 3NO cod stock, it has been assumed that all cod caught within NAFO Divisions 3NO belong to the 3NO stock. There will undoubtedly be some problems with this convention because of movements of fish across boundaries with adjacent stocks off southern Newfoundland (3Ps) and on the northern Grand Bank (2J+3KL stock).

Time-series of spawning-stock biomass and recruitment data

The most recent assessment of this stock was conducted by NAFO in 2003. Results of a sequential population analysis (SPA) are presented by Healey *et al.* (2003).

The estimates of biomass of cod 3 years and older (Figure 3.13.3) were near 200 000 t during the late 1950s, increased quickly to a peak of almost 400 000 t in 1967, and then declined rapidly to a low of 46 000 t in 1976. There was then a steady rise to a peak of 175 000 t in 1985, followed by a steady decline to 14 000 t in 1993. The biomass reached a nadir in 1995, started to increase a little toward the end of the decade, and has since declined once again.

The increase in 3+ biomass in the mid-1960s was a consequence of good recruitment in the early 1960s (notably the 1962–1964 year classes) (Figure 3.13.4). The rapid decline was primarily caused by intensive fishing. Fishing mortality was reduced considerably during the late 1970s and early 1980s (Healey *et al.*, 2003), and 3+ biomass increased, even though recruitment was not particularly strong (Figure 3.13.4).

The estimates of spawning-stock biomass (SSB) (Figure 3.13.3) follow a trend similar to that of the 3+ biomass, except that the peaks in 3+ biomass in the mid-1960s and mid-1980s were not followed by peaks in SSB.

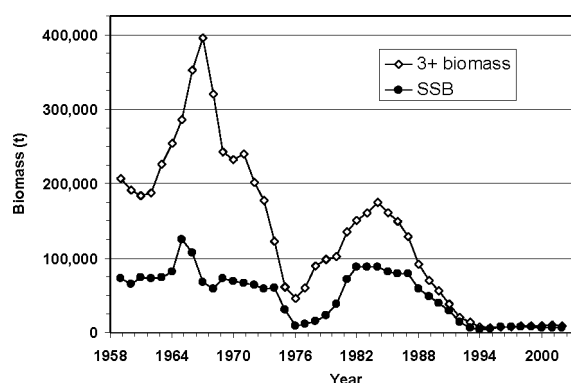


Figure 3.13.3. Cod in Divisions 3NO. Total (3+) biomass and spawning-stock biomass (SSB) (from Healey *et al.*, 2003).

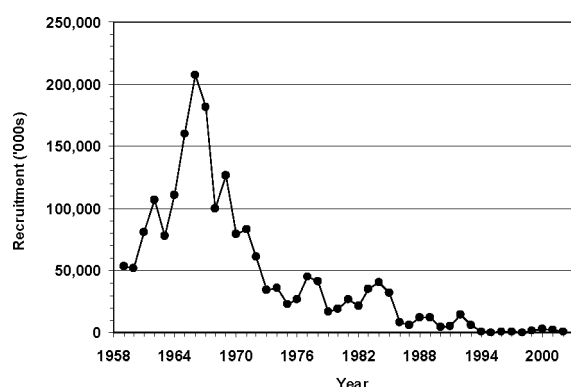


Figure 3.13.4. Cod in Divisions 3NO. Recruitment (numbers at age 3) (from Healey *et al.*, 2003).

Recruitment declined to low levels in the 1970s and 1980s and to very low levels in the 1990s (Figure 3.13.4).

What is the geographical location of the stock and does it change seasonally?

Distribution and migration patterns are summarized above. The cod tend to overwinter on the southeastern and southwestern slopes of Grand Bank, and to spread over the plateau of the bank during summer. The movement onto the slopes in late autumn or winter may be an avoidance of cold water, and the movement back onto the plateau in spring or early summer is presumably related to better feeding conditions on the plateau than on the slope. Colbourne and Murphy (2000) reported that catches during spring surveys tended to be larger during years when water temperatures were higher, supporting an hypothesis that cod migrate onto the plateau later when water temperature is low.

What is the depth range and temperature associated with the stock and does it change seasonally?

There has been no study of either the average depth occupied by the stock as a whole on an annual basis, or of the average temperature experienced by the stock.

The temperature on the southern Grand Bank at the time of the Canadian spring surveys has varied considerably between years. Stansbury *et al.* (2001) illustrated that in one, specific, cold year (1990) the cod were nearly randomly distributed with respect to the available temperature (with the median of the biomass-weighted temperature distribution only slightly above 0°C), whereas in one, specific, warm year (1995) the cod were distributed towards the warmer end of the available temperature distribution (with the median of the biomass-weighted temperature distribution at about 4°C). Colbourne and Murphy (2000) reported that when all data from surveys in 1972–1999 were combined, the cod biomass-weighted temperature distribution was broad, with the 10th percentile, median and 90th percentile at about -0.9°, 0.6° and 2.7°C respectively.

Time of spawning

Date of spawning and interannual variability or trend

In summarizing various reports of spawning time of 3NO cod, Templeman (1981) stated that “cod spawn mainly in April–June and usually in the latter half of April to early June”.

Spawning time was determined from analysis of the spawning stage of cod that were visually examined during research trawl surveys (Myers *et al.* 1993). The day of the year on which 50% of mature females were in a spent state was Julian day 133 ± 28 (May 13) for cod in 3N and day 137 ± 41 (May 17) for cod in 3O. The authors thought that the method would over-estimate the mean spawning date by about 2 weeks. The mean date of spawning in 3NO is about a week earlier than in 3Ps to the west, and 3–4 weeks earlier than 3L to the north.

Time of day when spawning occurs

No information.

Timing of spawning season in relation to planktonic production cycle

See Myers *et al.* (1993) for a comparison between cod spawning dates, *Calanus finmarchicus* seasonal cycles, and two indices from the physical environment (surface temperature and water column stability) for several areas from Greenland to southern Newfoundland (3Ps).

Timing of spawning season in relation to hydrographic events

No information.

Timing of spawning season in relation to other fish species that spawn in the same location

No information.

Location of spawning

Geographic location and extent of spawning area

Cod overwinter on the southwestern and southeastern slopes of the bank, and spread over the plateau of the bank during summer. Earlier reports indicated that the cod spawned while still on the slopes (see review by Fitzpatrick and Miller, 1979), but Hutchings *et al.* (1993) reported that catches of cod in spawning condition during spring surveys were greater on the plateau than on the slope. (See maps in the section on the cod of Labrador and eastern Newfoundland.) The actual locations of most of the spawning by 3NO cod are not well understood because of limited bottom-trawl surveys during spawning periods, the absence of acoustic surveys that might better locate spawning aggregations, the incomplete coverage of early egg surveys, and inadequate knowledge of the drift patterns of eggs, larvae and juveniles.

Does spawning regularly begin in one part of the spawning area and then move on to other parts?

No information.

Can the location be described in relation to hydrographic features?

No information.

Can location be described in relation to other species, including food organisms and predators?

No information.

Can location be described in relation to water mass circulation?

No information.

Biological details

Fecundity

May (1967) provided regression parameters for log-log regressions of fecundity vs. length and fecundity vs. age for cod sampled in 3N (actually 3N and southeastern 3L) in 1964–1965 and 3O (actually 3O and western 3N) in 1965.

	<i>Fecundity - length</i>		<i>Fecundity - age</i>	
Area	Slope	Intercept	Slope	Intercept
3N	3.81	-1.05	1.95	4.40
3O	3.88	-1.27	2.47	3.85

Evidence of changes in fecundity with time

No information.

Percentage mature-at-age

Historically, cod on the southwestern Grand Bank had the greatest size and age at sexual maturity of all cod in the Newfoundland-Labrador area. Fleming (1960) reported that the age at 50% sexual maturity (A_{50}) was 7.5 in 1947–1950.

Maturation has been determined visually during Canadian research trawl surveys in spring. The data are highly variable, particularly in recent years (partly as a consequence of small sample sizes). Female age at 50% maturity (A_{50}), estimated by cohort, was generally between 5.9 and 7.4 for cohorts from the 1950s and 1960s, but declined steadily through the 1970s to a low of about 5.6 for the 1976 cohort. A_{50} then increased to about 6.6 for the 1979–1981 cohorts, but declined once again to between 4.8 and 5.5 for cohorts of the 1990s.

Egg size and evidence of changes with age and with time during the spawning season

No information.

Typical densities, i.e. number per m^3 of eggs and larvae

No information.

Incubation rate of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larva

No information.

Larval development rate as a function of temperature

No information.

Condition factor and nutritional status

No information.

Egg and larval mortality rates

No information.

Time of first-feeding of larvae and food at first-feeding

No information.

Food of larvae during development

No information.

Evidence of predation during the egg and larval stages

No information.

Recruitment

Are there several spawning sites (sub-populations) that contribute to the same stock unit?

Cod that overwinter on the southeastern slope may have different spawning areas from those that spawn on the southwestern slope, but there has been insufficient study to identify the number of specific spawning sites within 3NO as a whole and the extent to which such sites are discrete.

Earliest time in the life history when year-class strength can be predicted

No information.

Hypotheses that have been put forward to account for year-to-year variability in year-class strength

Characteristics of spawning-stock have been explored (Morgan *et al.*, 2000).

Evidence of long-term trends in recruitment

The SPA output indicates that recruitment has experienced a dramatic decline since the mid-1960s. Recruits per spawner have been at a relatively low level since the mid-1980s (Morgan *et al.*, 2000; Healey *et al.*, 2003).

Evidence that variability in recruitment is linked to variability of other species in the same area, the same species in other areas, or other species in other areas

No information.

Evidence of inter- or intraspecific competition

No information.

Is recruitment related to SSB or any environmental factors?

Stock-recruit plots from SPA output (Morgan *et al.*, 2000; Healey *et al.*, 2003) illustrate that recruitment tends to be low when the SSB is low. However, the stock was much more productive at moderately high SSBs during the 1960s than at comparable levels during the

1980s, and more productive at relatively low SSBs during the late 1970s than at comparable levels during the early 1990s.

Morgan *et al.* (2000) explored the possible effect of spawning-stock characteristics on recruitment of 3NO cod and two other cod stocks (2J+3KL and 3Ps), plus one American plaice stock. A Beverton-Holt stock-recruit model was fitted to the output from an SPA, and residuals were compared to the weighted mean age of the spawning-stock, the proportion of first-time spawners and the proportion of females in the mature population. Because results were not consistent between stocks and were difficult to interpret, the reader is referred to the paper for details.

Migration

See under stock and geographic distribution above.

Adult growth

Evidence for density-dependent growth

No information.

Evidence of temperature-dependent growth

No information.

Evidence of size-selective effects on growth. What are the general growth characteristics?

Historically, cod on the southwestern Grand Bank had the fastest growth rate and largest theoretical maximum length (L_{∞} in von Bertalanffy growth curve) of all cod in the Newfoundland-Labrador area (Fleming, 1960; May *et al.*, 1965).

Mean lengths-at-age estimated from sampling during Canadian surveys in the springs of 1972–1997 are available by Division and for 3NO combined (Stansbury *et al.*, 1998). In general, mean lengths-at-age increased from the early 1970s to the early 1980s and then declined a little. There was little consistent change from the late 1980s to the late 1990s.

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3.14 Southern Gulf of St. Lawrence (NAFO 4T-Vn (November–April))

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Stock and geographic distribution

Southern Gulf cod have been exploited commercially since at least the 16th century (De la Morandière, 1962; Chaussade, 1983; De la Villemarqué, 1990). Landings varied between 20 000–40 000 t annually between 1917–1940, and then began to increase to a peak of over 100 000 t in 1958 (Chouinard and Frechet, 1994). The fishery was primarily prosecuted with hook and line until the late 1940s, when a ban on otter trawling was lifted (Paloheimo and Kohler, 1968). Landings remained relatively high in the 1960s and early 1970s, in the range of 60 000 t. TACs were first imposed in 1974, and these became restrictive as the stock declined in the mid-1970s. The stock recovered somewhat, and landings returned to the 60 000 t range during the 1980s. During the 1980s, the fixed gear fishery declined drastically, and the fishery was mainly prosecuted by mobile gear until it was closed in September 1993, due to low abundance. The fishery has been re-opened since 1998. The winter fishery has remained closed amid concerns for the resident stock in Sydney Bight (4Vn). Since the re-opening, catches have been in the order of 6000 t, only a fraction of historical levels. Productivity of the stock has been low in the 1990s and natural mortality is estimated to be about twice the historical levels (Sinclair, 2001). The increase in natural mortality corresponds to the increase in abundance of grey seals in the area (Chouinard *et al.*, 2002). Despite the moratoria and the low level of catches in recent years, the stock remains at a low level and is expected to decline slightly in the short term, even with no fishery (Chouinard *et al.*, 2003).

Evidence of stock discreteness

An early view of Southern Gulf of St. Lawrence cod stock structure was presented by Templeman (1962). Based largely on studies of vertebral counts and early tagging studies (e.g. McKenzie, 1956; McCracken, 1959), he concluded that there were distinct cod stocks off the Gaspé Peninsula, off the Baie des Chaleurs, off PEI, off western Cape Breton, and in the Sydney Bight region (Figure 3.13.1). He acknowledged that there was considerable mixing between the Gaspé, Baie des Chaleurs and PEI components, and indicated that they may not prove to be as separate as was then indicated. He also mentioned the possible existence of a Magdalen Island stock, but seemed doubtful that it was a distinct stock. Although there may be some separate components, the extent of mixing at various times of the year has led to the designation of cod in the Southern Gulf as one stock for fishery management purposes (Halliday and Pinhorn, 1982). The stock is considered to be discrete from adjoining areas although limited mixing can occur

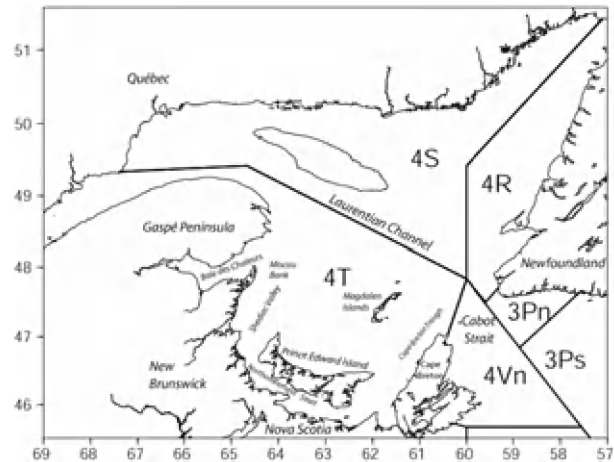


Figure 3.14.1. Gulf of St. Lawrence showing Northwest Atlantic Fisheries organizations (NAFO) areas and place names mentioned in the text.

with the Northern Gulf cod stock (3Pn, 4RS) within one area (Sept-Îles, Québec) in summer (Jean, 1963b). During the overwintering period, the stock also mixes with the resident Sydney Bight (4Vn) resident cod (McKenzie, 1941; 1948; Powles, 1959; Martin, 1962; Jean, 1964; Martin and Jean, 1964; Halliday, 1974; Templeman, 1974). Discreteness of cod from the Southern Gulf of St. Lawrence has also been confirmed with otolith elemental composition analyses (Campana *et al.*, 1999; 2000). Southern Gulf cod are also distinct from all neighbouring stocks on the basis of vertebral number (Swain *et al.*, 2001). Vertebral number did not differ between eastern and western regions of the Southern Gulf, and thus provided no evidence for separate eastern and western stock components (Swain *et al.*, 2001). During their feeding season in September in the Southern Gulf, mean vertebral number of cod increases steadily with depth from 25 to over 175 m. (Swain and Frank, 2000). This could be caused by mixing between Southern and Northern Gulf stocks on the Magdalen Shallows, but it would require much more extensive mixing than is indicated by tagging studies. Alternatively, this pattern may indicate fine-scale spatial structure within the population involving an association between vertebral number and habitat selection. During the overwintering period, vertebral numbers suggest that the cod on the southern flank of the Laurentian Channel in Cabot Strait come almost entirely from the Southern Gulf (Swain *et al.*, 2001).

Units for which assessment of spawning-stock biomass and recruitment are available

Historically, the unit for the assessment of this stock was the Northwest Atlantic Fisheries Organization (NAFO—see Figure 3.14.1) areas 4T and 4Vn (January–April). However, historical tagging information (Martin and Jean, 1964; Kohler, 1975) and fishery observations indicate (Lambert, 1993; Sinclair and Currie, 1994) that the fall migration begins in late October and cod become concentrated off western Cape Breton in November as they move into 4Vn (Sydney Bight) (Figure 3.14.2). As a result, since 1994 the management unit has been 4T and 4Vn (November–April) (Sinclair *et al.*, 1994). Recent analyses (Comeau *et al.*, 2002) indicated that the migration timing into 4Vn, which used to be in early December in the 1970s, is now in late October/early November. This is consistent with the units for which assessment data are available.

Annual stock assessments have been conducted since 1974. The stock was originally assessed under the auspices of the International Commission of Northwest Atlantic Fisheries (ICNAF) but since 1978 assessments have been conducted by the Canadian Department of Fisheries and Oceans.

Time-series of spawning-stock biomass and recruitment data

Trends in population abundance, biomass and recruitment are available from VPA from 1950 to the present (Figure 3.14.3). However, uncertainties in nominal catches and poor sampling intensity prior to 1970 (Maguire *et al.*, 1983) restrict the usefulness of the time-series. Since 1971, independent estimates of relative abundance, biomass and recruitment of the stock are available from an annual stratified random survey conducted in the Southern Gulf of St. Lawrence during September. Three survey vessels have been used, the “E. E. Prince” from 1971–1985, the “Lady Hammond” from 1985–1991, and the “Alfred Needler” from 1992 to the present. Comparative fishing experiments were conducted each time the vessel changed and conversion factors have been applied where necessary (Nielsen, 1989; 1994; Swain *et al.*, 1995). This index is used in the calibration of VPA. Data from the survey have also been used extensively to examine the population dynamics of the stock (e.g. Sinclair, 1998; 2001). Other indices of abundance include an otter trawl catch rate series (1983–1992) and a series of sentinel surveys started in the mid-1990s (Chouinard *et al.*, 1999a; 2003). Sentinel survey abundance indices for cod are constructed from limited removals by commercial fishing vessels following a scientific protocol.

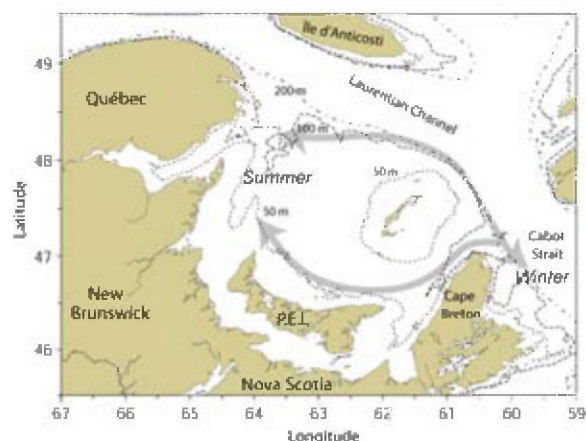


Figure 3.14.2. Southern Gulf of St. Lawrence showing the 50, 100, and 200 depth contours and general migration pattern for the Southern Gulf stock.

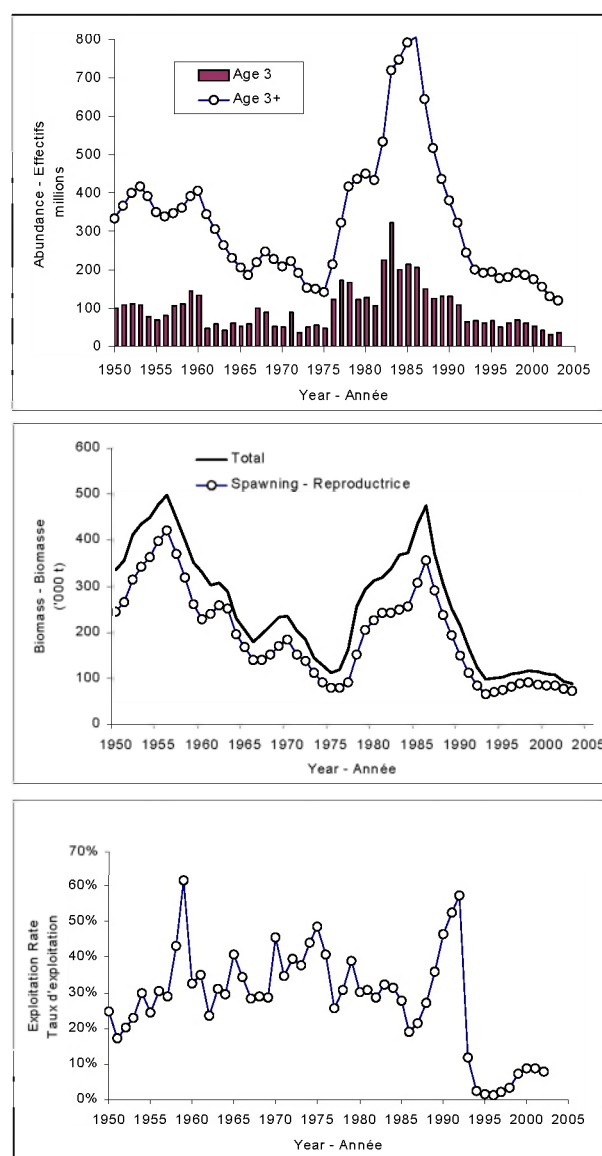


Figure 3.14.3. Recruitment (age 3) and population (age 3+) abundance (top), spawning biomass (middle) and exploitation rate (7+) (bottom) trends for the Southern Gulf of St. Lawrence cod stock.

Time of spawning

Date of spawning and interannual variability or trend

Spawning generally occurs from April to September. Based on the abundance of females in spawning condition, peak spawning was determined to occur likely in late June (Powles, 1958). However, Jean (1963a) examined seasonal samples of eggs and larvae and found the highest densities of cod eggs to occur in May. Based on ichthyoplankton surveys conducted in the mid-1970s, Lett (1980) concluded that the spawning season for cod in the Southern Gulf reached a peak by 20 May and was largely over by 15 June. Schwalme and Chouinard (1999) noted that gonadosomatic index (GSI) attained maximum values in April and May and that there was a large increase in the number of fish with low GSI values in samples collected in June in 1992 and 1993. This suggests that peak spawning tends to occur in May-June.

Time of day when spawning occurs

No information is available for this stock.

Timing of spawning season in relation to planktonic production cycle

The spawning period occurs shortly after the spring bloom which tends to occur during April (de Lafontaine *et al.*, 1991). Primary production is also very high in the area in the period from May to September (Pocklington, 1988; de Lafontaine *et al.*, 1991).

Timing of spawning season in relation to hydrographic events

The entire area where cod spawn is heavily influenced by the St. Lawrence River discharge (RIVSUM) through the Gaspé current. Net transport over the Southern Gulf is in a southeasterly direction (Trites, 1972).

Timing of spawning season in relation to other fish species which spawn in the same location

Although the exact spawning sites are not known, American plaice (*Hippoglossoides platessoides*) has a similar distribution to cod and also spawns in the late spring-early summer (Scott, and Scott, 1988). Most flat-fish (winter flounder, witch flounder) and numerous other marine fishes also spawn during that time (Scott and Scott, 1988). Spawning of mackerel also occurs in the Southern Gulf at about the same time (Sette, 1943). Spring spawning Atlantic herring also tend to spawn in inshore waters during that time (de Lafontaine *et al.*, 1984).

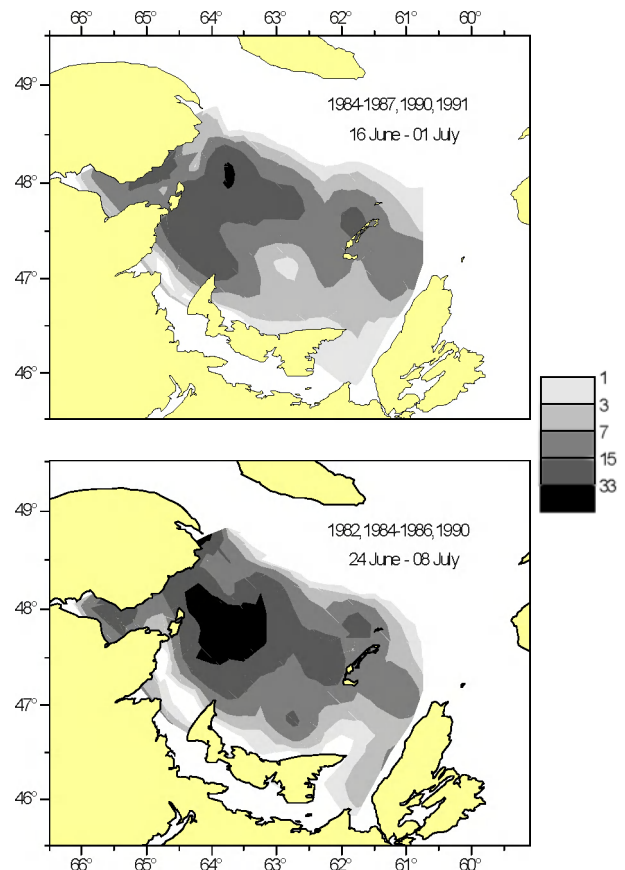


Figure 3.14.4. Distribution of cod eggs in mackerel egg surveys of the Southern Gulf of St. Lawrence, 1982–1991 (from Castonguay and Swain, 2001)

Location of spawning

Geographic location and extent of spawning area

The exact spawning areas are not precisely known. Fish in spawning condition can be found over a wide area in the western part of the Southern Gulf (Powles, 1958). Egg and larvae surveys indicate that the early life history stages are widely distributed over the Southern Gulf of St. Lawrence in June (Castonguay *et al.*, 1998). The distribution of cod eggs from samples collected during a mackerel egg and larvae survey in June suggest that the main spawning area is located in the western Southern Gulf in the area of the Gaspé Coast, Miscou Bank, the Shediac Valley, and the western coast of the Magdalen Islands (Castonguay and Swain, 2001 (Figure 3.14.4); see also de Lafontaine *et al.*, 1984). Larvae tended to be found to the south and east of the egg concentrations, which is consistent with the circulation patterns over the Magdalen Shallows (Trites, 1972).

Does spawning regularly begin in one part of the spawning area and then move to other parts?

Not precisely known but indications are that peak spawning occurs later (late June and July) in the Baie des Chaleurs (de Lafontaine *et al.*, 1984).

Can the location be described in relation to hydrographic features?

Spawning appears to occur in waters of 35 to 100 m depth. Eggs and larvae are found primarily at the thermocline (12–20 m) (de Lafontaine, unpublished).

Can location be described in relation to other species, including food organisms and predators?

Cod are thought to spawn in the same area as where mackerel are also spawning at that time of year. There are also herring spawning beds inshore from these areas. Both herring and mackerel are thought to be predators of the early life stages of cod (Lett, 1980; Swain and Sinclair, 2000). In recent years, herring is an important food component in the diet of large cod (Hanson and Chouinard, 2002).

Can location be described in relation to water mass circulation?

The main area of spawning is influenced by the strong (6–10 cm s^{-1}) coastal Gaspé current caused primarily by the freshwater discharge from the St. Lawrence estuary and wind forcing (Trites, 1972; Koutitonsky and Bugden, 1991). During summer, surface circulation patterns in the main area of spawning are generally in a north to south direction sweeping over the Magdalen Shallows then in an easterly direction to Cabot Strait in the eastern Southern Gulf.

Biological details

Fecundity

Two studies of fecundity have been conducted for this stock (Powles, 1957; 1958; Buzeta and Wainwood, 1982). As in other stocks, there is a strong relationship between fecundity and length (Powles, 1958). Powles (1958) found that a 51 cm cod can produce 200 000 eggs while a 140 cm fish could produce up to 12 million eggs. Buzeta and Wainwood (1982) estimated specific fecundity to be 379 eggs g^{-1} . Relationships between fecundity (number of eggs) and length (cm) derived from the studies above are as follows:

$$F = 0.38 \times L^{3.5}, n=30, r=0.81 \text{ (Powles, 1957)}$$

$$F = 1.10 \times L^{3.28}, n=43, r=0.83 \text{ (Buzeta and Wainwood, 1982)}$$

Evidence of changes in fecundity with time

Comparison of fecundity at length from the two fecundity studies (Powles, 1957; Buzeta and Wainwood, 1982) suggest that fecundity was lower in 1981 than in the mid 1950s. Depending on length, fecundity was 1.7 to 2.2 times higher in the 1950s.

Percentage mature-at-age (including the population not on the spawning grounds). Length at 50% maturity

Powles (1958) examined size at maturity for 1955–1956 and found that it ranged from 50 to 57 cm (about 5 and 6 years of age). Other visual maturity determinations of cod have been conducted routinely in fixed-station groundfish surveys conducted from 1959–1969 and in the stratified random surveys conducted in September in the Southern Gulf of St. Lawrence (1971–2002). These surveys were conducted well after the peak of the spawning season. Beacham (1983) determined the maturity-at-age from these surveys and found that maturity-at-age in the late 1950s and early 1960s was similar to that reported by Powles (1958). However, thereafter maturity of ages 3–5 increased continuously until the late 1970s when age at 50% maturity was 3.6 years for both sexes. However, Trippel *et al.* (1997) compared visual and histological maturity determination from surveys conducted during spawning and those conducted after the spawning season. They concluded that visual maturity determinations conducted after spawning were unreliable. Observations conducted at the end of the spawning seasons were performed from 1990 to 1995 for the stock and these are considered reliable. During that period, the age of 50% maturity for females increased from 4.5 to 5.1 years while male age at 50% maturity varied between 4.0 and 4.8 years. Average maturity-at-age over the time period from Sinclair *et al.* (1995) was as follows:

Age	3	4	5	6	7	8–15
% mature	0.121	0.368	0.721	0.905	0.974	1.000

Egg size and evidence of changes with age and with time during the spawning season

Mature eggs are greater than 250 microns (Buzeta and Wainwood, 1982). Ouellet *et al.* (2001) conducted a study on the neighbouring Northern Gulf of St. Lawrence stock and found mature egg size to range from 1.2 to 1.8 mm. Egg size was highest in the first batches produced and declined with batch number.

Typical densities, i.e. number per m^3 of eggs and larvae

In areas of concentration, densities can be around 2.5 eggs m^{-3} (Lett *et al.*, 1975). In egg and larvae surveys conducted between 1982 and 1991 (Castonguay *et al.*, 1998), the mean number of egg m^{-2} varied between 0 and 21.4 eggs m^{-2} . The overall average for all the surveys was 5.6 eggs m^{-2} .

Incubation rate of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larva

No information is available for this stock in particular.

Larval development rate as a function of temperature

No information is available for this stock in particular.

Condition factor and nutritional status

There is no information available for this stock on condition factor and nutritional status of larvae. For juveniles and adults, there is a strong seasonal cycle in condition. Body condition is low in early spring until after spawning (Schwalme and Chouinard, 1999). After spawning in spring and early summer, cod condition improves during the feeding season until late fall when cod migrate to Sydney Bight. Cod feed little over winter and condition progressively declines until the next spawning season.

In addition to seasonal patterns, age, depth and year have significant effects on the variation in cod condition. Generally, condition of cod varies according to depth (Chouinard and Swain, 2002). Cod in shallow and intermediate depths are in better condition than those found in deeper waters. However, the bathymetric pattern in cod condition also appears to be linked to density-dependent mechanisms. During the period of high abundance in the 1980s, the condition index was highest in the shallower waters, while in periods of low abundance (1970s and 1990s) condition was similar at shallow and intermediate depths. These results combined with the propensity of Southern Gulf cod to be found in shallower waters at low abundance (Swain, 1993; Swain and Wade, 1993) suggests that intrinsic habitat quality for cod is higher in shallower waters in the Southern Gulf of St. Lawrence.

The study also reveals significant interannual changes in condition. Generally, condition was high in the 1970s and low in the 1980s. Although condition was high during the 1970s, a period of low abundance, condition was only about average in the 1990s and did not return to the high levels of the 1970s.

Egg and larval mortality rates

Based on weekly samples over the spawning season, mortality from egg stage I to larvae is estimated to be 17.1% day⁻¹ (de Lafontaine, unpublished).

Time of first-feeding of larvae and food at first-feeding

No information is available for this stock.

Food of larvae during development

No information is available for this stock.

Evidence of predation during the egg and larval stages

Pelagic fish (primarily mackerel and herring) are thought to be important predators of egg and larval stages (Lett, 1980; Swain and Sinclair, 2000)

Recruitment

Are there several spawning sites (sub-populations) which contribute to the same stock unit?

This is not known precisely. Spawning appears to be widespread over the Southern Gulf. Lett (1980) identified about three concentrations but these were not completely discrete. Similarly, the analysis of Castonguay and Swain (2001) suggests a few adjoining areas of higher concentrations (Baie des Chaleurs, Miscou Bank –Shediac Valley and the western coast of the Magdalen Islands).

Earliest time in the life history when year-class strength can be predicted

Very large year classes can be detected at age 1 from research surveys (Chouinard and Sinclair, 1989). Relative year-class abundance can be reliably determined from analyses of research and sentinel survey abundance indices at age 2 (Sinclair and Chouinard, 1992; Chouinard *et al.*, 1999b).

Hypotheses which have been put forward to account for year-to-year variability in year-class strength

A number of hypotheses have been examined and tested (Swain *et al.*, 2000). Lett (1980) proposed that cod recruitment was negatively influenced by pelagic fish (mackerel) abundance. Swain and Sinclair (2000) found strong support for the hypothesis. Recruitment is also more strongly linked to spawning biomass of cod when the effect of pelagic biomass is taken into account.

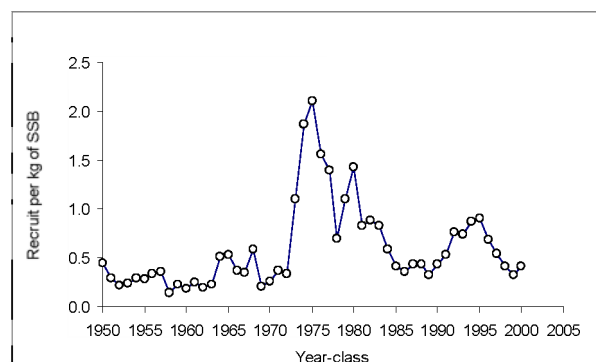


Figure 3.14.5. Recruitment rate (fish × kg⁻¹) of southern Gulf of St. Lawrence cod.

Variation in recruitment rate of cod was not linked to changes in seal population abundance. Several environmental factors (e.g. RIVSUM, air temperature, minimum cold intermediate layer temperature, North Atlantic Oscillation (NAO) index) were all found to be non-significant when accounting for auto-correlation in the series (Swain *et al.*, 2000). However, the last appearance of ice accounted for a small fraction of the variation in cod pre-recruit survival. Recruitment rate tends to be better when the timing of ice melt in the spring is near average. Recent analyses (D. P. Swain, unpublished analyses) have confirmed the strong negative effect of pelagic fish biomass (herring and mackerel) on cod recruitment rate in the Southern Gulf and also suggest that recruitment success is poor in warm springs. Recruitment rate of Southern Gulf cod appears to be unrelated to variation in spawning-stock characteristics, such as age diversity of spawners, mean age and size of spawners, proportion of old fish in the spawning-stock and measures of growth and condition such as weight-at-age (Swain and Chouinard, 2000).

Evidence of long-term trends in recruitment

Recruitment was highest in the late seventies and early eighties, however the number of recruits produced per unit of spawning biomass was highest in the mid-1970s (Figures 3.14.3 and 3.14.5).

Evidence that variability in recruitment is linked to variability of other species in the same area; the same species in other areas or other species in other areas?

Variability in recruitment appears to be inversely related to pelagic fish (mackerel and herring) biomass (Lett, 1980; Swain and Sinclair, 2000). Recruitment of large year classes tends to occur at about the same time in adjoining cod stocks (Northern Gulf cod stock (Chouinard and Frechet, 1994) and in northern stocks in the Canadian Atlantic (Sinclair, 1996)).

Evidence of inter- or intraspecific competition

Density-dependent distribution (Swain and Wade, 1993; Swain, 1993; Swain and Sinclair, 1994), condition (Chouinard and Swain, 2002) and growth (Paloheimo and Kohler, 1968; Crabtree and Ware, 1975; Sinclair *et al.*, 2002a; Swain *et al.*, 2003) suggest that there is intra-specific competition when abundance is high. Densities of cod on their feeding grounds in the Southern Gulf appear to be relatively high compared to other areas, perhaps resulting in unusually strong density-dependent effects in this population (Swain *et al.*, 2003). The strong density-dependent effects observed in this population may also reflect the exceptionally great increase in the abundance of this stock in the late 1970s and early 1980s. Abundance in the mid-1980s appeared to be twice the previous peak abundance in the early 1950s. Competitive effects would have been especially strong in the 1980s because size variation was small compared to the wide range of sizes and ages in the population during earlier periods of high abundance.

Migration

Evidence of adult migration

Adult Southern Gulf cod have long been known to migrate from the Southern Gulf in summer to the Sydney Bight in winter (McKenzie, 1941; Halliday and Pinhorn, 1982). Historically, the fishery has taken advantage of this characteristic by concentrating fishing activities on migratory aggregations in spring and fall (Chouinard and Frechet, 1994).

Where and when do they migrate?

During the summer, cod are widely distributed over the shallow shelf of the Magdalen Shallows from the Gaspé Peninsula and northern N.B. to Cape Breton Island (Jean, 1964; Swain, 1993). Early on, the Southern Gulf stock was known to move east out of the Gulf in winter, although the extent of the migration appeared to vary from between 4Vn and eastern Banquereau. Tagging studies (Martin and Jean, 1964; Kohler, 1975) and fishery observations indicate (Lambert, 1993; Sinclair and Currie, 1994) that the fall migration begins in late October and cod become concentrated off western Cape Breton in November as they move into 4Vn (Sydney Bight). It appears that the migration out of the Gulf in the 1990s occurred about one month earlier than it did in the 1970s (Comeau *et al.*, 2002). The stock over-winters in 4Vn and northern 4Vs, along the edge of the Laurentian Channel (Jean, 1964; Halliday and Pinhorn, 1982; Clay, 1991; Chouinard, 1994; Campana *et al.*, 1999). The return migration begins in mid-April, although in some years (1991–1992), it appears that this was delayed by the late break-up of the winter ice (Sinclair and Currie, 1994). As a result of this migration, the management unit for this stock includes all of 4T and catches in 4Vn during November–April. In some years, catches in 4Vs in January–April are attributed to this stock (Hanson, 1995).

Hypotheses for purpose of the migration

It is likely that cod migrate from the spawning and feeding grounds of the Southern Gulf to the overwintering areas in Sydney Bight to avoid freezing (Swain *et al.*, 1998). The shallow waters (<100 m) of the Southern Gulf are covered with ice over winter and temperatures throughout the water column are near the freezing point (-1.5°C) in winter. In winter, median temperatures occupied by Southern Gulf cod in the deeper waters of the southern flank of the Laurentian Channel vary from 4.9 to 5.2°C , which is considerably warmer than the median temperatures occupied on the feeding grounds in September (Swain *et al.*, 1998). Recent work has also shown that cod feed little while on the overwintering grounds (Schwalme and Chouinard, 1999). These high temperatures occupied over winter are energetically costly and result in a relatively rapid depletion of energy reserves over winter. However, they are thought to promote rapid gonad maturation in time for spring spawning (Castonguay *et al.*, 1999).

Comeau *et al.* (2000; 2001) examined the role of thyroid hormones in the migration. It appears that the seasonal variation in the thyroid hormone T4 was linked to the photoperiod and not water temperature (Comeau *et al.*, 2000). Increasing thyroid hormone production appeared to coincide with the onset of the fall migration suggesting that their production facilitates migration through enhanced metabolism, sensory physiology and swimming capacity (Comeau *et al.*, 2001). However, variation in the timing of the migration, although relatively low, also suggests that other factors (abundance of prey and abundance of older fish) may also play a role in determining the onset of migration (Comeau *et al.*, 2002).

Adult growth

Evidence for density-dependent growth

Growth has been shown to be inversely related to abundance in this stock (Paloheimo and Kohler, 1968; Crabtree and Ware, 1975; Sinclair *et al.*, 2002a; Swain *et al.*, 2003). Recent analyses (Sinclair *et al.*, 2002a; Swain *et al.*, 2003) have examined the effect of size-selective mortality, temperature and density on growth. Sinclair *et al.* (2002a) found that, when testing these factors simultaneously, size-selective mortality was most important but density also had a significant effect. Temperature was also found to have a significant positive effect but the effect was minor compared to the other two factors. However, Swain *et al.* (2003) found that the strengths of the effects of density and temperature on growth were similar. The latter two analyses differed in a number of aspects. Sinclair *et al.* (2002a) used survey estimates of population abundance and included ages 5–11 in the analysis while the study by Swain *et al.* (2003) used SPA population abundance, and included ages 4–10 in the analysis. However, the main difference was that Sinclair *et al.* (2002a) predicted length by accumulating length increments starting at age 4 and accounting for growth variation in earlier years by including mean back-calculated length-at-age 4 for each cohort as a covariate while Swain *et al.* (2003) predicted length by accumulating predicted length increments starting at age 1. This suggests that much of the temperature effect on growth of Southern Gulf of St. Lawrence cod occurs at early ages (1–4).

Evidence of temperature-dependent growth

Temperature-dependent growth has been documented for this stock with faster growth occurring at warmer temperatures. (Campana *et al.*, 1995; Sinclair *et al.* 2002a; Swain *et al.*, 2003). There were differences in the importance of the temperature effect on growth in the most recent studies as described above.

Evidence of size-selective effects on growth. What are the general growth characteristics?

Size-selective mortality likely caused by selectivity of fishing gear has been shown to affect size-at-age for this

stock (Hanson and Chouinard, 1992; Sinclair *et al.*, 2002a; 2002b). Striking changes in the direction and form of size-selective mortality occurred over the 1970s and 1980s (Sinclair *et al.*, 2002b). Survival was greatest for fast-growing fish early in this time period and for slow-growing fish later in the time period. There was an intervening period when size selection was disruptive, with lowest survival for fish with intermediate growth rates. This variation in size selection was the dominant factor in accounting for variation in size-at-age of adult cod after controlling for variation in juvenile growth (Sinclair *et al.*, 2002a). Swain *et al.* (2003) did not test for size-selective effects; however, they noted that strong residual patterns, which were similar for the stocks examined, could be caused by size-selective mortality. The effects of size-selective mortality may have led to a population made up primarily of slow-growing fish. There has been little change in growth rate despite greatly reduced fishing effort over the last 10 years (Chouinard *et al.*, 2003), even though density-dependent effects and recent temperature conditions should favour fast growth. This raises the possibility that there has been a genetic response to the strong selection against fast growth in the late 1980s and early 1990s.

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3.15 Southern Newfoundland —St. Pierre Bank (NAFO Subdivision 3Ps)

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Stock and geographic distribution

The stock of cod in NAFO Subdivision 3Ps (Figure 3.15.1) occupies the area south of Newfoundland from Cape St. Mary's in the east to just west of the Burgeo Bank, and adjacent offshore waters to about the centre of the Laurentian Channel, including St. Pierre Bank and most of Green Bank.

Water mass characteristics in the 3Ps region are largely determined by the general circulation, which consists of Labrador Current Water, the inshore branch of which flows through the Avalon Channel and around Cape Race (Colbourne, 2003). This branch then divides into two parts, one flowing to the west around the north of St. Pierre Bank, and the other flowing to the south between Green Bank and Whale Bank. Additionally, part of the offshore branch of the Labrador Current flows around the tail of the Grand Bank, westward along the continental slope (where it may interact with the Gulf Stream and

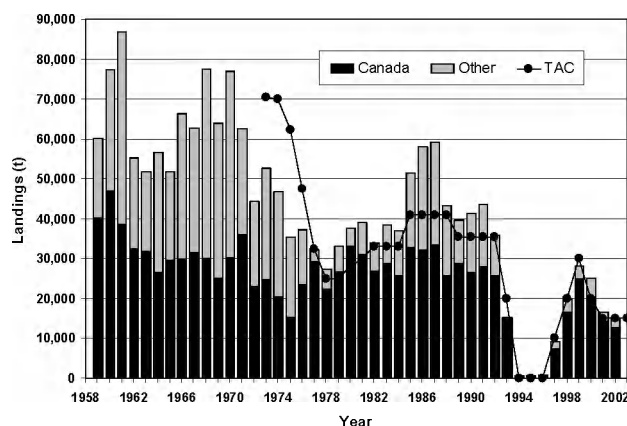


Figure 3.15.2. Cod in Subdivision 3Ps. Total allowable catches (TACs) and reported calendar year landings (t). The latter are subdivided into catches by Canadian and non-Canadian fleets. Note that TACs are by management year (1 April – 31 March) since 2000. (Modified from Bratley *et al.* (2003).

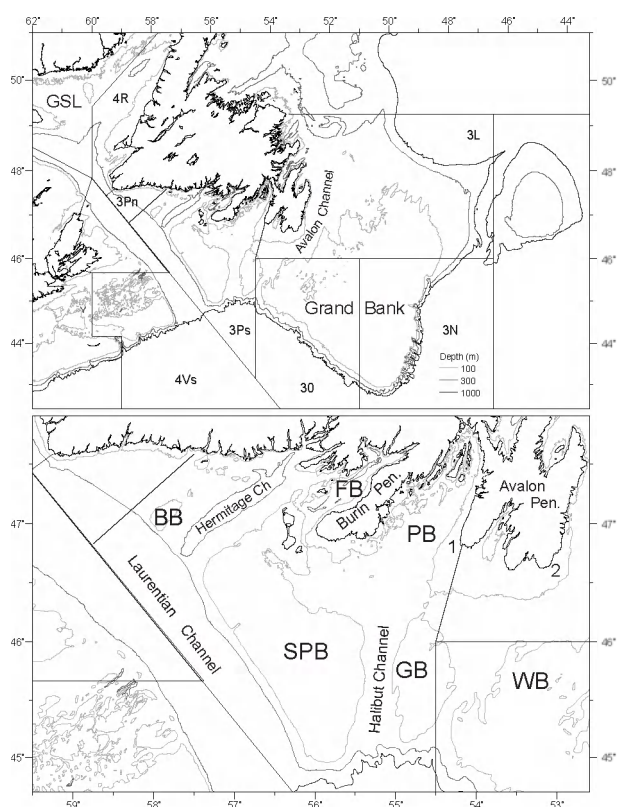


Figure 3.15.1. Area south of Newfoundland, illustrating NAFO Divisions (e.g. 3L) and Subdivisions (e.g. 3Ps). Place names are Gulf of St. Lawrence (GSL), Burgeo Bank (BB), St. Pierre Bank (SPB), Green Bank (GB), Whale Bank (WB), Fortune Bay (FB), Placentia Bay (PB), Cape St. Marys (1), and Cape Race (2).

slope waters), to the Laurentian Channel and into the Gulf of St. Lawrence. As a result the near-bottom habitat in the 3P region can be divided into two distinct oceanographic regimes. One, which includes much of St. Pierre Bank and regions to the east, is influenced by cold-fresh water from the eastern Newfoundland Shelf. Near-bottom temperatures are generally in the range 0–2°C, but are <0°C in many years. The other oceanographic regime includes the deeper regions of the Laurentian and Hermitage Channels and areas to the west of St. Pierre Bank. This region appears to be influenced mostly by warmer slope water from the south. As a result this region experiences high variability with temperatures ranging from 3–6°C.

Temperature measurements on St. Pierre Bank in the winter/spring show anomalous cold periods in the mid-1970s and from the mid-1980s to the mid-1990s (Colbourne, 2003). Temperatures moderated in 1996, decreased again during the spring of 1997 and returned to more normal values during 1998. During 1999 and 2000 temperatures continued to increase, reaching the highest values observed since the late 1970s in some regions. During the past 3 years, temperatures have cooled significantly to values observed during the mid-1990s.

This stock supported an inshore fixed gear fishery for centuries. Catches in the offshore have been taken with both fixed gear and mobile gear. The stock was heavily exploited in the 1960s and early 1970s by non-Canadian fleets, with reported landings peaking at about 87 000 t in 1961 (Figure 3.15.2). After Canadian extension of fisheries jurisdiction (1977), cod catches averaged between 30 000 t and 40 000 t until the mid-1980s when

increased fishing effort by France led to increased total reported landings, reaching a high for the post-extension of jurisdiction period of about 59 000 t in 1987. Subsequently, reported catches declined gradually to 36 000 t in 1992. Catches exceeded the total allowable catch (TAC) throughout the 1980s and into the 1990s. A moratorium was imposed on all directed cod fishing in August 1993. The fishery was reopened in 1997. The TAC was raised quickly but subsequently lowered. Under the terms of the Canada-France agreement, France is now allocated 15.6% of the TAC.

Evidence of stock discreteness

Stock definition does not always correspond closely to population structure. The delineation of geographic areas for the purpose of collecting fisheries statistics in the Northwest Atlantic is summarized by Halliday and Pinhorn (1990). They note that, although knowledge of cod biology was influential in the selection of statistical boundaries, simplicity and practicalities of data collection outweighed biological knowledge in some cases.

It is clear that cod distribution and migration patterns are such that it is not possible for each population to define an area that encompasses the whole of its distribution as it undergoes its annual migration cycle, and which at the same time excludes fish from other populations. Thus, stocks as designated for management purposes are often geographical constructs that encompass the distribution of several populations for all or part of the year. The 3Ps stock area off southern Newfoundland seems particularly complex.

Templeman (1962; 1979) used information from vertebral numbers, tagging studies, time and location of prespawning and other aggregations, times and places of spawning, and ancillary information such as growth patterns and relative year-class strength, to determine stock structure within Atlantic Canada. Several of his "stocks" occupy 3Ps for at least part of the year. He designated a St. Pierre Bank stock that forms winter — early spring concentrations on the western and southern slopes of the bank, with a large concentration at the southern entrance to the Halibut Channel. Many of these fish move onto the shallower parts of the bank from late spring to autumn, and some move to inshore waters along the south coast. His Avalon-Burin stock is an inshore stock that extends from the outer coast of the Avalon Peninsula (3L) westward past Placentia Bay and the Burin Peninsula to Fortune Bay. His Burgeo Bank stock, at the western end of 3Ps, occupies Burgeo Bank in winter and early spring and spends the summer in inshore waters. Cod from the Northern Gulf of St. Lawrence (3Pn+4RS) stock overwinter in part within western 3Ps, intermingling with the Burgeo Bank stock. There is also evidence of movement of cod between 3Ps and the southern Grand Bank (3NO). Bratley (1996) provides a more detailed overview of this information, with emphasis on the results of tagging studies.

More recent studies confirm the general patterns described by Templeman, but provide much additional detail. For example, the recent (1997–2002) tagging studies of Bratley and Healey (2003) provide evidence of strong inshore residency among fish tagged in spring in Fortune Bay and Placentia Bay. These fish appear to disperse widely along the inshore during summer, particularly in an easterly direction, with their distribution extending well into 3L in some years. There appears to be limited offshore movement of these cod with only a few offshore recaptures even several years after release.

The migrations of cod into and out of Placentia Bay, the largest bay in 3Ps, have been described from observations of fish harvesters (Davis *et al.*, 1994), the new series of tagging studies (Lawson and Rose, 2000b; Bratley and Healey, 2003) and hydroacoustic studies (Lawson and Rose, 2000a). There is a group of cod that overwinters in the inner reaches of the bay, spawns at various sites in the bay during the spring, and then leaves the bay along the eastern side. Some of these fish move around the southern Avalon Peninsula (3L) and return to the bay during the autumn. There are other fish that enter the bay during spring, primarily along the western side, and depart during the autumn. Many of these fish appear to come from Fortune Bay to the west, but some may come from the offshore.

The mixing between the 3Ps stock and the 3Pn+4RS stock is generally perceived to take place in the western portion of 3Ps during the winter months (approximately November to April). There is a long history of scientific investigations on mixing between these stocks (Bratley, 1996) and various techniques have been employed, including genetics (Ruzzante *et al.*, 1998; 2000; Beacham *et al.*, 2002), tagging (Lear, 1984; 1988; Taggart *et al.*, 1995; Bérubé and Fréchet, 2001; Bratley *et al.*, 2002a; 2002b; Bratley and Healey, 2003), meristics (Templeman, 1981), analysis of fleet activities, fishery statistics and general biology (Pinhorn, 1969), otolith elemental analysis (Campana *et al.*, 1999), and parasite infection levels (Templeman *et al.*, 1976). These studies have shown that the duration, timing and extent of mixing appear to vary annually and may be strongly influenced by oceanographic conditions.

Units for which assessment of spawning-stock biomass and recruitment are available

For the purposes of most assessments of the status of the 3Ps cod stock as a whole, it has been assumed that all cod caught within NAFO Subdivision 3Ps belong to the 3Ps stock (see Bratley *et al.*, 2003). Undoubtedly, there will be some problems with this convention because of migrations across boundaries with adjacent stocks in the Northern Gulf of St. Lawrence (3Pn+4RS), the east coast of Newfoundland (2J+3KL) and the southern Grand Bank (3NO). Thus, fish that may overwinter in 3Ps but spawn in 3Pn or the Northern Gulf of St. Lawrence are included within the 3Ps stock if caught in 3Ps, but are included in the Northern Gulf stock if caught in 3Pn or

4RS. Fish that spawn in 3Ps but move into 3Pn or the northern Gulf are included in the northern Gulf stock if caught in 3Pn or 4RS. That is, the area of spawning is not taken into account. (At present it is not possible to routinely assess the spawning location of fish that are taken in most commercial fisheries.) Migrations also occur across the eastern boundary of 3Ps. Cod that over-winter in 3Ps but move into 3L or even 3K during summer are included within the northern (2J+3KL) cod catch statistics if caught in 3KL. Similar movements also take place across the boundary with the southern Grand Bank cod stock (3NO). The actual spawning locations of fish that undertake spring migrations are not always clear.

Estimates of density and abundance are available for spawning aggregations within Placentia Bay (Lawson and Rose, 2000a; 2000b; Robichaud and Rose, 2002).

Time-series of spawning-stock biomass and recruitment data

Five sequential population analysis (SPA) model formulations were explored during the most recent assessment of this stock (Brattey and Healey, 2003). The models provided similar trends in spawning-stock biomass and recruitment, but differed considerably in level. One specific formulation (Run D) was chosen for illustration. It is emphasized that this run is not considered to be “preferred” relative to the other runs.

The estimate of biomass of cod 3 years and older shows a peak in the mid-1980s followed by a steady decline to a low in the 1993/1994 period (Figure 3.15.3). Following the onset of the moratorium in mid-1993, population biomass increased during 1994–1998. The increase was arrested during 1998–2000, coincident with the resumption of directed fishing. There appears to be a small increase in recent years.

The estimate of spawning-stock biomass (SSB) follows a trend similar to that in the 3+ biomass (Figure 3.15.3), except that the increase following imposition of the moratorium is more pronounced in the SSB. There have been marked changes in the age at maturity of cod within 3Ps (see below), and a declining age at maturity appears to be an important factor in the high estimates of SSB for the post-moratorium period. It is recognized that the size of the SSB may not be a sensitive measure of the reproductive and recruitment potential. The spawning biomass in the post-moratorium period appears to be comprised of a much higher proportion of younger females compared to the period prior to the late 1980s.

Recruitment has been variable, but with a downward trend from the mid-1970s to the mid-1990s (Figure 3.15.4). The 1997 and 1998 year classes appear particularly strong, but their strength is estimated with greater uncertainty than older year classes.

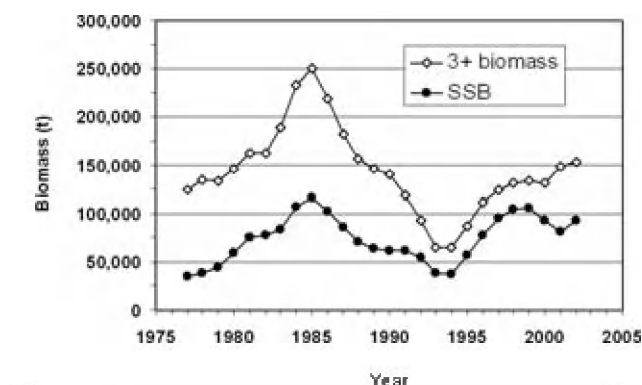


Figure 3.15.3. Cod in Subdivision 3Ps. Total (3+) biomass and spawning-stock biomass (SSB) from Run D in Brattey *et al.* (2003).

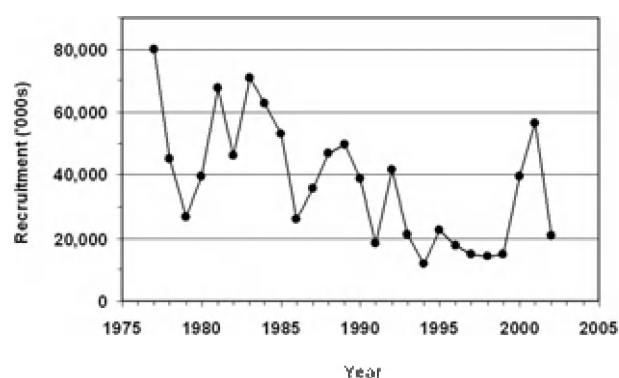


Figure 3.15.4. Cod in Subdivision 3Ps. Recruitment (numbers at age 3) from Run D in Brattey *et al.* (2003).

What is the geographical location of the stock and does it change seasonally?

Distribution and migration patterns are summarized above under the checklist question on evidence of stock discreteness.

Additional information regarding offshore distribution during winter-spring is available from catches during research bottom trawl surveys. In recent years, cod have tended to be caught over a considerable portion of 3Ps, with the largest catches typically in the southern Halibut Channel area, on Burgeo Bank and vicinity, and in the outer portion of Fortune Bay. Cod catches were small in the deep water south of the mouth of Placentia Bay and in the inner reaches of Hermitage Channel. The catch of cod on the plateau of St. Pierre Bank appears to vary with temperature (see below).

There is also considerable information from hydroacoustic studies regarding the distribution of cod within Placentia Bay at the time of spawning (see section on location of spawning).

What is the depth and temperature associated with the stock and does it change seasonally?

There has been no study of either the average depth occupied by the stock as a whole on an annual basis, or of the average temperature experienced by the stock.

Cod are taken over the full depth range in the winter-spring surveys (deepest tows about 550 m). The largest catches tend to be in deep water on the outer slopes of the banks where water is relatively warm (2°–6°C) (Colbourne and Murphy, 2003). There were very few cod on the plateau of St. Pierre Bank during years when the temperature was <0°C, but catches increased when the water was warmer.

Hydroacoustic studies within Placentia Bay (Lawson and Rose, 2000a; 2000b) indicated that cod were generally at depths less than 100 m during spawning, and were located at increasingly shallow depths over the course of spring and summer. The mean temperature occupied was about 0°C in April and varied around 1.5–2.8°C from May to October.

Time of spawning

Date of spawning and interannual variability or trend

Cod in 3Ps appear to spawn over a significant portion of the year and at many locations within the stock area. There appears to be no consistent peak in the spawning time.

Spawning time of fish in the offshore was determined from analysis of the spawning stage of cod that were visually examined during research trawl surveys (Myers *et al.*, 1993). The day of the year on which 50% of mature females were in a spent state was Julian day 141 ± 52 (May 21). The authors thought that the method would over-estimate the mean spawning date by about 2 weeks. Hutchings and Myers (1994) used a similar approach to examine interannual variability and found that spawning occurred on day 135 ± 24 (i.e. May 15).

Spawning time of fish within Placentia Bay is available from various studies. Bolon and Schneider (1999) observed the proportion of fish in spawning condition from March to December 1998 in the inner reaches of the bay. They found that females in spawning condition were found from March to August, and that the highest proportion of females in spawning condition occurred from May to August. Lawson and Rose (2000a; 2000b) used hydroacoustics and associated biological sampling to monitor the intensity and timing of spawning at three sites within the bay. They found that spawning peaked in April in 1997 but was about a month later (June–July) in 1998. Bradbury *et al.* (2000) found that peaks in mean egg density occurred in April in both 1997 and 1998, but that egg production continued later in 1998.

Time of day when spawning occurs

No information.

Timing of spawning season in relation to planktonic production cycle

See Myers *et al.* (1993) for a comparison between cod spawning dates, *Calanus finmarchicus* seasonal cycles, and two indices from the physical environment (surface temperature and water column stability) for several areas from Greenland to southern Newfoundland (3Ps).

Timing of spawning season in relation to hydrographic events

Hutchings and Myers (1994) found that the median date of completion of spawning in the offshore of 3Ps was positively correlated with water temperature. This was the opposite to what was found in nearby Division 3L, where a negative correlation was explained as a positive influence of temperature on gonad development. In 3Ps, they attributed “the early spawning dates in years characterized by cold bank temperatures to (1) a thermal barrier imposed by sub-zero temperatures on spawning migrations from the continental slope to the shelf, and to (2) increased rates of gonad development, and an earlier readiness to spawn, experienced by cod ‘forced’ to prolong their residence in warm slope waters.”

Timing of spawning season in relation to other fish species that spawn in the same location

No information.

Location of spawning

Geographic location and extent of spawning area

Spawning is spatially widespread and is known to occur on Burgeo Bank, St. Pierre Bank, and the Halibut Channel area, as well as inshore in Hermitage Bay, Fortune Bay, and Placentia Bay.

Sampling during research trawl surveys has shown that the cod tend to be aggregated during winter in warm, deep water along the outer slopes of the banks and in some of the deep channels. It is not clear whether the cod spawn in these overwintering areas or move somewhat onto the banks or into shallower channels prior to spawning. An analysis of maturity data collected over many years during winter-spring research surveys in offshore areas found that cod in spawning condition (containing hydrated eggs) were not concentrated in the overwintering areas in deeper water but instead appeared to be primarily on the shelf (Hutchings *et al.*, 1993). However, there was no indication of high densities of cod in spawning condition anywhere within the stock area. Since 1993, the surveys have been conducted primarily in April when a higher proportion of cod are in spawning condition (Bratley *et al.*, 2003). An analysis of maturity

stage in three sub-areas (Burgeo Bank/Hermitage Channel; southern 3Ps/Halibut Channel; and mid-3Ps) indicated that spawning fish were found in each area in April. An update of the finer spatial analysis of Hutchings and Myers (1993) might be highly informative.

Because of the hit-or-miss nature of the stratified sampling conducted during research trawl surveys, and the fact that some cod may be well off bottom at the time of spawning, the distribution of spawning aggregations may be more readily discerned with hydroacoustic surveys. Such studies within Placentia Bay have detected three discrete areas where dense aggregations of cod in spawning condition may be found (Lawson, and Rose, 2000a; 2000b). These are Bar Haven in the inner bay and Perch Rock (Cape St. Mary's) and Oderin Bank in the outer bay. There was substantial variation in the intensity and timing of spawning both between the three areas and between the two years in which the study was conducted.

Studies of the distribution of eggs and larvae in Placentia Bay (Bradbury *et al.*, 2000) found that stage I eggs were concentrated in the three spawning areas identified by Lawson, and Rose (2000a; 2000b).

Does spawning regularly begin in one part of the spawning area and then move on to other parts?

No information.

Can the location be described in relation to hydrographic features?

No information.

Can location be described in relation to other species, including food organisms and predators?

No information.

Can location be described in relation to water mass circulation?

Bradbury *et al.* (2000) found that the prevailing currents within Placentia Bay swept eggs from the eastern side of the bay northward toward the inner part of the bay and then outward along the western side. The eventual fate of the eggs and larvae advected from the bay remains unresolved. There has been very little additional study of eggs and larvae in 3Ps. Bradbury *et al.* (2000) should be consulted for further discussion and speculation.

Biological details

Fecundity

Pinhorn (1984) provided regression parameters for log-log regressions of fecundity vs. length and fecundity vs.

age for cod sampled in Placentia Bay in 1966 and on St. Pierre Bank in 1967–1970.

Area	Fecundity - length		Fecundity - age	
	Slope	Intercept	Slope	Intercept
Placentia Bay	2.42	1.73	0.84	5.52
St. Pierre Bank	3.37	-0.38	1.94	4.10

Evidence of changes in fecundity with time

No information. However, it seems likely that there have been changes, at least for the younger fish, because the age at maturity has declined.

Percentage mature-at-age

Maturation in cod was determined visually during research trawl surveys. The proportion of female cod mature-at-age has increased among younger cod. For example, the proportion of 5 year-old females that are mature has increased from about 10–20% in the 1970s and early 1980s to over 80% in the early 2000s (Bratney *et al.*, 2003).

Female age at 50% maturity (A_{50}), estimated from sampling within a given year, was generally between 6 and 7 during the 1970s and 1980s, and declined quickly from a high of 7.2 during 1988 to a low of 5.0 during 1994 (Bratney and Morgan, 1996). Age at 50% maturity (A_{50}), estimated by cohort rather than by year (Bratney *et al.*, 2003), was generally between 6 and 7 for cohorts from the mid-1950s to the early 1980s, but declined dramatically thereafter to a low of 5.1 for the 1988 cohort. A_{50} remained low but fairly constant for the 1988 to 1994 cohorts, increased somewhat for the 1995 and 1996 cohorts, but declined again for the 1997 and 1998 cohorts, with the latter having the lowest A_{50} in the time-series at 4.6 yr. Males show a similar trend over time, but tend to mature about one year younger than females.

Female length at 50% maturity (L_{50}), estimated from sampling within a given year, was generally between 55 and 65 cm during the 1970s and 1980s, and declined quickly from 63.2 cm during 1988 to a low of 46.7 cm during 1994, with the 1996 value at 47.8 (Bratney and Morgan, 1996). Males declined from a high of 57.4 during 1979 to a low of 42.4 during 1994, with the 1996 value at 43.4. Lengths at maturity have not been updated for recent years, and have not been determined by cohort.

Similar changes in maturity have been observed in the 2J+3KL cod stock off eastern Newfoundland. See the section on that stock for some discussion of factors that have contributed to these changes.

Egg size and evidence of changes with age and with time during the spawning season. Specific gravity of eggs and larvae

No information.

Typical densities, i.e. number per m³ of eggs and larvae

No information.

Incubation rate of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larva

No information.

Larval development rate as a function of temperature

No information.

Condition factor and nutritional status

No information.

Egg and larval mortality rates

No information.

Time of first-feeding of larvae and food at first-feeding

No information.

Food of larvae during development

No information.

Evidence of predation during the egg and larval stages

No information.

Recruitment

Are there several spawning sites (sub-populations) that contribute to the same stock unit?

As noted in sections above, several different “stocks” (populations or sub-populations) spawn within 3Ps. As noted in the section on location of spawning, spawning is widespread in both the offshore and inshore. Some specific sites have been identified within Placentia Bay. However, there has been insufficient study to identify the number of specific spawning sites within 3Ps as a whole and the extent to which such sites are discrete. Indeed, there has been little effort to identify the geographic distribution of the various life-stages of any specific population, where one might be interested in identifying ontogenetic changes in distribution (from spawning site, to drift trajectories of eggs, larvae and early juveniles, to areas of successful settlement, to nursery areas) and seasonal changes in distribution of adults (from spawning areas to feeding areas to overwintering areas).

Earliest time in the life history when year-class strength can be predicted

No information.

Hypotheses that have been put forward to account for year-to-year variability in year-class strength

Characteristics of spawning-stock have been explored (Morgan *et al.*, 2000).

Evidence of long-term trends in recruitment

The SPA output indicates that recruitment has been variable, but that there has been a long-term decline between the year classes of the 1970s and those of the mid-1990s (Figure 3.15.4). However, the 1997 and 1998 year classes appear to be strong as 3 year-olds.

Evidence that variability in recruitment is linked to variability of other species in the same area, the same species in other areas, or other species in other areas

No information.

Evidence of inter- or intraspecific competition

No information.

Is recruitment related to SSB or any environmental factors?

Morgan *et al.* (2000) explored the possible effect of spawning-stock characteristics on recruitment of 3Ps cod and two other cod stocks (2J+3KL and 3NO), plus one American plaice stock. A Beverton-Holt stock-recruit model was fitted to the output from a specific SPA (several SPAs are available for 3Ps cod – see above), and residuals were compared to the weighted mean age of the spawning-stock, the proportion of first time spawners and the proportion of females in the mature population. Because the results were not consistent between stocks and were difficult to interpret, the reader is referred to the paper for details.

Migration

Evidence of adult migration

See above under evidence of stock discreteness.

Where and when do they migrate?

See above under evidence of stock discreteness.

Adult growth

What are the general growth characteristics, e.g. typical length and size at age? Has it undergone changes over time?

Mean lengths-at-age (Figure 3.15.5) varied over time. A peak occurred in the mid-1970s for young ages (3–4) and progressively later to 1980 for older ages. This peak does not track individual year classes particularly well, but in general year classes born in the 1970s experienced faster growth than those born in the 1980s (Lilly, 1996; Chen and Mello, 1999b). From the mid-1980s to the present, length-at-age tended to increase at young ages (2–3) and to vary with no clear trend at older ages. During the past decade or so there has been considerable year-to-year variability at older ages (as much as 20 cm at age 10).

There has not yet been a thorough analysis to determine if these differences were caused mainly by environmental factors (e.g. temperature or prey availability), cohort factors (e.g. cohort or population abundance, distribution) or any of the numerous additional possibilities, such as changes in maturation schedules (Chen and Mello, 1999a) or size-selective fishing mortality. Variability associated with sampling or processing could also be important.

An exploration of the effects of environmental factors such as temperature has not been conducted because there appears to be negative growth for at least 2 cohorts during each of the intervals 1977–1978, 1980–1981, 1989–1990, and 1993–1994 (Lilly, 1998). Such extreme year effects could result from the existence within 3Ps of groups of fish with different growth rates, coupled with annual variability in the proportion of the age sample taken from each of those groups. This possibility is discussed further by Lilly (1996), but has not yet been explored.

Much of the high variability in length-at-age at older ages (say 7–10) in recent years appears to be caused by cohort effects (Brattey *et al.*, 2003). For example, the 1989, 1990 and 1992 year classes were relatively long at age, whereas the 1988, 1991 and particularly the 1987 year classes were relatively short. The small length-at-age of the 1991 year class, compared with the adjacent 1990 and 1992 year classes, is striking. There has not yet been an investigation of the reasons for such cohort effects.

As expected, the patterns in mean weight-at-age (Brattey *et al.*, 2003) appear to be very similar to those in length-at-age. The high year-to-year variability at older ages in recent years, noted above for length-at-age, is much more pronounced in weight-at-age, with weights-at-age in some years being more than twice that in others. The weight-at-age estimates may include more sampling variability than the length-at-age estimates in years prior to 1990 because they are based on much smaller sample sizes (Lilly, 1998). The weight-at-age data also include variability associated with between-year and within-year variability in weight at length (condition).

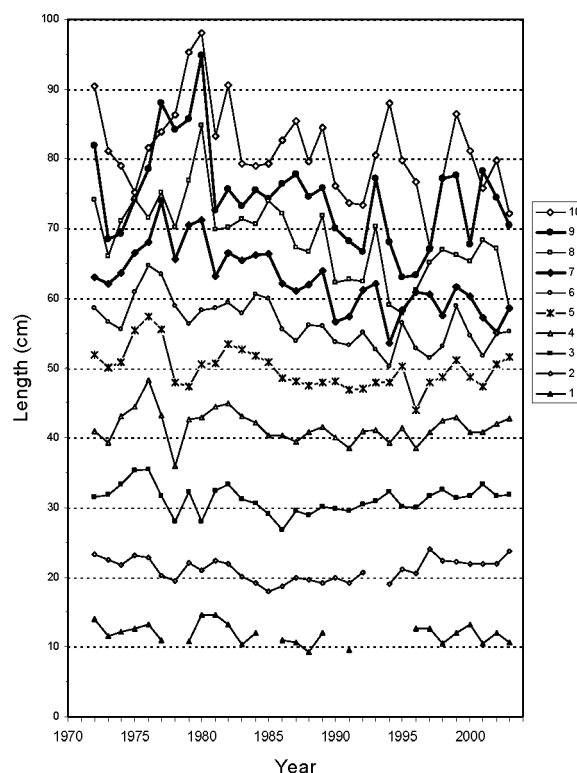


Figure 3.15.5. Cod in Subdivision 3Ps. Mean length-at-ages 1–10 of cod sampled during bottom-trawl surveys in the offshore in winter-spring 1972–2003 (from Brattey *et al.*, 2003).

Mean somatic (gutted) condition and liver index (both at age and within size classes) declined from early winter to a minimum in roughly late April to early June, and then increased rapidly. This pattern was apparent in samples from both the offshore (Brattey *et al.*, 2003) and the inshore (Lilly, 1996). An examination of between-year variability in condition of cod in the offshore was confounded by the combination of seasonal variability in condition and variability in the timing of the surveys.

Evidence for density-dependent growth

See above.

Evidence of temperature-dependent growth

See above.

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3.16 Southern Labrador and eastern Newfoundland (NAFO Divisions 2J+3KL)

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Stock and geographic distribution

The term “northern cod” is used in reference to a complex of cod populations found in NAFO Divisions 2J, 3K and 3L (Figures 3.16.1 and 3.16.2). At one time the term included those cod off northern and central Labrador (NAFO Div. 2GH), but 2GH has been considered separately for management purposes for many years (Pinhorn 1976). The 2GH stock was severely reduced by fishing during the 1960s, when catches averaged 72 000 t in 1965–1969 (peaking at 94 000 t in 1966). Catches fell below 1000 t after 1984 and have been essentially zero since the early 1990s (Murphy *et al.*, 1992; Murphy and Bishop, 1995). There has been little research activity on cod in 2GH during the past two decades or so. Because so little is known about the cod in 2GH, the present report will focus on the cod in 2J, 3K and 3L.

The continental shelf in 2J+3KL 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) of Grand Bank lies within the stock area. Depths greater than 400 m occur in the saddles or channels northwest of Hamilton Bank and between Hamilton Bank and Belle Isle Bank, and also in basins landward of Belle Isle Bank and Funk Island Bank.

The Labrador Current flows southeastward along the shelf and keeps temperatures low. Local cooling in autumn and winter contributes to the existence of a water column that is often below 0°C from the surface to 200 m or more. Local ice formation and the drift of ice from the Arctic often result in ice cover as far south as the northern Grand Bank. Warming in the spring and summer results in a three-layer system, the middle of which (the Cold Intermediate Layer at roughly 100–200 m) remains below 0°C.

The marine environment off Labrador and eastern Newfoundland has experienced considerable variability since the start of standardized measurements in the mid-1940s (Colbourne 2003; Colbourne and Anderson, 2003) (Figure 3.16.3). A general warming phase reached its maximum by the mid-1960s. Beginning in the early 1970s there was a general downward trend in ocean temperatures, with particularly cold periods in the early 1970s, early to mid-1980s and early 1990s. Ocean temperatures started to warm in 1995. The decade of the 1990s experienced some of the greatest extremes, with particularly cold conditions in 1991 and very warm conditions in

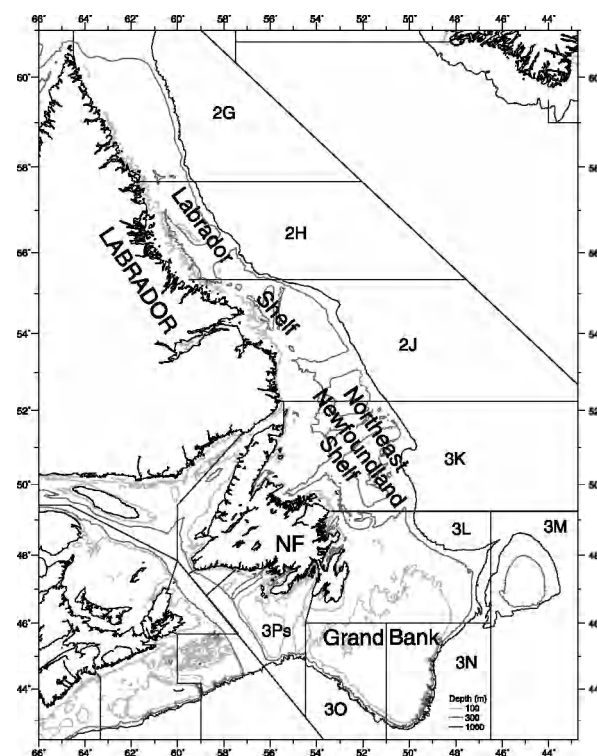


Figure 3.16.1. Labrador-Newfoundland area, illustrating major geographic features and NAFO Divisions and Subdivisions.

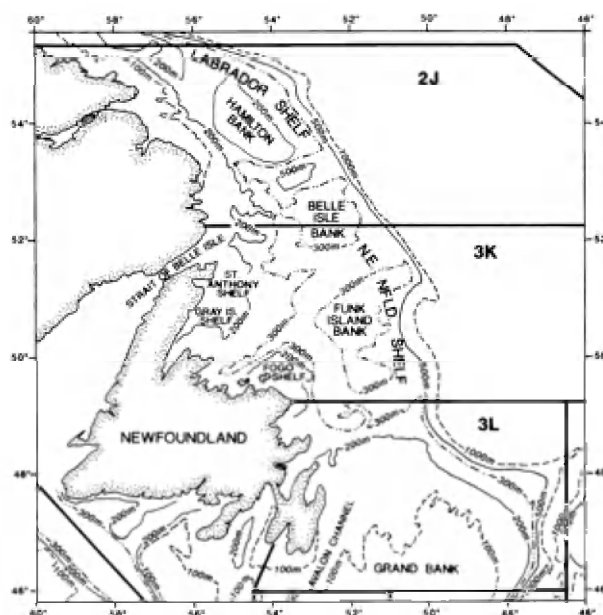


Figure 3.16.2. Shelf area off southern Labrador and eastern Newfoundland, illustrating NAFO Divisions and locations of some geographic features.

various years of the late 1990s. For about 3 decades there was a good association between a meteorological index (the North Atlantic Oscillation or NAO) and the strength of northwesterly winds over the Labrador Shelf, low water temperature, and high ice extent and duration. This association has largely broken down since the late 1990s.

The northern cod has been exploited for centuries. Annual landings increased through the 18th and 19th centuries to about 300 000 tonnes during the early decades of the 20th century. The early fishery was limited to shallow water. Deep waters ceased to be refugia when, in the 1950s, longliners were introduced to nearshore waters and distant water trawlers from Europe located and exploited the dense aggregations of cod overwintering along the shelf break. Total landings escalated from 360 000 tonnes in 1959 to 810 000 tonnes in 1968 (Figure 3.16.4), and then plummeted to 140 000 tonnes in 1978. The landings by distant water fleets declined substantially when Canada declared a 200 mile fishing zone in 1977. Canadian trawlers soon replaced the non-Canadian fleets on the winter fishing grounds, and catches once again rose to above 200 000 tonnes. In 1988–1989 it was recognized that the stock size had been overestimated for several years, and that fishing mortality during the 1980s had been higher than intended. Quotas were reduced, but not sufficiently to prevent an increase in fishing mortality. During the early 1990s the fishery experienced difficulty finding cod in the north. By the winter of 1992, the trawlers had difficulty finding fish anywhere. In July 1992 Canada declared a moratorium on directed cod fishing. In 1998 a directed fishery was reopened for small (< 65 feet) vessels operating in the inshore, but all directed fishing was closed once again in 2003.

Evidence of stock discreteness

Stock definition does not always correspond closely to population structure. The delineation of geographic areas for the purpose of collecting fisheries statistics in the Northwest Atlantic is summarized by Halliday and Pinhorn (1990). They note that, although knowledge of cod biology was influential in the selection of statistical boundaries, simplicity and practicalities of data collection outweighed biological knowledge in some cases.

It is clear that cod distribution and migration patterns are such that it is not possible to define for each population an area that encompasses the whole of its distribution as it undergoes its annual migration cycle, and which at the same time excludes fish from other populations. Thus, stocks as designated for management purposes are often geographical constructs that encompass the distribution of several populations for all or part of the year.

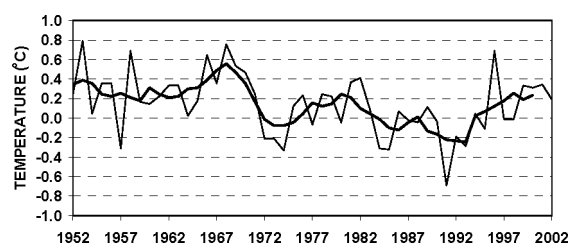


Figure 3.16.3. Cod in Divisions 2J+3KL. An index of temperature in the stock area. The light line shows the annual depth-averaged (0–176 m) temperature anomalies from Station 27, near St. John's. The heavy line is a 5-year running mean (from Colbourne, 2003). Additional indices of temperature and ice coverage are available.

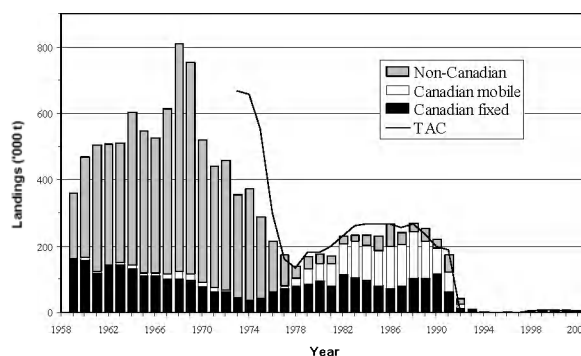


Figure 3.16.4. Cod in Divisions 2J+3KL. Total allowable catches (TACs) and landings (thousands of tons) by non-Canadian fleets and Canadian fleets, with the latter divided into mobile gear (offshore) and fixed gear (mainly inshore). (Modified from Lilly *et al.*, 2003.)

Templeman (1962; 1979; 1981) used information from vertebral numbers, tagging studies, time and location of prespawning and other aggregations, times and places of spawning, and ancillary information such as growth patterns and relative year-class strength, to determine stock structure within Atlantic Canada. The 2J+3KL cod stock intermingles with the 3NO stock on the plateau of Grand Bank, with the 3Pn+4RS stock in the area of the Strait of Belle Isle (between Labrador and the island of Newfoundland), and with the 3Ps stock near the coastal region of 3L.

Numerous studies have indicated the likelihood of sub-stock structure within the northern cod stock complex (see, for example, overviews by Lear, 1986; deYoung and Rose, 1993; Smedbol and Wroblewski, 2002). The evidence includes a north-south cline in size-at-age and spawning time, and a change in vertebral counts at approximately the north slope of Grand Bank. Cod tagged at specific locations in the offshore in winter tended to migrate to specific but broad areas of the inshore during summer and then returned to approximately the area of tagging in subsequent winters. It was also known that cod overwintered in various locations inshore and that some spawning occurred inshore.

After the stock as a whole collapsed in the early 1990s, it became clear that some aggregations of cod could still be found inshore. Several sources of information are consistent with the hypothesis that there are distinct inshore or bay stocks along the east coast of Newfoundland. Tagging studies conducted during the collapse period indicate that the inshore of 3KL is inhabited by at least two groups of cod: (1) a northern resident coastal group and (2) a migrant group from inshore and offshore areas of 3Ps that moves into 3L during late spring and summer and returns to 3Ps during the autumn. It is not known if there is currently movement to the inshore from the offshore of 2J+3KL.

Genetic studies suggest that the northern cod conforms to an isolation-by-distance structure, with cod from more distant locations tending to be more distinct (Beacham *et al.*, 2002). There appear to be differences between the inshore and the offshore, and among various areas of the offshore (Ruzzante *et al.*, 1998; Beacham *et al.*, 2002; but see Carr *et al.*, 1995). Subpopulation structure at the level of individual bays is less strongly supported.

Units for which assessment of spawning-stock biomass and recruitment are available

For the assessment of the status of the 2J+3KL cod stock as a whole, it has been assumed that all cod caught within NAFO Divisions 2J, 3K and 3L belong to the 2J+3KL stock. There will undoubtedly be some problems with this convention because of migrations across boundaries with adjacent stocks on the southern Grand Bank (3NO), on the south coast of Newfoundland (3Ps), and in the northern Gulf of St. Lawrence (3Pn+4RS). The area in which the fish spawn is not taken into account. (At present it is not possible to routinely assess the spawning location of fish that are taken in most commercial fisheries.) Thus, cod that overwinter in 3Ps but move into 3L during summer are included within the northern (2J+3KL) cod catch statistics if caught in 3L. (Note that many of these fish may complete their spawning in 3Ps, but it is possible that others may spawn in both 3Ps and 3L during their migration, or may even spawn entirely within 3L. We simply have insufficient information on the actual spawning locations.)

As described below, information is available for the stock as a whole from sequential population analysis (SPA). Information for the offshore alone is also available from research bottom-trawl surveys conducted throughout 2J+3KL during the autumn. Information for the inshore alone from the mid-1990s to recent years is available from an SPA conducted on inshore data alone, from the results of tagging studies, and from hydroacoustic studies conducted in a small, but important, inlet.

Time-series of spawning-stock biomass and recruitment data

Biomass

There is currently no model or index that adequately captures the dynamics of the 2J+3KL cod stock as a whole from the 1960s to the present. Sequential population analysis (SPA) of the stock became problematic in the early 1990s and annual updates were discontinued for awhile after 1993. There have been several subsequent attempts, including “illustrative” SPAs in 1998 and 2002.

Biomass of the stock as a whole (1962 — early 1990s)

Total (3+) biomass of the stock as a whole collapsed from almost 3 000 000 t in 1962 to about 500 000 t in 1976, and then increased to just over 1 000 000 t in the mid-1980s (Figure 3.16.5). There then followed a steady decline toward a crash in the early 1990s. The actual time course from the mid-1980s onward is somewhat uncertain, but the stock clearly reached an extremely low point by about 1994.

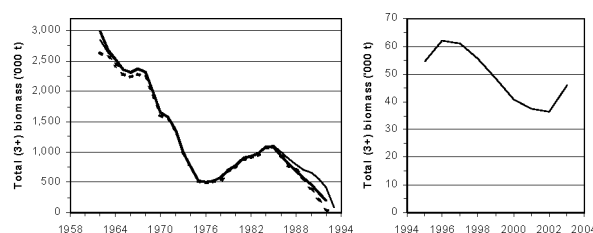


Figure 3.16.5. Cod in Divisions 2J+3KL. Trend in total (3+) biomass (thousands of tons) of northern cod as estimated by sequential population analyses (SPA). In the left panel, the solid bold line shows the biomass from the 1993 assessment ((Bishop *et al.*, 1993), reconstructed by P. Shelton), the dashed line shows an “illustrative” model with no alteration of catch (Lilly *et al.*, 1998) and the thin solid line shows an “illustrative” model with sufficient unreported catch added to allow the model to fit the pattern in the survey index (Smedbol *et al.*, 2002). The right panel shows biomass of fish from an SPA based on catches and indices from the inshore only (Lilly *et al.*, 2003).

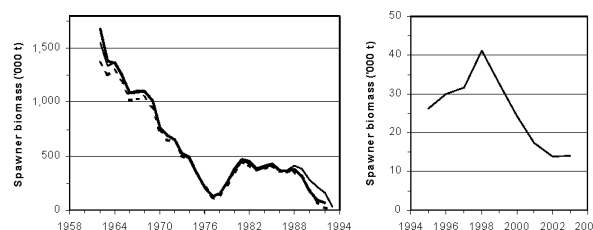


Figure 3.16.6. Cod in Divisions 2J+3KL. Trend in spawner stock biomass (SSB, thousands of tonnes) of northern cod as estimated by sequential population analyses. Panels and lines as in Figure 3.16.5.

The spawning-stock biomass (SSB) collapsed from about 1 500 000 t in 1962 to about 125 000 t in 1977, and then increased to 400–500 000 t through most of the 1980s (Figure 3.16.6). The SSB declined rapidly after 1988, with perception of the time course varying between models.

Biomass in the offshore alone (1984–2003)

The trend in biomass in the offshore is deduced from indices derived from the autumn bottom-trawl surveys. The spawning biomass index has in recent years been at 1–2% of the level during the 1980s (Figure 3.16.7).

Biomass in the inshore alone (1995–2003)

Information on the size and behaviour of inshore populations started to accumulate only after the offshore populations declined to an extremely low level. The recent trend in biomass in the inshore is derived from a sequential population analysis (SPA) that incorporated catches and indices for the period 1995–2002. Stock biomass (ages 3–10) decreased from about 60 000 t in 1996–1997 to less than 40 000 t in 2002, and then increased a little in 2003 (Figure 3.16.5). Spawner biomass increased from 26 000 t in 1995 to 41 000 t in 1998, but subsequently declined to less than 15 000 t at the beginning of 2003 (Figure 3.16.6). [It may be noted that the inshore SPA incorporated an assumption (based on analysis of tagging data) that the instantaneous rate of natural mortality was 0.5, which is much higher than the value of 0.2 that was used in the whole stock SPAs cited above.]

A second source of information on biomass of cod in the inshore comes from analysis of tagging data (Cadigan and Brattey, 2003). The biomass estimated to be available to the fisheries in 3KL during 1999–2002 increased from 43 000 t in 1999 to 59 000 t in 2001, but declined to 24 000 t in 2002. Taken together, the estimates for the 4 years suggest that the biomass of cod available to the fishery has been less than 60 000 t.

Additional information on biomass trends in the inshore comes from hydroacoustic surveys conducted during winter in Smith Sound, a fjord-like inlet on the western side of Trinity Bay (48°10'N; 53°40'W). A dense aggregation of cod that overwinters in the sound has been by far the largest single overwintering aggregation known in the 2J+3KL area since the collapse of the stock. The hydroacoustic biomass estimates increased from about 10 000 t in 1995 to about 26 000 t in 2001, and then declined to about 20 000 t in 2003 (Rose, 2003; Lilly *et al.*, 2003).

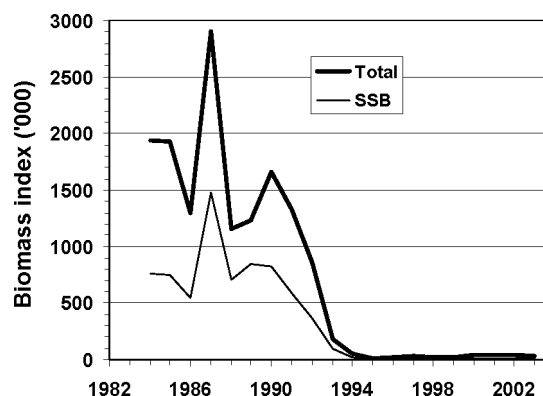


Figure 3.16.7. Cod in Divisions 2J+3KL. Trend in the index of total biomass and spawner stock biomass (SSB) computed by areal expansion of the stratified mean catch-at-age per tow during autumn bottom-trawl surveys in 2J+3KL. The catch in autumn of year t has been used to compute biomass on 1 January of year $t+1$. Note that the survey trawl was changed in 1995, and data collected prior to 1995 have been converted so as to be equivalent to data collected from 1995 onward. (from Lilly *et al.*, 2003).

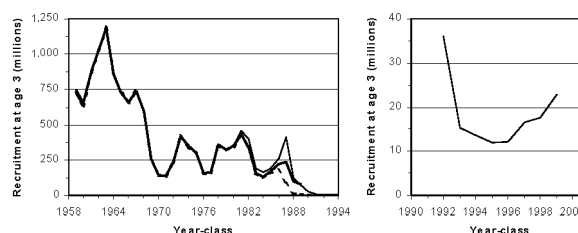


Figure 3.16.8. Cod in Divisions 2J+3KL. Recruitment at age 3 (in millions). Panels and lines as in Figure 3.16.5.

Time-series of spawning-stock biomass and recruitment data

Recruitment to the stock as a whole (1959–1990)

Recruitment increased from about 700 000 000 individuals at age 3 for the 1959–1960 year classes to a peak of almost 1 200 000 000 for the 1962 year class, and then declined steadily to a low of about 140 000 000 for the 1970–1971 year classes (Figure 3.16.8). There were then 3 periods of moderately good recruitment. The last of these (the 1986 and 1987 year classes) is of great interest. These year classes appeared to be moderately strong when young, but they seemed to disappear rapidly. Perception of the strength of these year classes, especially the 1987 year class, varies considerably depending on the data and models that are chosen.

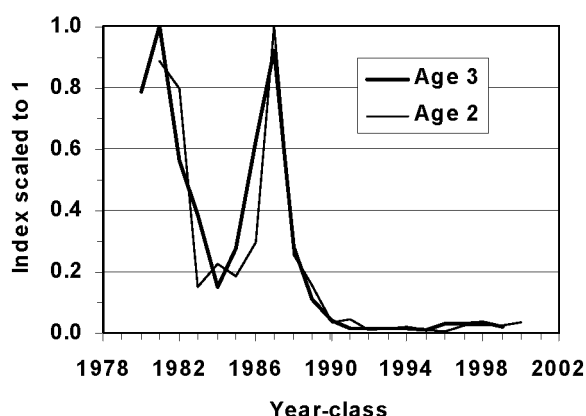


Figure 3.16.9. Cod in Divisions 2J+3KL. Relative size of the 1980–1999 year classes, as measured by the mean catch per tow at ages 2 and 3 during the autumn bottom-trawl surveys in the offshore. Number per tow has been scaled to a maximum of 1 within each age. Note that the survey trawl was changed in 1995, and data collected prior to 1995 have been converted so as to be equivalent to data collected from 1995 onward. (data from Lilly *et al.*, 2003).

Recruitment in the offshore alone (1980–1999)

The index of recruitment derived from mean catch-rate-at-age during the autumn bottom-trawl surveys (Figure 3.16.9) shows the 1980–1982 year classes to be relatively strong, and the 1986 and especially the 1987 year classes to be equally strong. As noted above, this latter peak of young fish seemed to disappear rapidly and made only a very small contribution to the spawning-stock. All year classes since the very late 1980s have been very weak in the offshore.

Recruitment in the inshore alone (1992–1999)

Analyses of catch-rates-at-age in the sentinel surveys reveal that the 1990 and 1992 year classes were stronger than other year classes during the 1990s (Lilly *et al.*, 2003). The relative strength of the 1992 year class and the weakness of subsequent year classes are also evident in output from the inshore SPA (Figure 3.16.8). Year-class strength improved during the late 1990s.

What is the geographical location of the stock and does it change seasonally?

Distribution changes ontogenetically. Most scientific studies (Anderson and Gregory, 2000; Lilly *et al.*, 2000) agree that the major nursery area for the northern cod stock is shallow water along the coast of southern Labrador and eastern Newfoundland, although young cod also occur on the plateau of Grand Bank. For the coastal areas, the young-of-the-year (age 0) cod are mainly inshore. By age 1 the cod are starting to appear in the offshore, and by age 3 or 4 they have a distribution that largely overlaps that of the older fish.

Historically, much of the northern cod stock overwintered near the shelf break in 300–500 m from Hamilton

Bank in Division 2J to the Nose of the Bank in Division 3L. At some time in the spring most of these fish moved onto the shelf, and many of them migrated during late spring and summer into the shallow, coastal waters where they fed on capelin (*Mallotus villosus*) that had approached the coast to spawn. The cod then moved back across the shelf during the autumn. There is evidence from tagging studies (Rose, 1993; Taggart, 1997) that the fish that overwinter toward the edge of the southern Labrador Shelf and the Northeast Newfoundland Shelf approach the coast in a southwesterly direction, move northward while inshore, and then move back offshore, thereby completing clockwise circuits. The details are, of course, much more complex. For example, north-south oscillations may be seen in both the offshore, winter habitat (Wroblewski *et al.*, 1995; Taggart, 1997) and the inshore, summer habitat (Taggart, 1997). It is unclear whether the offshore-inshore migration pattern has persisted since the collapse of the offshore populations in the early 1990s.

Not all cod had this offshore-inshore migration pattern. For example, some cod moved during summer to feeding areas on the plateau of Grand Bank. Others spent the whole year in inshore waters, moving from deep inlets during winter to shallow feeding areas in summer. The aggregation that overwinters in Smith Sound moves northward during late spring and summer, and returns to the sound in late autumn or early winter.

What is the depth range and temperature associated with the stock and does it change seasonally?

There has been no study of either the average depth occupied by the stock as a whole on an annual basis, or of the average temperature experienced by the stock.

Cod occur over a very broad depth range. They may be found in very shallow water, occasionally only a metre or two in depth, in inshore waters during late spring and early summer. Historically they tended to occur at 300–500 m along the shelf break in winter, but have been found at 900 m or more.

Cod have been found in water well below 0°C, even as low as -1.6°C, but most tend to occur in warmer water. The dense overwintering aggregations that at one time occurred toward the edge of the shelf were in 2–4°C water.

Time of spawning

Date of spawning and interannual variability or trend

Cod in 2J+3KL spawn over an extended period. There is a geographic cline, with cod in the north spawning earlier than those in the south. Templeman (1981) summarized various reports on the spawning of cod. With respect to the cod in 2GHJ+3K, he stated that “most of the spawning of this stock occurs during March–May (mainly March–April) in deep water along the slope ...

there is also some later spawning in June in the deep channels and bank slopes closer to the coast ... Cod spawning off northeast Newfoundland (Division 3K) begins in March but occurs mainly in April to early May with some spawning continuing to June.” He also stated that “on the northeastern Grand Bank (Division 3L), spawning occurs mainly in April-June, but occasionally, in years when temperature conditions are below normal, spawning is delayed until May-July.”

Spawning time of fish in the offshore was determined from analysis of the spawning stage of cod that were visually examined during research trawl surveys (Myers *et al.*, 1993b). The day of the year on which 50% of mature females were in a spent state was Julian day 97 ± 20 (April 7) for cod near Hamilton Bank (2J), Julian day 110 ± 28 (April 20) for cod near Belle Isle Bank (2J, 3K), Julian day 138 ± 36 (May 18) for cod near Funk Island Bank (3K), and Julian day 160 ± 37 (June 9) for cod in 3L (< 201 m). The authors thought that the method would over-estimate the mean spawning date by about 2 weeks. Hutchings and Myers (1994b) used a similar approach to examine inter-annual variability and found that spawning in 3L occurred on day 157 ± 18 (i.e. June 6).

Time of day when spawning occurs

No information.

Timing of spawning season in relation to planktonic production cycle

See Myers *et al.* (1993b) for a comparison between cod spawning dates, *Calanus finmarchicus* seasonal cycles, and two indices from the physical environment (surface temperature and water column stability) for several areas from Greenland to southern Newfoundland (3Ps).

Timing of spawning season in relation to hydrographic events

Hutchings and Myers (1994b) found that the median date of completion of spawning in the offshore of Division 3L was negatively correlated with water temperature. This was explained as a positive influence of temperature on gonad development.

Timing of spawning season in relation to other fish species that spawn in the same location

There is information on the timing of spawning of other species in the area (see, for example, Ollerhead *et al.*, 2004), but no statistical analyses of the similarity in spawning times.

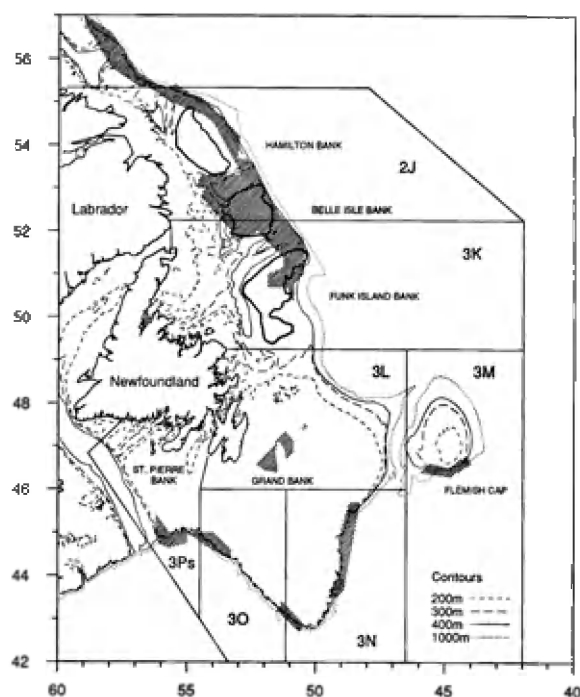


Figure 3.16.10. Cod in Divisions 2J+3KL. Spawning locations identified in the review by Fitzpatrick and Miller (1979). This illustration is from Hutchings *et al.* (1993), who combined the information that Fitzpatrick and Miller (1979) had presented by month (March-July).

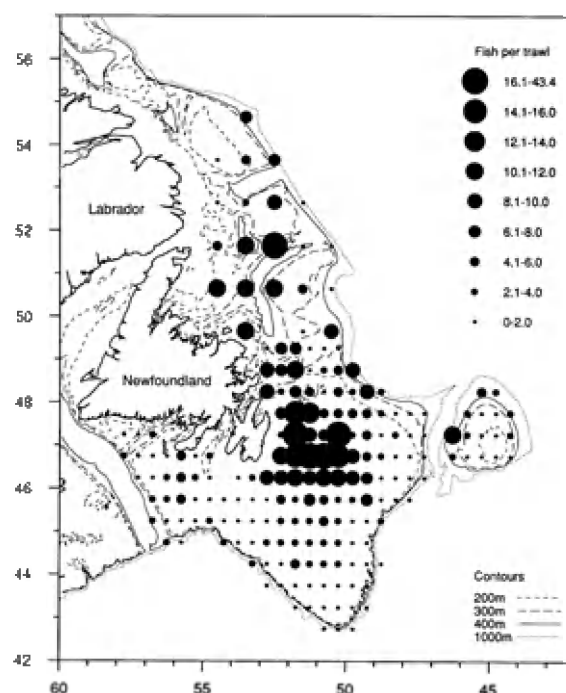


Figure 3.16.11. Cod in Divisions 2J+3KL. Relative abundance of fish in spawning condition, as determined from sampling of catches during bottom-trawl surveys. (from Hutchings *et al.*, 1993).

Location of spawning

Geographic location and extent of spawning area

A review by Fitzpatrick and Miller (1979) indicated that spawning occurred on the outer slopes of the continental shelf (Figure 3.16.10). However, Hutchings *et al.* (1993) argued that this perception was based to a considerable extent on sampling that was biased toward the outer parts of the shelf. Their analysis of maturity data, collected over many years during winter-spring research surveys in offshore areas, found that cod in spawning condition (containing hydrated eggs) were not concentrated in the overwintering areas in deeper water, but instead appeared to be primarily on the shelf (Figure 3.16.11).

The dense concentrations of cod that at one time overwintered near the shelf break were frequently referred to as prespawning and spawning concentrations. Wroblewski *et al.* (1995) reported that cod in spawning condition were indeed caught in these aggregations. An ongoing question has been whether the cod actually spawn at their overwintering locations (essentially below the jet of the Labrador Current), or whether they move somewhat onto the shelf, perhaps through the channels, before spawning. Such movement might increase the likelihood that their eggs will remain on the shelf rather than be advected away. Pepin and Helbig (1997) provided a thorough review of the issue, and presented evidence that spawning may occur over the entire shelf.

Spawning also occurs on the plateau of Grand Bank (Hutchings *et al.*, 1993; Ollerhead *et al.*, 2004) and in inshore waters (Hutchings *et al.*, 1993; Smedbol and Wroblewski, 1997).

Does spawning regularly begin in one part of the spawning area and then move on to other parts?

As noted above, spawning is earlier in the north than in the south.

Can the location be described in relation to hydrographic features?

As discussed above, the locations of spawning in the offshore have been discussed and debated within the scientific literature. Additional information is required on the exact locations at which eggs are shed into the water.

Can location be described in relation to other species, including food organisms and predators?

No information.

Can location be described in relation to water mass circulation?

As discussed above, the locations of spawning in the offshore, and the relationships between those locations and

water mass circulation, have been discussed and debated within the scientific literature. Additional information is required on the exact locations at which eggs are shed into the water.

Biological details

Fecundity

May (1967) provided regression parameters for log-log regressions of fecundity vs. length and fecundity vs. age for cod sampled offshore in 1964 in 2J,3K (combined) and 3L. Pinhorn (1984) provided similar information for cod sampled in three inshore areas of 3L: Bonavista Bay (1967–1968), Trinity Bay (1967–1968) and the St. John's area (1966, 1968).

Area	Fecundity - length		Fecundity - age	
	Slope	Intercept	Slope	Intercept
2J,3K	3.63	-0.64	2.26	3.84
3L (offshore)	2.51	1.52	0.96	5.34
Bonavista Bay	3.50	-0.45	1.34	4.92
Trinity Bay	3.13	0.25	1.91	4.34
St. John's	1.41	3.42	0.92	5.23

Evidence of changes in fecundity with time

Pinhorn (1984) found differences in fecundity between years, but sampling had been conducted during only two years within each geographic area, so it was not possible to determine if there was any systematic pattern in such variability.

It seems likely that there have been changes in fecundity over time, at least for the younger fish, because the age at maturity has declined.

Percentage mature-at-age

Analyses of biological samples collected during 1947–1950 demonstrated a north-south cline in maturation of cod in the Labrador-Newfoundland area (Fleming 1960). In general, both the age and length at maturation were lowest off Labrador and highest on the southwestern Grand Bank. The age at 50% sexual maturity (A_{50}) was 5.36 off Labrador (2HJ), 6.13 off the northern part of the Newfoundland coast (3K), 5.82 off the southern part of the Newfoundland coast (3L), 6.26 on the northeastern Grand Bank (3LN), and 7.47 on the southwestern Grand Bank (Division 3O, with some 3N).

More recent information has come from analyses of samples collected during offshore research surveys by Canada. Morgan *et al.* (1994) calculated A_{50} and length at 50% maturity (L_{50}) by sex and Division from samples collected within each year (1978–1992 in 2J3K; from 1981 in 3L). They found that females matured at an older age and larger size than males. A_{50} for females did not differ significantly by Division, whereas the A_{50} for

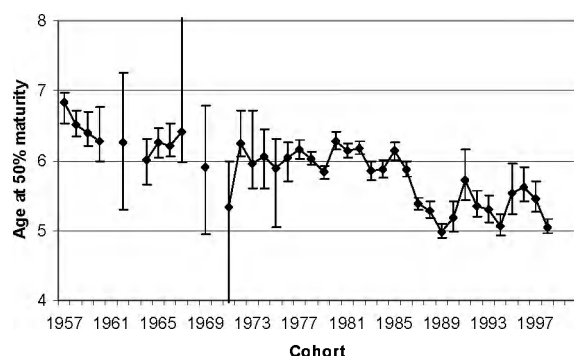


Figure 3.16.12. Cod in Divisions 2J+3KL. Age at 50% maturity ($\pm$ 95% CI) by cohort for female cod in Divisions 2J+3KL combined based on sampling during autumn research bottom-trawl surveys. (from Lilly *et al.*, 2003).

males increased from north to south. A_{50} for both males and females decreased over the period of sampling. For females, the decrease was from about 6.0 to about 5.5. The L_{50} for both females and males increased from north to south and decreased over the period of sampling. For females, L_{50} decreased from about 53 cm to 40 cm in 2J, from about 55 cm to 42 cm in 3K, and from about 57 cm to 47 cm in 3L. (Note that there was considerable annual variability, and these numbers are just approximations.) The declines in L_{50} were much more distinct than the declines in A_{50} .

Annual estimates of age at 50% maturity (A_{50}) for females from the 2J+3KL cod stock as a whole have recently been calculated by cohort rather than by year, using data extending back to 1960 (Lilly *et al.*, 2003) (Figure 3.16.12). The estimated age at 50% maturity (A_{50}) was generally between 6.0 and 7.0 among cohorts produced in the mid-1950s and around 6.0 among those produced during the late 1960s to the early 1980s, but declined dramatically thereafter to a low of 5.0 for the 1989 cohort. Age at maturity remained low but variable for cohorts produced during the 1990s. Some of the high year-to-year variability in recent years may be caused by small sample sizes. Males tend to mature about one year younger than females. Olsen *et al.* (2004) provide evidence supporting the hypothesis that the changes in the maturation schedule are a consequence of fisheries-induced evolution.

Egg size and evidence of changes with age and with time during the spawning season. Specific gravity of eggs and larvae

Anderson and deYoung (1994) reported the density (kg m^{-3} , but for consistency the dimensionless term “specific gravity” is used here) of eggs reared in laboratory situations and measured directly, as well as the specific gravity of eggs and larvae estimated from their vertical distribution in the wild. The specific gravity of eggs decreased with increasing age and development. Initial specific gravity increased with the density of the water in which the cod spawned. The initial specific gravities of eggs

obtained from cod that were raised in tanks in relatively low salinity surface waters inshore were 1023.0 to 1024.9. These specific gravities were lower than the initial specific gravity of 1026.5 estimated for eggs obtained from cod that lived in relatively high salinity at 380 m in offshore waters. This latter value is similar to the specific gravity (1026.2 to 1026.3) estimated from the vertical distribution of eggs in the offshore. Initial specific gravity was in all cases less than the density of the ambient water.

Specific gravity increased as a function of poor condition.

The specific gravity of larvae, determined from their vertical distribution in the offshore, was about 1025.1.

Typical densities, i.e. number per m^3 of eggs and larvae

Densities (number per 1000 m^3 of water) of eggs and larvae are, of course, highly variable in time and space. Examples are available from studies of ichthyoplankton in a bay on the east coast of Newfoundland, where Laprise and Pepin (1995) reported mean densities of cod eggs and larvae of 217.9 and 3.7 respectively in 1990, and 35.2 and 0.6 respectively in 1991. Additional examples of the densities of larvae come from repeated sampling in a limited portion of the same bay during 1985 and 1986 (Pepin and Penney, 2000). Additional examples of the densities of eggs come from sampling in the inner portion of the next bay to the north during 1991, 1993 and 1995 (Smedbol *et al.*, 1998).

Incubation rate of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larvae

Pepin *et al.* (1997) reported that the development rate of cod eggs increased with temperature. They also noted that cod eggs from the Northeast Newfoundland Shelf can develop normally at temperatures as low as -1°C . Development rate of eggs was not significantly related to egg size.

Pepin *et al.* (1997) reported that larval length at hatch was significantly greater in larger eggs, but egg size explained only a small portion of the variation in larval length. They also found that size at hatch increased with temperature.

Larval development rate as a function of temperature

No information.

Condition factor and nutritional status

No information.

Egg and larval mortality rates

No information.

Time of first-feeding of larvae and food at first-feeding

No information.

Food of larvae during development

No information.

Evidence of predation during the egg and larval stages

No information.

Recruitment

Are there several spawning sites (sub-populations) that contribute to the same stock unit?

As noted above, cod spawn in many areas of 2J+3KL. For cod that spawn in the offshore from Hamilton Bank to the northern slope of Grand Bank, there is uncertainty regarding whether spawning occurs over the shelf break or somewhat onto the shelf. There is also uncertainty regarding whether spawning tends to be broadly spread, as indicated by the catch rates of cod in spawning condition during bottom-trawl surveys, or whether there are more discrete sites that are not being detected in such data.

Earliest time in the life history when year-class strength can be predicted

No information.

Hypotheses that have been put forward to account for year-to-year variability in year-class strength

Characteristics of spawning-stock have been explored (Morgan *et al.*, 2000).

Evidence of long-term trends in recruitment

There has been a considerable decrease in recruitment.

Evidence that variability in recruitment is linked to variability of other species in the same area, the same species in other areas, or other species in other areas

No recent analyses.

Evidence of inter- or intraspecific competition

No information.

Is recruitment related to SSB or any environmental factors?

Numerous studies have demonstrated a positive association between spawning-stock biomass and recruitment (e.g. Rice and Evans, 1988; Myers *et al.*, 1993b; Hutchings and Myers, 1994a; Morgan, *et al.*, 2000).

However, Drinkwater (2002) pointed out that both spawning-stock biomass and recruitment experienced a long-term decline from the 1960s to the late 1980s, and that a statistical demonstration of the influence of spawning biomass on recruitment does not hold if the data are first-differenced to remove trends.

Morgan *et al.* (2000) explored the possible effect of spawning-stock characteristics on recruitment of 2J+3KL cod and two other cod stocks (3Ps and 3NO), plus one American plaice stock. A Beverton-Holt stock-recruit model was fitted to the output from a specific SPA (several SPAs are available for 2J+3KL cod – see above), and residuals were compared to the weighted mean age of the spawning-stock, the proportion of first-time spawners and the proportion of females in the mature population. Because the results were not consistent between stocks and difficult to interpret, the reader is referred to the paper for details.

It may be noted that atresia and skipped spawning were observed in cod overwintering in inlets on the east coast (Div. 3L) of Newfoundland during the 1990s (Bratley 1997; Rideout *et al.*, 2000). Such phenomena reduce the spawning potential of the stock. There have been no such observations in cod caught in the offshore of 2J+3KL.

With respect to environmental influences, there is an expectation that recruitment in 2J+3KL cod might be influenced positively by warm temperatures, because the stock is at the northern limit of the species' range in North America (Planque and Fredou, 1999). However, there have been conflicting reports of whether such a relationship can be detected (deYoung and Rose, 1993; Hutchings and Myers, 1994b; Planque and Fredou, 1999; Taggart *et al.*, 1994). Similarly, a reported relationship between recruitment and salinity (Sutcliffe *et al.*, 1983) was subsequently supported (Myers *et al.*, 1993a) and later rejected (Hutchings and Myers 1994b; Shelton and Atkinson, 1994) as data for additional years became available.

Migration

See section on stock and geographic distribution.

Adult growth

What are the general growth characteristics, e.g. typical length and size at age? Has it undergone changes over time?

Analyses of biological samples collected from the late 1940s to the early 1960s demonstrated a north-south cline in growth of cod in the Labrador-Newfoundland area. In general, growth rate and theoretical maximum length (L_{∞} in von Bertalanffy growth curve) were lowest off Labrador and highest on the southwestern Grand Bank (Fleming 1960; May *et al.*, 1965). These differences were attributed by May *et al.* (1965) to differences

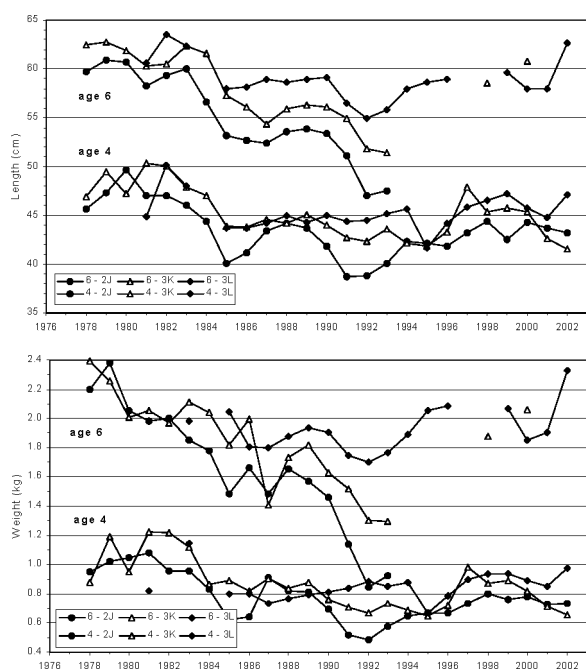


Figure 3.16.13. Cod in Divisions 2J+3KL. Mean lengths and weights at ages 4 and 6 of cod in Divisions 2J, 3K and 3L in 1978–2002, as determined from sampling during bottom-trawl surveys in autumn. Values calculated from fewer than 5 aged fish are not plotted. There were no surveys in Division 3L in 1978–1980 and 1984. (from Lilly *et al.*, 2003).

in environmental temperature. They noted that there was a trend from north to south of increasing surface temperature and decreasing volume of cold Labrador Current water. Lilly (1982) postulated that seasonal access to prey might also be a factor. Cod off southern Labrador do not feed for a long period during the winter and spring, whereas cod on the northern Grand Bank have access to prey throughout most of the year.

Growth, as indicated by size-at-age of cod sampled during autumn surveys by Canada since 1978 in 2J+3K and since 1981 in 3L (Figure 3.16.13), declined during 1983–1985 and again in the early 1990s, especially in 2J (Lilly, 2001; Lilly *et al.*, 2003). Size-at-age has increased in recent years but is below the peak values observed in the late 1970s. Much of the long-term variability in growth is associated with variability in water temperature (Krohn *et al.*, 1997; Shelton *et al.*, 1999). The water temperature used in the above-referenced papers was an index of the temperature in the environment, and not some measure of the temperature experienced by the cod. The decline in cod growth associated with a decline in environmental temperature could therefore be a direct effect of temperature *per se* or the effect of some broader ecosystem change for which temperature is a proxy.

Condition (weight at length) may be expressed in many ways. In the following it is discussed as an index (W/L^3) at age, and is provided for two body components; the gutted body mass and the liver, which is the energy storage organ. Condition has varied considerably between Divisions, years and ages. This variability is not well understood (Lilly, 2001). In Division 2J, both gutted condi-

tion and liver index declined in the early 1990s. During the second half of the 1990s gutted condition returned to approximately normal, whereas the liver index improved but did not fully recover. There has been variability with little trend since the mid-1990s (with the exception that the liver index appears low for 2001–2002). In Division 3K, gutted condition declined during the early 1990s and improved during the latter half of the 1990s. Liver index changed little during the 1990s. As in Division 2J, there has been variability with little trend since the mid-1990s. In Division 3L, gutted condition has remained relatively unchanged over time whereas liver index increased considerably in the early 1990s and has since declined to an intermediate level. Contrary to the data collected during the autumn bottom-trawl surveys, data collected during acoustic studies in 2J in June of several years have been interpreted to indicate that the cod in that area are in poor condition (Rose and O'Driscoll, 2002). Fish harvesters have reported that fish caught during the index/commercial fisheries (1998–2002) were in good condition.

Evidence for density-dependent growth

No information.

Evidence of temperature-dependent growth

See above.

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3.17 West Scotian Shelf

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Stock and geographic distribution

In the early 1970s, the 4X area was recognized as including a number of inshore cod spawning-stocks whose distributional boundaries were unclear (Halliday, 1971; 1974). Assessments were conducted for the offshore (primarily Browns and LaHave banks) which was thought to be a discrete stock. The treatment of cod in 4X and the Canadian portion of 5Yb as a single stock for assessment purposes commenced in 1985 (Campana and Simon, 1984). This step was taken partly because tagging results indicated mixing between inshore and offshore stocks appeared to be more extensive than had previously been thought, and because landings data did not have sufficient resolution to distinguish among components. While it is managed as a unit stock and a single assessment is done for the area, it is clearly a stock complex which encompasses a number of spawning components.

A time-series of stock biomass and recruitment from a VPA is available from 1948. Estimates of age composition of landings from before 1980 are thought to be less precise due to the limited sampling of the commercial fishery, but still sufficient to provide evidence of long-term trends.

Cod are found throughout the Southern Scotian Shelf and Bay of Fundy area and are landed as part of a mixed species groundfish fishery, which includes haddock, pollock (*Pollachius virens*), white hake (*Urophycis tenuis*), and lesser amounts of other species. Relative landings by species have fluctuated over time, but in general cod has been the primary species landed by the fixed gear and haddock the primary species landed by otter trawl. Recent declines in cod abundance have been less pronounced in the Bay of Fundy and Gulf of Maine than in eastern parts of 4X.

Results of tagging as well as morphometric and parasite studies indicate that cod in 4X are largely separate from adjacent management areas (Hunt *et al.*, 1999; Martin and Jean, 1964; McKenzie, 1956; Scott and Martin, 1959; Templeman, 1962). Analysis of allelic variation from microsatellite DNA has been used to discriminate 4X cod from those in 5Z (Georges Bank) and 4W. This analysis also resolved cod from Browns Bank, and the Bay of Fundy within 4X (Ruzzante *et al.*, 1999). Recent tagging work has shown little mixing between cod from eastern 4X and those in the Bay of Fundy, with Browns Bank forming the dividing line. Length-at-age for cod differs between the Bay of Fundy and Scotian Shelf; a pattern also apparent for haddock and pollock.

Time of spawning

Cod spawn in this region in both spring (February–March) and fall (October–November); however the amount of interannual variability in timing of spawning is unknown. The presence of both spring and fall spawned cod results in a bimodal length frequency for cod at age 1 in summer groundfish surveys. Both spring and fall spawning appear to coincide with plankton blooms (Brander and Hurley, 1992).

Those pollock which spawn inshore appear to coincide with cod inshore spawning in fall, while cod spawning is slightly earlier than haddock on Brown's Bank in spring.

Location of spawning

Spawning is distributed broadly through the area, both spatially and temporally. Spawning occurs in the fall in a number of areas along the coast of Nova Scotia from Halifax Harbour to Yarmouth, and at the mouth of St. Mary's Bay (McKenzie, 1940). Spawning occurs in the spring, primarily on Brown's Bank, but also off Digby Neck and Grand Manan at the mouth of the Bay of Fundy. Egg and larval studies in the 1980s support these observations. Cod eggs and larvae were distributed along the coast of Nova Scotia and into the Bay of Fundy in fall, and on Brown's Bank and in the Bay of Fundy in spring (Hurley and Campana, 1989; Hanke *et al.*, 2000).

Inshore spawning takes place in vertically well-mixed areas at the mouth of the Bay of Fundy and most eggs and larvae would be swept into the Bay. Fall spawning along the Nova Scotia coastline occurs at a time when the thermocline extends quite deep, and the coastal waters are well mixed. Offshore spawning occurs primarily on Browns Bank. The tidal influence results in a permanent gyre which circulates around the bank (Smith, 1989). In some years this gyre appears to retain most eggs, while in others wind-induced currents carry most eggs northwest towards the coastline (Suthers and Frank, 1989; Campana *et al.*, 1989b).

Biological details

Based on samples from the 1980s, Trippel *et al.* (1997) determined that cod in 4X mature at 2–3 years of age (25% at age 2; 75% at age 3: $A_{50} \sim 2.5$) and at about 45cm. Cod in adjacent areas, and also haddock in 4X, have shown a trend to decreasing length-at-age, and length-at-maturity, but this does not appear to be the case for 4X cod, with recent data showing no change. Condition factor (Fulton's K) has been calculated from July survey data back to 1970. Condition

was high through the 1990s in the Bay of Fundy (>1). On the Scotian Shelf, condition declined from about 1 in the 1970s, to 0.96–0.98 in the 1980s and the early 1990s, and has since returned to about 1.

Egg densities of 10–20 m^{-2} are reported for cod on Browns Bank (Hurley and Campana, 1989). Mortality rates for eggs and larvae were estimated at 0.15–0.3 day^{-1} (Campana *et al.*, 1989b). Since the mid-1980s, no additional field studies on egg and larval distribution and development have been conducted.

Recruitment

There are several spawning grounds for cod in 4X stretching from Halifax Harbour in the east to Grand Manan Island in the west. Spawning in coastal areas peaks in October–November, while on the banks it is February–March. Browns Bank was thought to be the primary spawning grounds in the 1980s (Campana, 1994). Given the shifts in relative abundance between areas in recent years, Bay of Fundy spawners may now be the largest component. Based on data from a three-year program in the mid-1980s, Campana *et al.* (1989a) reported a correlation between year-class strength and pelagic larval abundance. There is no ongoing larval sampling programme, and abundance at age 2 in bottom trawl surveys is currently used as the earliest index of abundance.

There has been a long-term decline in recruitment for cod in 4X. This has been correlated to a similar trend in spawning-stock biomass (Clark, 2000). The declines are more severe for some spawning groups than others, with abundance low in the east of 4X, and relatively stronger in the west. Recruitment levels for cod in 4X, 5Z, and 5Y show some correlation (Werner *et al.*, 1999). There is little correlation with haddock recruitment in 4X, which is currently high; however, length-at-age for haddock has declined considerably in the past decade. In general, pollock recruitment in 4X has followed a similar pattern. Pollock recruitment has been low in the last decade, and abundance for pollock is similarly low in eastern 4X, with both the cod and pollock fisheries now focussed primarily in the Gulf of Maine and the Bay of Fundy. Despite a restricted age range for spawners, the recruit/SSB ratio was high for the 1998–2000 year classes.

Migration

Cod which aggregate in the Bay of Fundy in summer move out of the Bay in November – December. Most of these move just to the mouth of the Bay, or into the adjacent, deep basin waters. These fish return to the Bay of Fundy in May/June. Many of the cod which congregate on the western side of the Bay appear to move well south in winter, returning to the deep basin waters in April and moving back into the Bay in May/June. Cod tagged on the Scotian Shelf show some limited movement to the shelf edge in winter and back onto the banks in summer. Cod tagged on Browns Bank during spawning disperse

broadly through the region, and appear to return to the south edge of Browns Bank in early February to spawn. Inshore cod appear not to undertake any extensive migration, remaining close to the location of tagging.

Adult growth

Unlike other NW Atlantic cod stocks, growth of 4X cod does not appear to be density or temperature dependent (Swain *et al.*, 2003). Despite similar temperature conditions in the two areas (1961–1990 average: 6.7°C for Fundy, 6.9°C for Scotian Shelf) length-at-age for 4X cod differs between the Bay of Fundy and Scotian Shelf; a pattern also apparent for haddock and pollock. There has been no temporal trend in length-at-age for cod; however haddock growth has shown a sharp decline in the past decade.

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