INVITED REVIEW

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THE POPULATION BIOLOGY AND EXPLOITATION OF CAPELIN (*MALLOTUS VILLOSUS*) IN THE BARENTS SEA

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The life history of the Barents Sea capelin stock through the various phases from egg to maturity is reviewed, including distribution, feeding, growth, mortality at the different life stages. The ecological role of the capelin is discussed, as well as its population dynamics. The stock history, its abundance and exploitation is dealt with, together with the history of stock assessment and management. The main aim of the review is to compile and bring to light many not readily available sources of knowledge concerning the Barents Sea capelin stock. These include Russian literature, cruise reports, theses, various kinds of working documents.

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KEYWORDS: Capelin; *Mallotus villosus*; Barents Sea; biology; ecology; stock history; fishery; stock assessment; fisheries management.

Йосетер Х. Популяционная биология и эксплуатация мойвы (Mallotus villosus) Баренцева моря.

В данном обзоре, посвященном запасу баренцевоморской мойвы, обсуждаются многие аспекты указанного вида. Рассматривается жизненный цикл мойвы, включая ее распределение, питание, рост и смертность на разных стадиях жизни. Обсуждается экологическая роль и динамика популяции мойвы. Рассматривается история запаса, его численность и эксплуатация одновременно с историей оценки запаса и его управления. Основная цель данного обзора - выявить и представить многие не всегда доступные источники информации, касающиеся запаса баренцевоморской мойвы. Сюда относится литература на русском языке, рейсовые отчеты, диссертации, различные рабочие документы.

Ключевые слова: мойва Mallotus villosus, Баренцево море, биология, экология, история запаса, промысел, оценка запаса, управление рыболовством.

1 INTRODUCTION

The Barents Sea capelin (*Mallotus villosus* Müller) stock is potentially the largest capelin stock in the world, its biomass in some years reaching 6-8 million tonnes. It is the largest stock of pelagic fish in the Barents Sea, with a key role as an intermediary of energy conversion from zooplankton production to higher trophic levels, annually producing more biomass than the weight of the standing stock. It serves as a forage fish for other fish species as well as marine mammals and sea birds, and has provided an annual fishery harvest of up to 3 million tonnes. The stock became a special object of interest to the fishing industry when the fishery on the Norwegian spring-spawning herring was banned in the early 1970s. A comprehensive research program for studying the capelin stock was initiated by the Institute of Marine Research in Bergen, Norway around 1960, and this species has for many years also been studied by scientists from the Polar Institute of Fisheries and Oceanography PINRO in Murmansk, Russia. Unlike for the Icelandic capelin, where a detailed review was recently published (VILHJÁLMSSON 1994), and despite the ecological importance of capelin and its key role as target for the fishing industry, no comprehensive review of its biology and ecological role in the Barents Sea has been compiled. Much of the existing information can only be found in unpublished cruise reports, unpublished papers presented to various meetings and symposia, and in theses and other kinds of 'grey' literature. The aim of this article is to present a synopsis of the knowledge of the Barents Sea capelin stock, based on the information found in these sources. In addition, I will present some results of ongoing studies, utilising the steadily growing capelin data base at the Institute of Marine Research in Bergen.

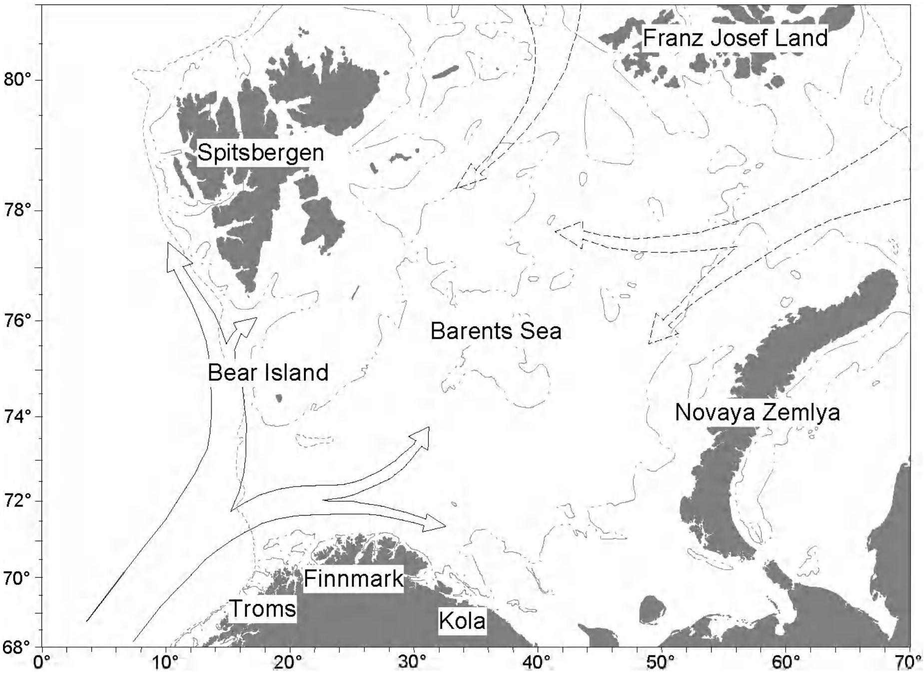

Fig. 1. The Barents Sea and adjacent areas, with main ocean currents, bathymetry (200 m and 500 m depth contours) and names of places mentioned in the text. The currents entering the Barents Sea from the south-west are the North Atlantic current carrying warm high-salinity water and the Norwegian Coastal Current carrying warm low-salinity water. The currents entering from the north and east are carrying cold low-salinity Arctic water.

2 SHORT DESCRIPTION OF THE AREA

Fig. 1 is a map of the Barents Sea, showing some topographical and hydrographical features and names of places mentioned in the text. The Barents Sea is a high-latitude, shallow continental shelf area. It is bounded in the north by the archipelagos of Spitsbergen and Franz Josef Land, in the east by Novaya Zemlya, and in the south by the coasts of northern Norway and Russia (Fig. 1). In the west, the boundary between the Barents Sea and the Norwegian Sea is usually drawn along the continental edge at about 10° to 15°E. More than 20 % of the area is shallower than 100 m, but troughs deeper than 400 m enter the area from the west and north-east.

The Norwegian Coastal Current flows along the coast of Norway and Russia, given the name Murman Coastal Current when it crosses the border between the two countries. The Norwegian Atlantic Current flows into the Barents Sea from south-west, dividing into two branches flowing eastwards and north-eastwards. Arctic water enters the Barents Sea through the channel between Spitsbergen and Franz Josef Land and, more important, between Franz Josef Land and Novaya Zemlya (Loeng 1991).

The three main water masses of the Barents Sea, Coastal Water, Atlantic Water and Arctic Water, are linked to these current systems. In addition, locally formed water masses resulting from processes taking place inside the area, e.g. seasonal freezing and melting of ice, can be found. Where the Atlantic and Arctic water meet, a well-defined Polar Front is formed. Its position is rather stable in the area south of Spitsbergen, where it is governed by the bottom topography, but is more variable in the eastern parts of the Barents Sea.

3 STOCK DISCRIMINATION

Rass (1933) divided the Barents Sea capelin into three 'forms' or 'races' which he called the Finnmarken, the Murman and the Novaya Zemlya capelin, after their spawning places. These groups spawned in spring, summer and autumn respectively. However, Prokhorov (1965) and Luka (1978) were of the opinion that spring and summer-autumn spawning capelin were not ecologically isolated groups. Collett (1903) mentions one oceanic stock of capelin and several fjord stocks living in Norwegian fjords in Finnmark, Troms, Nordland and Trøndelag counties. He argued that the fjord stocks are not completely isolated from the oceanic stock, although

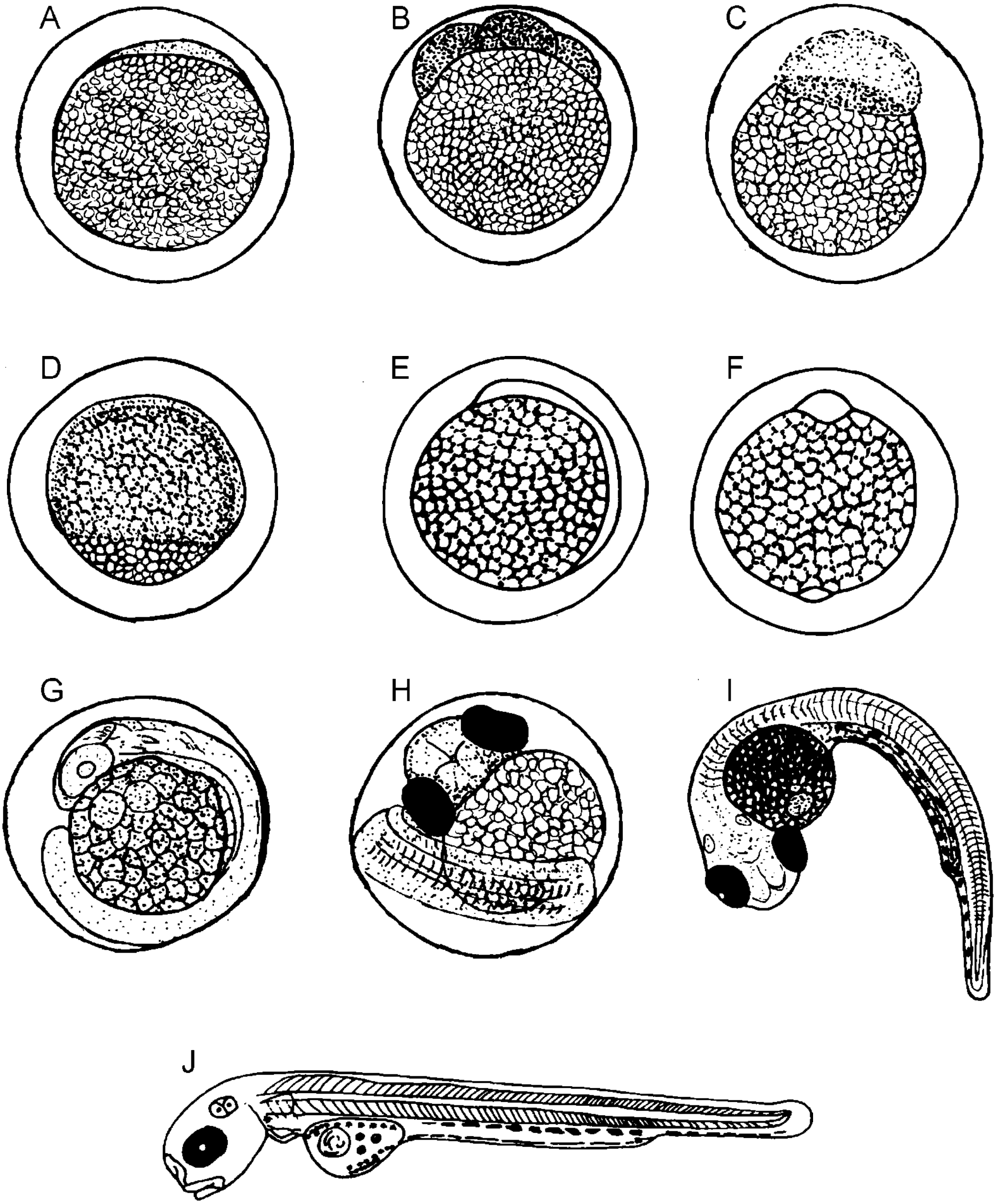

Fig. 2. Development of the capelin egg at 4 °C. A: 5 hours after fertilisation. B: About 12 hours after fertilisation. C: About 24 hours after fertilisation. D: Age 4 days. E: Age 7 days. F: Same age, frontal view. G: Age 12 days. H: Age 20 days. I: Age 25 days. Embryo is dissected out of the egg). J: Newly hatched capelin larva. From Gjøsæter & Gjøsæter (1986).

they mainly spawn within the fjords. Dushchenko (1985), who used electrophoretic studies of variability of myogens, non-specific esterases and malic enzyme, found no reasons to distinguish any reproductively isolated groups. He concluded that his results confirmed the opinion, already existing, that early and late spawning capelin were not independent reproductive groups. In Balsfjorden, Troms, Northern Norway, there is what is normally considered a local fjord stock of capelin. However, using genetic methods Mork & Friis-Sørensen (1983) argued that inter-sample differences in allele frequencies at four polymorphic loci were not significant and thus did not indicate genetic isolation between the fjord stock and the oceanic stock. On the other hand, Kennedy (1979), who

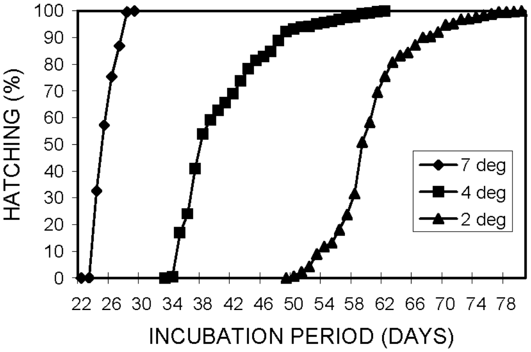

Fig. 3. Hatching curves for three batches of eggs incubated at 2, 4, and 7 °C. Redrawn after Gjøsæter & Gjøsæter (1986).

studied infestation by the cestode parasite *Eubothrium parvum* in capelin from the Barents Sea and Balsfjorden, concluded that the difference in frequency distribution and the failure to find any heavily infested fish in the Barents Sea confirm the suggestion that the capelin of Balsfjord form a local isolated population, which does not migrate into the Barents Sea.

It seems reasonable to conclude, for the moment, that there is one large oceanic stock of capelin in the Barents Sea and, in addition, one or more populations in fjords like that in Balsfjorden, although not completely isolated genetically from the oceanic stock, may be self-contained. This paper deals with the Barents Sea stock.

4 THE LIFE HISTORY

4.1 THE PLANKTONIC STAGES

4.1.1 Embryonic and larval development

Gjøsæter & Gjøsæter (1986) kept artificially fertilised eggs from capelin of the Barents Sea stock under controlled temperature conditions comparable to those observed on the spawning beds. They gave a description of the development and the effect of temperature on the embryonic growth, the eggs' ability to adhere to the substrate, and the fertilisation rate at different salinities.

The description of the embryonic development given below is based on a temperature of 4 °C, a typical temperature at the spawning beds of the Barents Sea capelin. The embryonic stages referred to in the description of the development are more or less identical to those used by Fridgeirsson (1976) when describing the development of the Icelandic capelin. The duration of each stage at 4 °C is given for the fastest developing eggs in the study group which hatched after 34 days (Gjøsæter & Gjøsæter 1986).

Stage 1. Blastodisc formation. Duration: from fertilisation to age six hours. Appearance: About two hours after fertilisation a fertilised egg may be distinguished from an unfertilised as it has a clear periviteline space. After about five hours the blastodisc is seen as a cap on top of the yolk (Fig. 2A).

Stage 2. Cleavage of blastodisc, morula, blastula. Duration: from age seven hours to age two days. Appearance: At age seven hours the egg is at the two-cell stage, and continues through the four-cell stage (Fig. 2B) *et. seq.* As the cleavage progresses, the individual cells become progressively more difficult to discern. The morula (Fig. 2C) is visible after about 24 hours and, in the course of the second day, the morula begins to be hollowed out, forming the blastoderm.

Stage 3. Gastrulation, closure of blastopore. Duration: from age two to six days. Appearance: Around day three the blastoderm starts to grow around the yolk, a process which can easily be observed in the egg. At day four the rim of the blastoderm reaches about three fourths of the distance around the yolk (Fig. 2D). Simultaneously, gastrulation takes place. At age five days the embryo is seen as an oval thickening of the blastoderm , which at day six can be seen to reach about half way around the yolk sac.

Stage 4. Organogenesis I. Formation of pre-organs. Duration: from age six to twelve days. Appearance: On day seven the head end of the embryo has become broader and higher than the tail end (Fig. 2E and F) and on the next day the optic bulbs begin to form. During this stage there are only minor changes in the outer appearance of the embryo. There is some growth in length, but the embryo does not reach around the circumference of the yolk sac (Fig. 2G). Towards the end of this stage the inner ear can be observed to contain structures which are probably the primordial otoliths.

Stage 5. Organogenesis II. Further organ development. Duration: from age twelve to twenty-four days. During this stage the embryo begins to move, the heart starts to beat, and the eyes become pigmented. The body grows in length, and the tail continues developing. Fig. 2H shows the embryo 20 days after fertilisation. At day 22 a faint pigmentation appears below the gut, and during the two last days of this stage the pigmentation becomes more distinct.

Stage 6. Preparation for independent feeding. Duration: from age 25 days to hatching, which may start around day 33 and last for more than 20 days for a batch of eggs. Appearance: At the beginning of this stage melanophores are present both below and above the gut, and pigmentation is also more pronounced under the tail and on the yolk sac (Fig. 2I). The head separates from the yolk sac. Three to four days later the segmentation reaches the tail, and in the yolk sac the oil globules begin to aggregate into one large sphere. About age one month the pectoral fins appear, and the mouth starts to form. At days 33-34 the pigmentation resembles that of a newly hatched larva (Fig. 2J). The mouth seems fully developed and is open.

Hatching curves for three batches of eggs, incubated at 2, 4 and 7 °C (Fig. 3) show that the incubation period is to a large degree dependent on temperature, varying from about 20 days for the fastest developing eggs at 7 °C to 80 days for the slowest developing eggs at 2 °C. At hatching, the mean total length was 7.55 mm (N = 102, range 6.1-8.2 mm) and the mean yolk sac diameter was 1.15 mm (N = 102, range 0.7-2.0 mm).

Pozdnjakov (1960) also studied the embryonic development of the Barents Sea capelin, but used a somewhat less detailed stage description than the one adopted here. He reported length at hatching to be from 4.8 to 7.5 mm, but it is not quite clear whether he measured the total length of the larvae.

4.1.2 Growth of larvae

Feeding, growth and survival of capelin larvae from the Barents Sea stock were studied in an outdoor basin by Moksness (1982). He sampled naturally spawned eggs from a spawning site at the coast of Finnmark, which hatched in the laboratory and were released in a 2000 m^3 outdoor basin. Approximately 100 000 larvae were released in the basin, and 2.1 % survived after 127 days, when the experiment was terminated.

Mean growth in length during the first 12 days was 0.29 mm day^{-1}, but decreased to about 0.2 mm day^{-1} from age 40 days until the end of the experiment. The growth rate is expected to be determined by the density of zooplankton, and in another experiment, when two batches of capelin larvae were given zooplankton in densities more than 10 times higher than observed in the basin experiment, they grew at rates of 0.44 mm and 0.31 mm day^{-1} during the first 26 and 15 days respectively (Øiestad & Moksness 1979). The temperature conditions in the basin during these experiments (8-20 °C at the surface and 6-12 °C near the bottom (Moksness 1982)) were higher than experienced in the natural habitat in the southern Barents Sea. This probably increased the growth rate but it is uncertain to what extent.

A larval survey of capelin in the Barents Sea has been conducted annually since 1981 (Alvheim 1985; Fossum 1992; ICES 1996a). The aim of that survey has been to describe the distribution and abundance of the larvae. The survey has normally been carried out in the last half of June, i.e. when most of the larvae are about one month old (Section 4.1.4). The larvae caught at each station (Gulf III high speed plankton sampler, Zilstra 1971) were length measured. In most years, the majority of the larvae were of 5 to 15 mm standard length, while the number of larvae > 20 mm was low. The mean length in the period 1981 to 1990 varied from 8.9 mm to 12.9 mm. If an age of one month and a standard length at hatching of 6 mm are assumed for all years, these mean lengths correspond to a mean daily growth rate of 0.10-0.23 mm day^{-1}. Based on counts of primary rings in otoliths of field sampled 0-group capelin, Gjøsæter & Monstad (1982) calculated a mean growth rate of 0.174 mm day^{-1}.

Annual 0-group surveys have been carried out in the Barents Sea in August since 1965. The main aim of this survey has been to describe the distribution of the 0-group of various species and to calculate abundance indices. Loeng & Gjøsæter (1990) analysed the growth of various 0-group species in relation to temperature conditions based on data from 1965 to 1989. The mean total length of capelin varied from 35-58 mm, with a mean for all years of 45 mm. As pointed out by the authors, offspring from summer spawning capelin (see section 4.2.3) may have influenced the mean length in some years. However, in only 6 out of the 32 years of data, capelin smaller than 20 mm were included in the measurements and then in very low numbers. A length of 20 mm in late August would, if these specimens derived from the main spawning in spring, correspond to a mean growth rate in the order of 0.15 mm day^{-1}. Assuming an age of three months for the 0-group capelin with mean length of 45 mm, measured in August, gives a mean growth rate over the period of 0.4 mm day^{-1}. These results indicate that the growth rate in terms of length is higher in the period July-August than it is in the period May-June. Loeng & Gjøsæter (1990) found some evidence for a positive relationship between mean length in August and variations of temperature conditions in the Barents Sea.

4.1.3 Larval feeding

Larvae kept in the basin at Flødevigen (Moksness 1982) were observed to reach the end of the yolk sac stage (EYS) at age 10 days (at 8 °C). They began to feed at age 4 days (laboratory) and 5 days (basin) while the yolk sac volume was 0.020 mm^3. In the basin, the feeding incidence was low (< 10 %) during the first 25 days, but had increased to 70 % on day 40. The length of the longest prey organisms increased from 300 to 1230 μm at a larval length from 7 to 20 mm, and further to 1400 μm for larval lengths up to 40 mm. The smallest prey organisms found in the larval guts consisted of various phytoplankton organisms of 9-50 μm in length. The zooplankton in the basin was dominated by larvae of *Spionidae* spp. (10 organisms l^{-1}) during the first part of the experiment while veligers of *Littorina* spp. (5 organisms l^{-1}) dominated during the remainder of the period. The gut content of the larvae reflected the composition of plankton in the basin. Thus, the larvae were apparently preying upon the dominant organisms of suitable size in their surroundings.

Moksness (1982) also reported on a field study of

Table 1. Comparison of gut content of larvae from a station with mean length 7.97 mm, 64 % without yolk sac, and of surrounding plankton. From Bjørke (1976).

Food items	In plankton		In diet	
	Number per m^3	%	Number	%
Calanus eggs	100	3	21	54
Calanus nauplii	1100	30	17	44
Copepods	2300	64	-	-
Other food	100	3	1	2

capelin feeding in spring 1971. The number of food items in the gut of larvae caught in the field was at the same level as that in the basin and no particular prey group dominated. Larvae caught in the field (yolk sac larvae with yolk sacs from 0.03 mm^3 to EYS, and larvae from 6 to 15 mm) mostly fed on copepod nauplii and harpacticoid and calanoid copepods.

Bjørke (1976) studied feeding of larval capelin near the coast of Finnmark in May 1971. The food items eaten by larvae 4.8-21.0 mm in length, mainly consisted of *Calanus* eggs (52 %) and *Calanus* nauplii (42 %). By comparing the gut content with the composition of plankton in the sampling area (Table 1) he concluded that the larvae preferred eggs over nauplii.

The larvae began to feed while still having large yolk sacs, but the feeding incidence increased with decreasing yolk sac size. Inspection of larvae, sampled during a 24 hour cycle, led to the conclusion that feeding started shortly after sunrise and declined at nightfall.

4.1.4 Geographical distribution of larvae and 0-group

From 1967-1980, investigations of larval capelin distributions were carried out in most years, but no abundance estimates were made (Hognestad 1969a, b, & c, 1971; Buzeta & al. 1975; Gjøsæter & Martinsen 1975; Hamre & Røttingen 1977; Dommasnes & al. 1978; Dommasnes 1978b; Dommasnes & al. 1979a; Dommasnes & al. 1979b; Ellertsen & al. 1980; Serebryakov & al. 1984). Since 1981, annual surveys for the purpose of describing the geographical distribution and abundance of capelin larvae have been carried out in June (Alvheim 1985; Fossum & Bakkeplass 1989; Bakkeplass & Lauvås 1992; Gundersen 1993a, 1993b; Kryssov & Toresen 1993; Hamre & Kryssov 1994; Tangen 1995; Tangen & Bakkeplass 1996). From 1965, an international 0-group survey of the Barents Sea has been carried out annually in August-September (ICES 1965, 1966, 1967, 1968, 1969, 1970, 1971, 1973a, 1973b, 1974, 1975, 1976, 1977, 1978, 1979, 1980, 1981, 1982b, 1983, 1984a, 1985a, 1986, 1987, 1988, 1989, 1990, 1991b, 1992, 1994, 1995, 1996b, 1996c). Based on the distribution maps and textual information presented in these reports, the approximate western, northern and eastern boundaries as well as the characteristics (types) of the larval and 0-group distribution in April-June and August-September are given in Table 2. Distribution maps of larvae in May-June, together with spawning areas (See section 4.2.1.4), have also been constructed (Figs 4-6). Before 1981, the total distribution area of the capelin larvae was not always covered. Consequently, maps for earlier years do not show the northern extension of the distribution area. In general, larvae are found east to about 36-37°E in May-June, while

Table 2. Geographical distribution of capelin larvae in April-June (larval surveys), and in August-September (0-group surveys), shown by its western, northern and eastern limits. The distribution type is characterised according to the main distribution areas. See text for data sources.

	Larval survey			0-group survey		
Year	Western limit (°E)	Eastern limit (°E)	Northern limit (°N)	Western limit (°E)	Eastern limit (°E)	Distribution type
1965				15	41	central
1966				22	46	central-east
1967	18	unknown	unknown	22	48	central-east
1968	16	31	unknown	16	50	west-east
1969	14	31	unknown	5	45	west-east
1970	22	31	unknown	22	50	central-east
1971	15	40	73	10	52	west-east
1972	15	40	73	10	50	west-east
1973	27	unknown	73	15	50	central-east
1974	32	unknown	70	20	45	central-east
1975	30	40	unknown	28	50	east
1976	25	38	73	18	50	central-east
1977	27	35	72	20	45	central-east
1978	30	37	72	26	43	east
1979	25	37	73	20	55	central-east
1980	25	38	73	15	50	central-east
1981	16	34	73	5	55	west-east
1982	16	33	73	5	N.A.	west-east
1983	16	36	74	<5	50	west-east
1984	18	36	73	<2	55	west-east
1985	17	34	73	5	46	west-east
1986	29	31	70	26	50	east
1987	30	33	71	25	50	east
1988	22	33	73	20	50	west-east
1989	18	34	74	7	42	west-east
1990	21	35	74	18	55	west-east
1991	17	36	74	5	55	west-east
1992	19	37	73	20	55	west-east
1993	18	38	74	25	56	central-east
1994	31	36	71	30	50	east
1995	30	35	70	30	50	east
1996	18	37	73	5	56	west-east

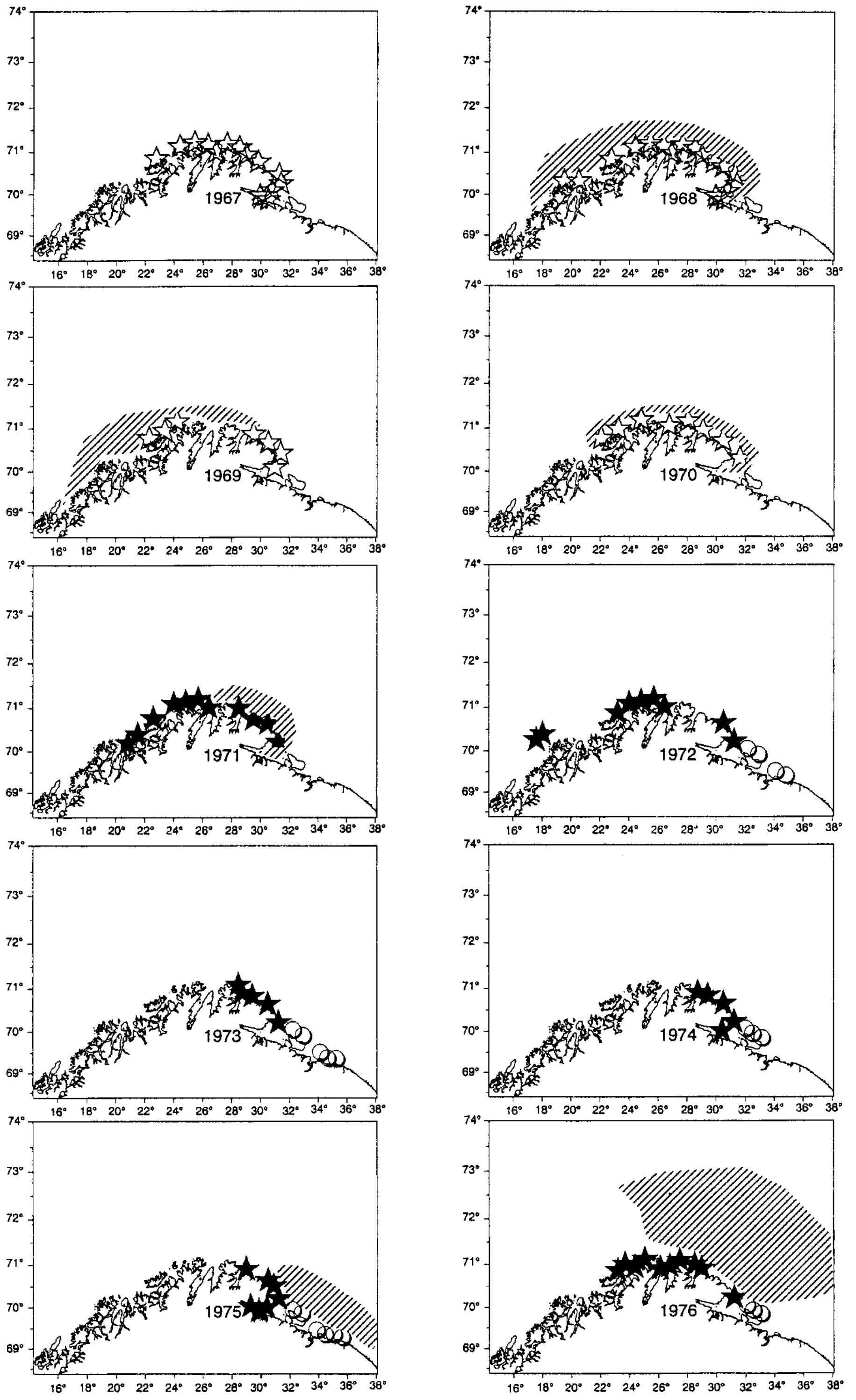

Fig. 4. Spawning areas and spring larval distribution during the period 1967-1976. See text for data sources. Open stars: Assumed spawning areas, filled stars: known spawning areas, Norwegian surveys. Circles: Known spawning areas, Russian surveys.

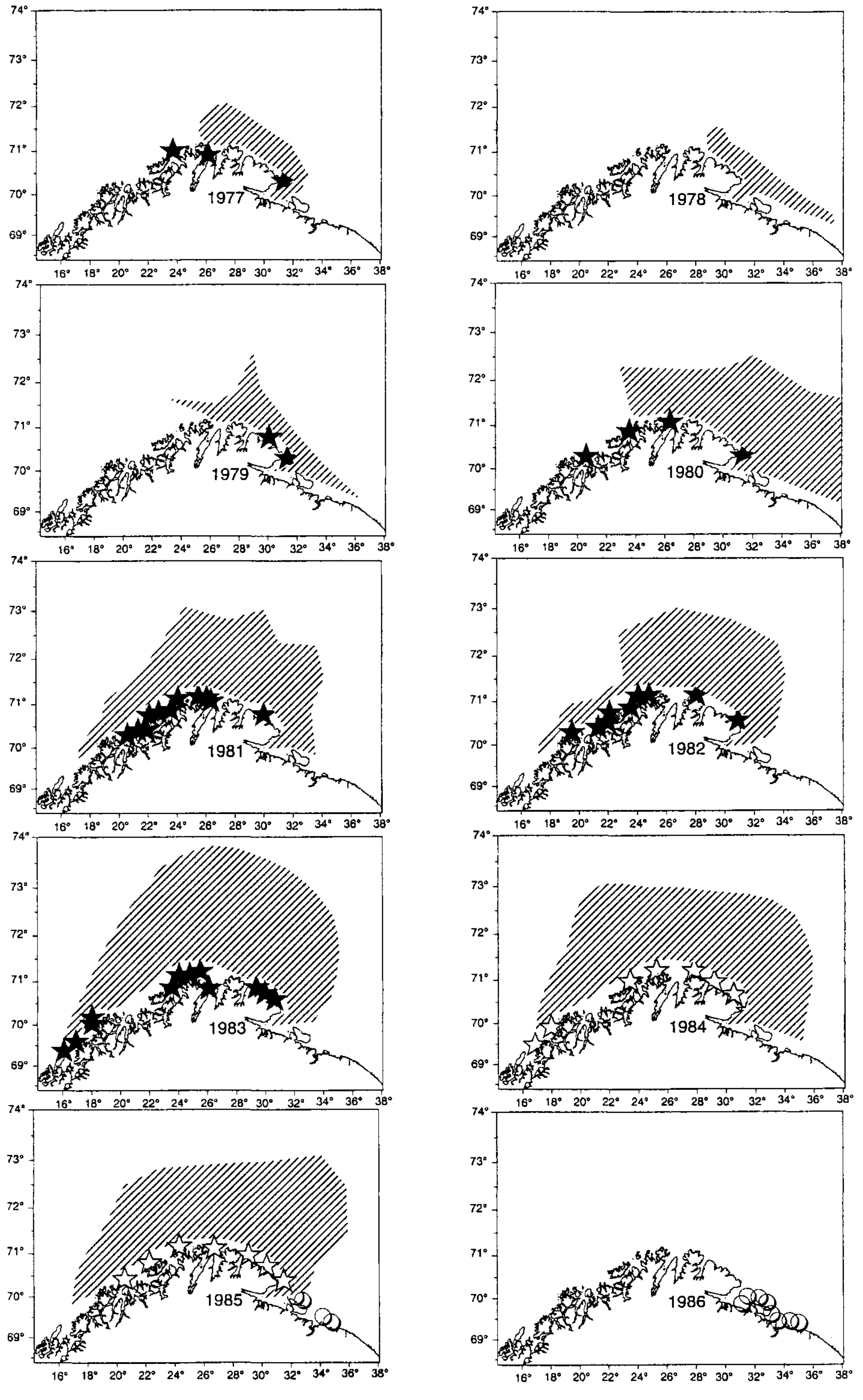

Fig. 5. Spawning areas and spring larval distribution during the period 1977-1986. See text for data sources. Open stars: Assumed spawning areas, filled stars: known spawning areas, Norwegian surveys. Circles: Known spawning areas, Russian surveys.

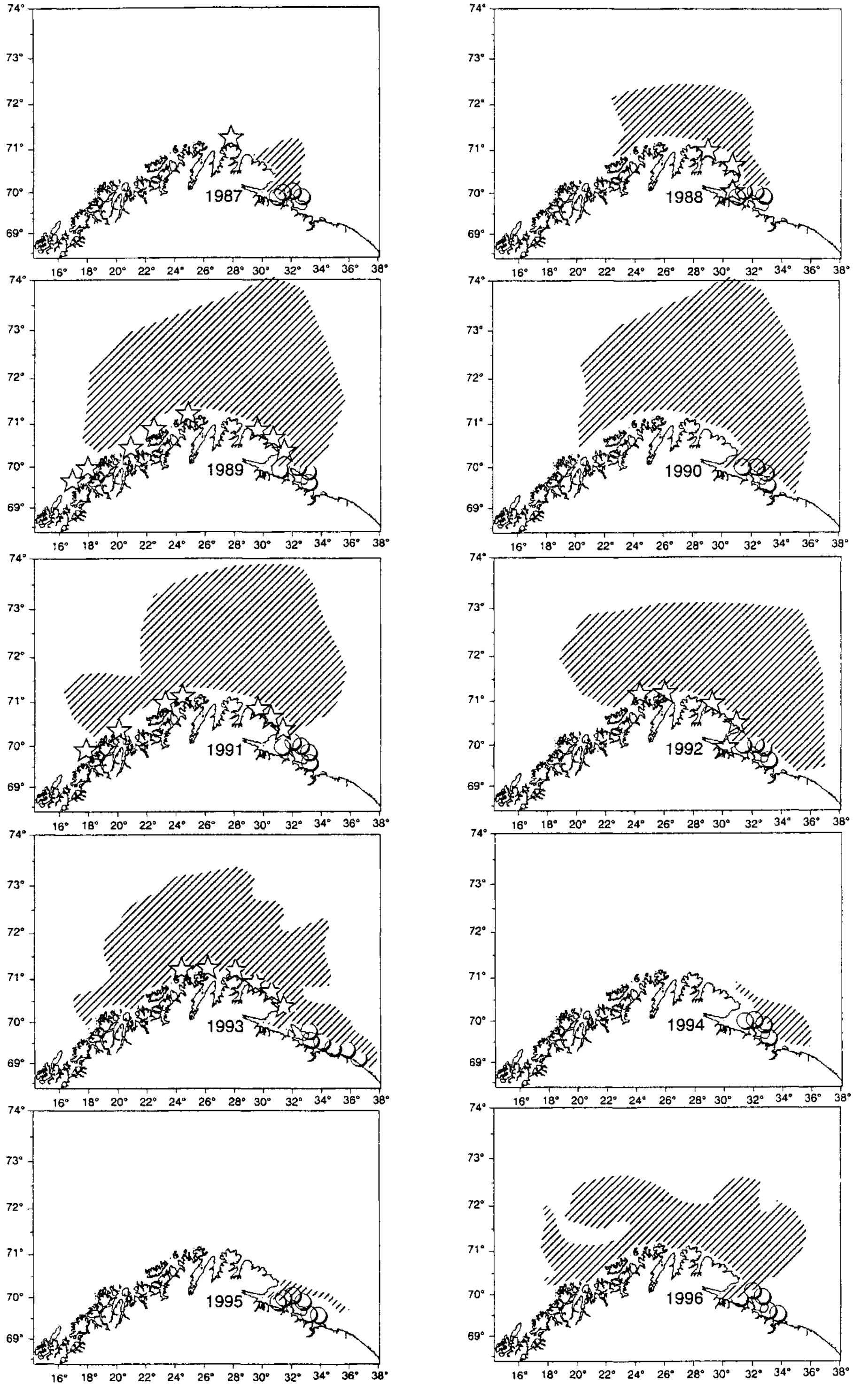

Fig. 6. Spawning areas and spring larval distribution during the period 1987-1996. See text for data sources. Open stars: Assumed spawning areas, Norwegian surveys. Circles: Known spawning areas, Russian surveys.

the western extension of the distribution is quite variable. In some years, the western limit is at 14-16°E, i.e. at Vesterålen. In other years, the western limit is at about 30°E, at the Varanger Peninsula in Eastern Finnmark. The northern extension at this time is normally at 73-74°N. However, in years when distribution is easterly, the northern limit is often displaced as far south as 71-72°N.

In August-September, the 0-group capelin has a much wider distribution, in most years extending eastwards beyond 50°E. The western boundary is much more variable. Thus, in some years, 0-group capelin is found to the west of Spitsbergen, i.e. at about 3-5°E, while in other years no 0-group capelin is found west of 25-30°E. In all years except 1992, there is a fairly close correlation between larval and 0-group distribution. In years with a western larval distribution there will also be a western 0-group distribution and an eastern larval distribution will lead to an eastern 0-group distribution.

4.1.5 Depth distribution

The vertical distribution of larvae along the coast of Troms and Finnmark in April-June was described by Hognestad (1969a, 1969b, 1969c, 1971). He used Clarke-Bumpus plankton samplers to monitor the horizontal and vertical distribution of capelin larvae. Hognestad's observations indicate that the newly hatched larvae reside in the uppermost 25 m, but gradually disappear, to be subsequently found in deeper layers. In 1967, the proportion of larvae found in the uppermost 25 m decreased from 62 % to 20 % over a period of three weeks. In 1968, the corresponding values were 56 % to 29 % over a period of 14 days. In 1969, however, 93 % of the larvae were found in the uppermost 25 m in late April, and 56 % were still found there in the beginning of June. A similar trend was observed in 1970. The larvae found at depths greater than 25 m seemed to be more or less evenly distributed in the layers 30-50 m and 50-75 m. It is not clear whether the changed depth distribution was caused by depth-selective mortality or if there was an active vertical migration of the larvae (Hognestad 1969a, 1969b, 1969c, 1971). Diurnal changes in vertical distribution were not discussed in these reports. Salvanes (1984) analysed the depth distribution of capelin larvae in the years 1972-1975. She showed that when the material from April, May and June was pooled, all length groups seemed to be found at somewhat shallower depths at night than during the day. The depth distribution of larvae was studied during a capelin larval survey in 1989 (Fossum & Bakkeplass 1989), using a submersible pump. Fifty litres of water were filtered through a plankton net from 10, 20, 30, 40, 50, and 60 m depth at 0800, 1100, 1400, and 1700 UTC. The larvae were mainly found from 20-40 m, and there was no sign of any vertical migration in the twilight hours (from 1700 UTC). Neither could any difference be detected between larval length groups of 6-9 mm and 10-14 mm.

Beltestad, Nakken & Smedstad (1975) found that in August the 0-group capelin descended down to the thermocline during night while they partly stayed in the surface layer during daytime.

4.2 THE IMMATURE AND ADULT PHASE

The capelin undergo metamorphosis when they are about 7.5 cm long (Vesin & al. 1981). The changes from a typical larval appearance, (e.g. slender body, sparse pigmentation) to a more adult appearance are gradual, and individuals which are not fully pigmented at lengths up to 8-10 cm may be found. The metamorphosis normally takes place in spring/summer in the second year of life, (i.e. when the offspring from the main spawning season are about 12 months old).

The immature phase lasts from metamorphosis until first maturation, which normally takes place in the third or fourth year of life. Since most capelin spawn only once and then die (see section 6.5.2), practically all growth takes place during this stage. If the life history prior to maturity is classified in this way, the adult phase only lasts for a relatively short time interval, i.e. from maturity is reached until spawning.

4.2.1 Distribution and migrations

4.2.1.1 General distribution

Usually, the capelin stock stays in the Barents Sea during all life stages, but perform extensive seasonal migrations. During winter and early spring, there is an 'upstream' spawning migration towards the coast of northern Norway (Troms and Finnmark counties) and Russia (Kola county) (Fig. 1), while during summer and autumn there is a north- and north-eastward feeding migration. During autumn, the adult capelin are found in both Atlantic and Arctic water, with ambient temperature from –1 °C to 2 °C, (Gjøsæter & Loeng 1987). The fry, upon hatching on the spawning sites at the coast, drift offshore with the ocean currents, and spread out into the central and eastern parts of the Barents Sea where the young capelin mainly stay during the first months of their life.

The position of both spawning areas, nursery areas and feeding areas vary with hydrographic conditions (Loeng 1981, 1989a, 1989b; Ozhigin & Luka 1985; Ozhiging & Ushakov 1985; Gjøsæter & Loeng 1987; Ushakov & Ozhigin 1987). In 'warm years', characterised by strong inflow of Atlantic water from the west and high temperatures in the Barents Sea, the distribution of capelin is displaced north- and eastwards. In 1973 and 1974, typical warm years, the capelin reached the extremity of their distribution area off Franz Josef Land

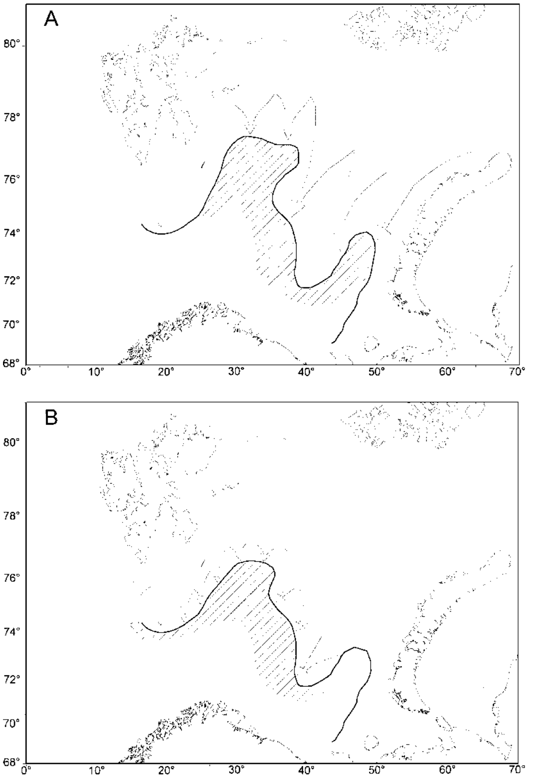

Fig. 7. Wintering migrations (arrows) of capelin in October and wintering areas (hatched) in November-December in a typical warm year (A), and a typical cold year (B). The position of the polar front is indicated by a continuous black line. Redrawn from Ozhigin & Luka (1985).

and the northern coast of Novaya Zemlya. In 'cold years', characterised by weak inflow and low temperatures, such as in the period 1979-1982, the capelin are found further to the south and west. Under such hydrographic conditions, a part of the capelin stock is also found west of Bear Island and along the west coast of Spitsbergen.

Loeng (1981) compared the northern extension of the capelin distribution area with temperature conditions at 100 m depth, and found linear correlation coefficients r of 0.85-0.90. Similarly, Ozhigin & Ushakov (1985) compared the northern limit of the feeding areas of capelin (measured along a series of southwest-northeast transects) with a number of different hydro-meteorological indices, and found high correlations. On the basis of multiple regression analysis they were able to forecast the position of the main capelin concentrations with a fairly high precision two months in advance.

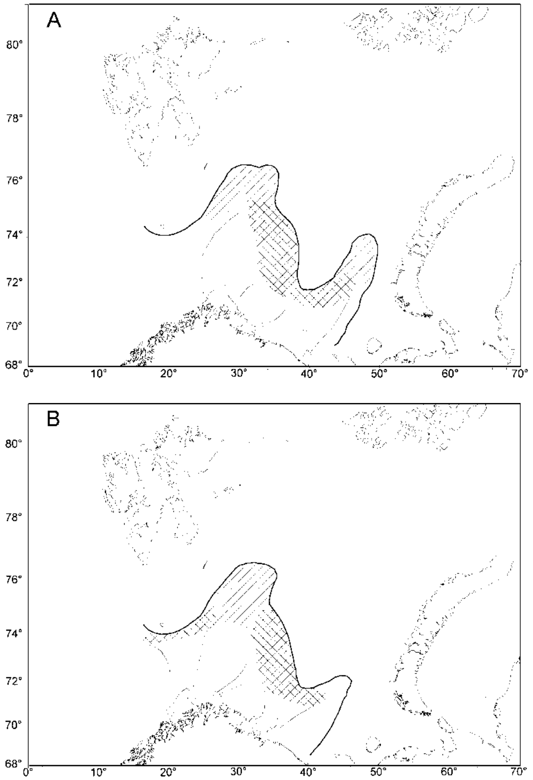

Fig. 8. Wintering areas of immature (hatched) and mature (cross-hatched) capelin and main routes of spawning migrations (arrows) in January in a typical warm year (A) and a typical cold year (B). The position of the polar front is indicated by a continuous black line. Redrawn from Ozhigin & Luka (1985).

4.2.1.2 Winter distribution

During winter (December-February), the capelin are normally found south of the ice edge in the central parts of the Barents Sea. In warm years, the overwintering areas extend further to the east (Fig. 7A) than in cold years (Fig. 7B). During January the maturing part of the stock gradually segregates from the immature part, occupying the southern part of the common distribution area.

4.2.1.3 Spawning migration

During February, the maturing part of the stock begins to move towards the coast. The migration routes and the time and place where the spawning stock approaches the coast are determined by hydrographic factors (Martinsen 1933; Penin 1971, Luka & Ponomarenko 1983; Shevchenko & Galkin 1983; Ozhigin & Luka 1985). In most years, the migration follows two or even three different routes towards the coast. In warm years, the maturing capelin mostly approaches the coast of Finnmark and the Kola peninsula from the north-east (Fig. 8A), while in cold years there may be additional spawning migrations from the areas south of Bear Island to the west coast of Troms and Finnmark (Fig. 8B). USHAKOV & OZHIGIN 1987 showed that the capelin do not immediately respond to thermal changes in the water. There appears to be a certain inertial, delaying responses with respect to changes of temperature conditions. After a series of cold years (1965-1969 and 1977-1982) the spawning of capelin in warm years (1970-1971 and 1983-1984) still continued to be restricted to areas near the Norwegian coast.

4.2.1.4 Spawning

The location of capelin spawning areas have been described on a general basis by several authors, e.g. RASS (1933), PROKHOROV (1968), SÆTRE & GJØSÆTER (1975) USHAKOV & OZHIGIN 1987, as well as in numerous cruise reports and other documents dealing with capelin spawning in particular years. Based on the information contained in these reports, and on material provided by N.G. Ushakov at PINRO, Murmansk, charts have been produced where the spawning areas are indicated, together with the resulting larval distribution in May-June (Figs 4-6). In the years from 1971 to 1984 the spawning areas were located by sampling eggs with a Petersen grab. In other years, the most probable spawning areas have been more subjectively determined, e.g. from sampling of spawning or newly spent capelin, observations of capelin eggs in fish stomachs, and by observations of diving ducks feeding on capelin eggs.

Before 1967, only sporadic information exists on the location and extent of spawning areas. MØLLER & al. (1961) describe the spawning migration in 1961 as consisting of two separate approaches, one towards western Finnmark and one towards eastern Finnmark and the Kola coast. In 1966, the capelin migrated to the spawning areas from the east, along the Kola coast towards eastern Finnmark (LAHN-JOHANNESEN & al. 1966).

Apparently, the spawning in 1967-1970 took place along the Norwegian coast from about 18-22°E to 32°E (STRØM & VESTNES 1967; STRØM; & al. 1968; STRØM & MONSTAD 1969; LAHN-JOHANNESEN & MONSTAD 1970). Nothing is known about spawning on the Russian side of the border in these years. According to the larval distribution in 1968-1970 (Fig. 4) spawning has probably also taken place further west than 18°E. In 1971, and in particular in 1972, spawning occurred along a wide area at the Troms, Finnmark and Kola coasts, while in 1973-1976 a more typical eastern spawning took place (DRAGESUND & al. 1971; BJØRKE & al. 1972; GJØSÆTER & SÆTRE 1973a; GJØSÆTER & al. 1974; GJØSÆTER & MARTINSEN 1976; HAMRE & SÆTRE 1976; N.G. Ushakov, PINRO, pers. commn). In 1972-1974 no information on larval distribution exists, but for the other years the larval distribution confirms the position of spawning. In 1977, spawning began near Vardø on 18 March and at Fruholmen on 29 March. These were the main spawning areas, but there was 'occasional spawning on a smaller scale along the coast' (DOMMASNES & HAMRE 1977). Although an extensive survey was carried out in 1978, no spawning areas were located (DOMMASNES & al. 1979a). Nonetheless, capelin larvae were detected off eastern Finnmark and Kola in June, and some spawning must have taken place in these areas (Fig. 5). In 1979, three spawning invasions were detected (HAMRE & MONSTAD 1979), but only at the Varanger peninsula was spawning confirmed by the detection of eggs. However, the larval distribution (Fig. 5) shows that additional spawning must have taken place further west. In 1980 the main spawning area was also near Vardø, but additional spawning areas were found at Magerøy, Sørøy and Arnøy (HAMRE & MONSTAD 1980). In 1981, 1982 and in particular in 1983, the main spawning areas were displaced westwards (ALVHEIM & al. 1983a; ALVHEIM & al. 1983b; GJØSÆTER 1983). From 1984 onwards, spawning areas were no longer detected by grab surveys on the Norwegian side of the border. Based on information from other surveys along the coast, spawning was found to take place off the coast of Troms and Finnmark in 1984 (DOMMASNES 1984), and along the Troms, Finnmark and Kola coasts in 1985 (GJØSÆTER 1985d). In 1986, mature capelin were only found in the Varanger fjord on the Norwegian side of the border, and observations of newly hatched larvae there in late June show that some spawning took place in these localities (SOLEMDAL & BRATLAND 1986), even if no larvae were detected during the annual larval survey in June. Some spawning was observed along the Rybachi peninsula and further east (N.G. Ushakov, PINRO, pers. commn). In 1987 no spawning was observed off the Norwegian coast in spring, but on 31 July spawning was observed outside Berlevåg (28°E) (G. Sangolt, Norwegian Directorate of Fisheries, pers. commn). Furthermore, in 1987 and subsequent years spawning took place along the Rybachi peninsula (N.G. Ushakov, PINRO, pers. commn). In 1988, GJØSÆTER (1988) found indications of spawning only off eastern Finnmark and in the Varanger fjord in mid-April. However, observations of larvae all along the Finnmark coast in June (Fig. 6) show that some spawning must have taken place over a wider area.

In 1989, spawning seemingly took place from 17°E to 34°E (SANGOLT 1989; N.G. Ushakov, PINRO, pers. commn). Judging from the larval distribution in June (Fig. 6), spawning also occurred over a large area in 1990, but no surveys were carried out off the Norwegian coast in

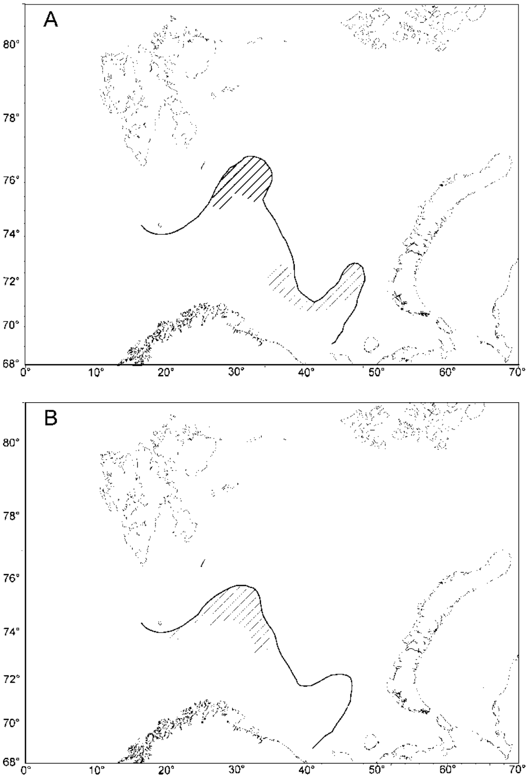

Fig. 9. Main capelin concentrations in June (hatched) in a typical warm year (A) and a typical cold year (B). The position of the polar front is indicated by a continuous black line. Redrawn from Ozhigin & Luka (1985).

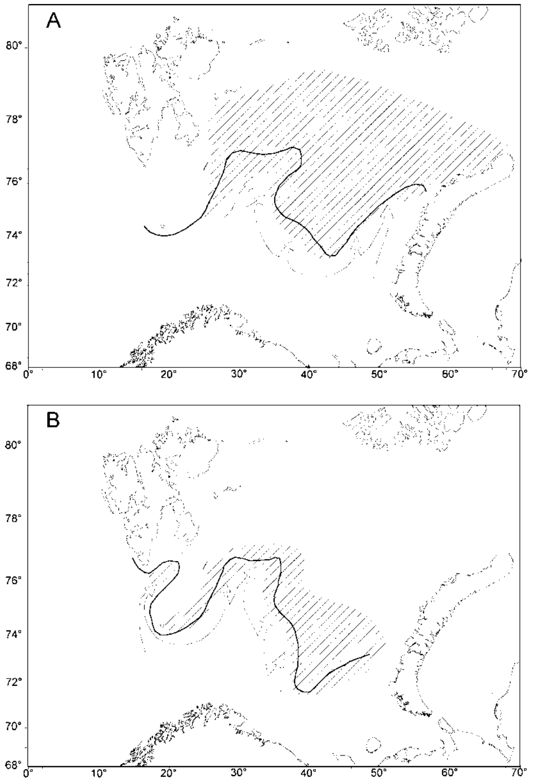

Fig. 10. Main feeding migration routes of capelin in July-August (arrows) and concentrations in September (hatched) in a typical warm year (A) and a typical cold year (B). The position of the polar front is indicated. Redrawn from Ozhigin & Luka (1985).

that year. Gjøsæter (1991) found spawning and spent capelin along the coast of Troms and Finnmark in March 1991, and Sangolt (1992) observed spawning and spent capelin along the coast, east of 24°E, in March 1992 (Fig. 6). In 1992, a spawning area was also detected near the island Dolgiy (69°21'N, 58°57'E) on 22 July (S. Dahle, Akvaplan AS, Tromsø, pers. commn). In 1993, spawning capelin were observed along the coast of Finnmark, east of Hjelmsøy (Fig. 6) (Anthonypillai & al. 1993). During spring 1994, only scattered concentrations of capelin were detected, except for one single concentration to the north-east of the Varanger peninsula (Gjøsæter 1994). The distribution of the larvae found in June (Fig. 6) also indicates an easterly spawning in 1994. During 1995 and 1996, no surveys were carried out to locate capelin spawning off the coast on the Norwegian side of the border.

4.2.1.5 Feeding migration, summer and autumn distribution

The immature fish will generally move towards the south from the area of overwintering and are found not far from the coast in late spring. The spring bloom starts earlier in coastal areas and on the banks than further offshore, and the capelin utilise the food base in these areas in spring and early summer. Spent fish that have survived the spawning will probably join the immatures in these areas. In June these concentrations are found further to the north (Fig 9A and B). When the ice starts to melt and the ice edge recedes northwards, the capelin migrate northwards as well. Following the receding ice edge is a phytoplankton and then a zooplankton bloom, resulting from the stabilisation of the relatively nutrient rich water masses (Skjoldal & Rey 1989). The capelin feed on this zooplankton bloom, moving with it until the northernmost feeding areas have been reached in September-October. Gjøsæter & al. (1983) presented a conceptual model of the development of the processes linked to the ice edge, where the processes taking place behind the receding ice edge are conceived as a continuous 'spring bloom' moving with the ice. These feeding areas will change according to the hydrographic situation as shown in Fig. 10A and B. In late October and November, the

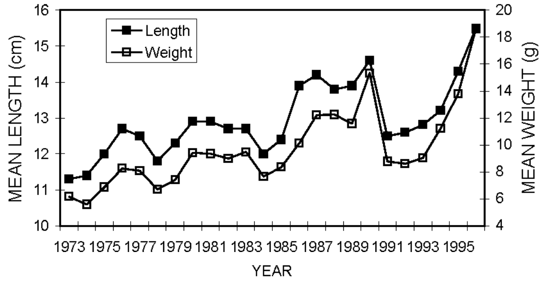

Fig. 11. Mean length- and weight-at-age of 2 years old Barents Sea capelin measured during the annual autumn surveys in the Barents Sea.

capelin concentrations move back south- and south-westwards, and eventually overwinter south of the ice edge in the areas indicated in Fig. 7A and B.

4.2.1.6 Vertical distribution

The vertical distribution of capelin larvae was discussed in section 4.1.5. The vertical distribution and migration of immature and adult capelin was studied by Luka & Ponomarenko (1983) and Luka (1984). The vertical migrations of capelin change during the year. In spring (March to April), when light reappears after the polar night, the capelin descend into the near bottom layers at sunrise, but ascend from these layers at the onset of twilight in the evening. In summer (May-August) when the light endures during 24 hours, the vertical migrations become less distinct. However, some changes in vertical distribution are still evident, but the migration rhythms are not clearly diurnal. During September, when the changes in light intensity between day and night become more clear-cut, the diurnal rhythm of vertical migrations reappears, but is most evident among the older age groups. Apparently, the immature capelin remain in the upper water layers both during day and at night. In late autumn (October-November), with the onset of the polar night, the amplitude of vertical migrations is reduced as the light intensity decreases. At this time of the year, the mature capelin descend to near bottom depths, disperse, and start migrating south towards the spawning areas. In December, mature capelin are mainly observed near the bottom. In January, the pre-spawning capelin more often form schools in intermediate and upper layer during their migration to the spawning areas, especially at night. As the light intensity increases in February, the diurnal vertical migrations become more evident. Young capelin (age groups 1 and 2) are often observed in the upper layers during the winter period.

Although it is generally considered a pelagic species, capelin is quite commonly caught in small numbers in bottom trawl, both during day and night and throughout the year. The general impression is that the capelin found there are large, old individuals, but any systematic investigation of this bottom dwelling component has not been undertaken. Therefore, it is unknown whether there is a separate component of the stock mostly staying at near bottom depth, or these are just individual fish staying there for shorter periods.

4.2.2 Growth

The growth of capelin is extremely flexible with large variations within and between years. Various authors have studied the growth of Barents Sea capelin, Olsen (1968), Prokhorov (1968), Monstad (1971), Shulga & Belusov (1976), Monstad & Gjøsæter (1977), Gjøsæter (1985c, 1986), Gjøsæter & Loeng (1987), Skjoldal & al. (1992). The capelin grow to a maximum length of about 20 cm (males) and 18 cm (females), and the weight seldom exceeds 50 grams (Prokhorov 1968).

The growth has been found to vary with stock size (Ulltang 1975; Gjøsæter 1986), with water temperature (Shulga & Belusov 1976; Gjøsæter & Loeng 1987) and with geographical distribution (Gjøsæter 1985c, 1986). The length- and weight-at-age of two year old capelin, as measured during the annual acoustic surveys carried out jointly by PINRO, Murmansk and Institute of Marine Research (IMR), Bergen, have varied substantially in the period 1972-1996 (Fig. 11). The general trend is an increase in length and weight over this period. However, the last half of the 1980s and the period 1995-96 are characterised by high values while 1978-1979, 1984-1985 and 1991-1993 are periods of low growth. The decrease in mean length and weight, observed from 1990 to 1991, and the increase observed from 1993 to 1996 coincide with a sudden increase and decrease in the stock size during these periods respectively. The general trend of increasing mean lengths and weights during the period 1973-1996 also coincides with a general trend of decreasing stock size in this period. Although mean length and weight of two years old fish reflects the accumulated growth over three growth seasons and, therefore, cannot be directly compared to stock abundance in one particular year, this indicates that the growth is density dependent, or more precisely, stock abundance dependent. There are, however, no clear-cut relationships between stock size and individual growth when analysed on a yearly basis. Monstad & Gjøsæter (1977), studying the growth of the year classes 1967-1969, noted that their data showed no correlation between growth and year class strength. Gjøsæter (1986) came to the same conclusion regarding growth of the year classes 1974-1985. He was not able to demonstrate density or abundance dependent growth, neither between growth and density within geographical sub-areas nor between growth and abundance of the total stock in each year. Both of these investigations were undertaken before the dramatic stock collapses in the 1980s and 1990s and similar analyses, including the year classes from these periods, which are now being made, may produce different results.

Gjøsæter (1985c, 1986) found clear differences between growth of capelin in different parts of the Barents Sea. He compared estimated growth rates in the current growth season (based on back-calculation of length from otoliths) for seven subareas of the Barents Sea, and found that growth was always more rapid in the southern and western parts than in the eastern and northern areas. These differences persisted regardless of whether the growth was generally high or low in one particular year. These differences should probably be attributed either to temperature conditions, to food abundance, or both. Gjøsæter & Loeng (1987) found correlation coefficients r of 0.70 and 0.53 between capelin growth and ambient temperature for two- and three-year-olds respectively, when all the material from 1974-1985 was considered, and r between 0.85 and 0.91 for within-year data. They concluded that there is a general pattern of increased growth in length with increasing temperature within the observed temperature interval, but that any growth differences observed and ascribed to temperature variations will be a combination of direct, physiological effects and indirect effects through increased availability of food.

Shulga & Belusov (1976) found a negative correlation between the length of two and three years old capelin and temperature, using the mean temperature of the 0-200 m layer along the Kola section in July in as an indicator of temperature conditions in the Barents Sea. However, the relevance of using temperatures along the Kola section as an indicator of the temperature conditions in the various feeding areas of capelin, and to compare such an indicator with accumulated growth during three to four growth seasons, is questionable.

4.2.3 Maturation

Monstad (1971) established a maturity classification for both sexes of Barents Sea capelin (Table 3) based on macroscopic criteria. The classification was modified from that presented by Nikolsky (1963). Monstad stated that the classification was difficult, especially for males.

Forberg (1982, 1983) made a histological study of the capelin ovaries and established an alternative maturity scale with 10 stages. This scale is currently used at the IMR, Bergen for maturity classification of female capelin, while the scale described in Table 3 is still in use for the classification of males.

Forberg (1982) classified oocytes in two growth phases, first (FGP) and second (SGP) growth phase. The FGP was further divided into three stages; the chromatin nucleolus stage (oocyte diameter – OD 5-15 µm), the early perinucleolus stage (OD 15-150 µm), and the late perinucleolus stage (OD 100-190 µm). This third stage can be found in capelin larger than 10 cm throughout the year in the Barents Sea, and is a ‘resting stage’. The SGP was classified into five stages; yolk vesicle stage I (OD 180-280 µm), yolk vesicle stage II (fat vesicle stage) (OD 250-450 µm), primary yolk stage (OD 430-550 µm), secondary yolk stage (550-650 µm) and, finally, the tertiary yolk stage (OD 650-1020 µm).

Table 3. Maturity scale used for both sexes prior to 1982, but after that only for males. From Monstad (1971).

Code	Stage	Description	Females	Males
1	Juvenile (a)	Gonads threadlike, sexes difficult to separate		
2	Juvenile (b)	Gonads increasing in volume. Sex can be determined	Ovaries transparent, without colour	Testes transparent, without colour
3	Maturing (a)	Gonads opaque, blood vessels can be seen	Ovaries with yellow/white grains	Testes white or with white spots
4	Maturing (b)	Gonads increasing in volume. Blood vessels distinct	Ovaries pink or yellowish white filling up 2/3 or more of body cavity	Testes light gray or white. No milt-drops appear under pressure
5	Maturing (c)		Ovaries occupy whole of body cavity. Most eggs transparent	Testes gray. Milt runs with some pressure applied
6	Spawning	Running gonads		
7	Spent	Gonads emptyied. Some residual eggs and sperm may occur		
8	Spent/ Recovering	Gonads small and collapsed		

Forberg (1982) found that the number of FGP oocytes of various sizes always exceeded the number of synchronously growing SGP oocytes, indicating that female capelin have a potential for repeated spawning. It was also found that the SGP lasted less than one year, and consequently it was concluded that the presence of a significant number of yolk vesicle oocytes or more mature SGP oocytes was a good indication that the fish was going to spawn within one year.

It has been observed in many years that the Barents Sea capelin may have a prolonged spawning season. The main spawning takes place in spring, while parts of the stock may spawn in early summer and even in late summer (Rass 1933; Møller & Olsen 1962a).

The age distribution of the spawning stock in different years has been described by many authors. Dommasnes (1985) reviewed the literature and presented a synopsis of this information for the period 1954-1983 (Table 4). In a few years (1954, 1956-1959, 1965-1967) the three years old fish represented the highest proportion of spawners, while four-year-olds dominated in the spawning stock in the other years during this period.

Table 4. Percentage age distribution of maturing and spawning capelin during the period 1954-1983. From Dommasnes (1984b).

Year	Age					Number
	2	3	4	5	6	
1954	1.6	78.1	19.9	0.4	0	238
1955	0	1.7	56.3	41.4	0.6	174
1956	0	52.4	42.7	4.9	0	61
1957	5.1	77.2	17.2	0.5	0	611
1958	0	88.8	11.2	0	0	98
1959	2.2	68.8	29.0	0	0	224
1960	0	40.5	58.8	0.7	0	973
1961	0.4	14.3	83.6	1.7	0	699
1962	0	12.4	67.0	20.4	0.2	917
1963	0	4.9	90.0	5.1	0	752
1964	0.2	4.2	52.6	43.1	0	-
1965	0.9	91.0	7.8	0.3	0	-
1966	32.3	64.3	4.4	0	0	300
1967	33.8	57.4	8.8	0	0	591
1968	2.6	35.7	61.7	0	0	863
1969	0	25.9	73.8	0.3	0	3380
1970	0	29.2	70.2	0.6	0	5304
1971	0	4.3	91.1	4.7	0	6215
1972	0	9.6	65.1	25.4	0	2450
1973	0	5.8	74.2	20.0	0	1837
1974	0.3	10.0	65.1	24.2	0.4	-
1975	0.1	9.9	79.3	10.4	0.3	-
1976	0.1	4.8	57.8	37.0	0.3	-
1977	0	5.5	58.5	32.2	3.9	-
1978	0	17.5	53.9	23.9	4.7	-
1979	0	22.4	62.9	13.7	1.1	-
1980	0	4.0	87.4	8.3	0.4	-
1981	2.6	6.0	61.7	27.7	2.4	-
1982	3.0	37.2	46.5	13.1	0.2	-
1983	0	21.2	63.9	14.1	0.9	-

The age distribution in the spawning stock will obviously reflect the strength of the year classes taking part in the spawning. However, since maturation is closely linked to fish size (Tjelmeland 1985), the growth rate of the immature stock will also affect the age distribution of the spawning stock. In periods with a high growth rate of the immatures, the year classes will mature and spawn at a young age, while in periods of slow growth the spawning will be postponed to an older age.

It is difficult to discriminate between early and late spawners by visual inspection of the gonads during the main capelin investigations in the autumn. However, Tjelmeland & Forberg (1984) developed a model for that purpose. Because of the difficulties in obtaining acoustic measurement of the amount of capelin spawning in the different seasons, it has not been possible to test the predictive reliability of this model. Therefore, Forberg & Tjelmeland (1985) and Tjelmeland (1996) have modelled the maturation of capelin as a monotonically increasing function of fish length, according to the equation

$$m(l) = \frac{1}{1+e^{4P_1(P_2-l)}}$$

where *m(l)* is the proportion of fish in length group *l*, measured during the autumn survey, that will mature and spawn next spring, P_2 is the length at 50 % maturity and P_1 is the *shape parameter*, the change of maturation with length at P_2. The shape parameter was determined from a fit to the empirical maturation data according to the maturation scale described in section 4.2.3, while the length at 50 % maturity was determined by comparing the immature stock in one year to the total stock in the following year, assuming total spawning mortality. Tjelmeland (1996) found that the estimated maturation function fitted the maturation data remarkably well, for P_2 values in the range 13.5-14.5 cm. The parameter values varied both with maturity stage and age. It was found that the most likely values of 50 % maturing length was 13.8 cm and 14.6 cm for females and males respectively.

Forberg & Tjelmeland (1985) studied the spatial and temporal variation of the maturing length P_2 of Barents Sea capelin during the period 1978-1983. They found a significant variation in P_2 between subareas of the Barents Sea, but the variation was not consistent from year to year. They estimated P_2 for the different maturity stages according to Forberg (1982), and found that there was a significant variation of P_2 between years when 'mature' was defined as all female capelin in SGP. However, when only those individuals classified in yolk vesicle stage II and above were classified as mature, the corresponding

P_2 was quite stable from year to year. They argued that this group probably consisted of spring spawners only. The observed variability between years could reflect actual differences in average maturing length or, more probably, differences in timing of sexual maturation. These authors also compared P_2 for two and three years old capelin and found that in most years the maturing length was significantly larger for the two-year-olds. A two year old fish must have invested much more energy per unit time in somatic growth than a three year old fish of the same length. Therefore, competing energy requirements may explain differences in maturity rates and in length at maturing between fishes of different age (Forberg & Tjelmeland 1985).

Using the maturation model just described, and accounting for natural mortality, growth, and fishing mortality during the period from measurement to spawning, the maturing stock in spring can be forecast based on the measurements of the total stock in autumn.

4.2.4 Behaviour

The behaviour of capelin associated with the spawning process was studied at the coast of Finnmark in the period 1971-1975 and reported on by Bakke & Bjørke 1973; Bjørke & al. 1972; Gjøsæter & al. 1974; Gjøsæter & Martinsen 1976; Gjøsæter & Sætre 1973a; Sætre & Gjøsæter 1975. Scuba divers observed the capelin at the spawning grounds, and echo sounders were used to observe the capelin schools approaching the spawning grounds.

The capelin approached the spawning grounds in dense pelagic schools, consisting of several hundred tonnes of fish. Males and females often formed separate schools. When the schools reached the spawning grounds, they settled to the bottom, and often formed a dense layer above the sea floor. At the spawning grounds, the divers observed two kinds of schools. The first type consisted of more or less regularly oriented capelin swimming forward or in circles. The distance between the individual capelin in these kinds of schools was usually between 15 and 30 cm. The second type of schools was often pyramidal and consisted of irregularly oriented fish. The lower part of the schools, with a diameter of 3-5 m, was close to the bottom. The mean distance between individuals was only 5 cm or less. Pre-spawning and spawning males were totally dominant in both types of schools, and females were seldom observed on the spawning grounds. The spawning act was never observed by divers, possibly because it mainly takes place during night.

Spent males were occasionally seen at the spawning grounds. They seemed to be in very bad condition, and many were found dead on the bottom.

Serebrov (1985) studied the schooling behaviour of capelin in the Barents Sea, by means of underwater photography. He found that during daytime the average density of fish in the schools was 1.4 specimens m^{-3} (SD = 2.3) but could, at maximum densities, reach 15-20 specimens per m^3. At night, the density never exceeded 3.5 specimens m^{-3}, and the average density was 0.8 specimens m^{-3} (SD=0.74). The schools normally consisted of sub-groups of 3-4 individuals and 5-7 individuals during daylight and at night respectively, separated by an average distance of about three body lengths. The average fish density in these subgroups was about 4 and 20 times (for day and night respectively) higher than for the school as a whole. While moving quickly, schools condense because these subgroups move towards each other, and eventually the average density of the whole school increases to that of the subgroups. In exceptional cases, e.g. when attacked by predators, the school may become very dense with 150 specimens m^{-3}.

Schooling by size was observed by Olsen (1965), who noted that the length distribution of capelin caught in purse seines varied considerably from one catch to another in the same area. This phenomenon was also reported by Gjøsæter & Korsbrekke (1990), who analysed the age- and length-distribution of trawl catches of capelin. The mean length of two years old capelin caught together with one-year-olds was significantly lower than the mean length of those caught together with older capelin. Their interpretation was that two-year-olds choose to school with fish of their own size. Consequently small two-year-olds school together with smaller fish (one-year-olds) while large two-year-olds school with older, (and larger) capelin. The tendency to school by size is probably linked to swimming speed, which is known to increase with increasing body length (e.g. Harden Jones 1968).

5 THE ECOLOGICAL ROLE OF THE CAPELIN

5.1 FOOD AND FEEDING

The capelin play a key role in the transportation of energy upwards through the food web in the Barents Sea. It is the only fish stock capable of utilising the zooplankton production in the central and northern areas including the marginal ice zone. Young herring (*Clupea harengus*), in some years present in large quantities in the Barents Sea, seldom penetrates to the north of the 74th parallel. Polar cod (*Boreogadus saida*) feed in the northern areas, but this species is not a specialised plankton feeder and is probably not able to compete with the capelin or take its place in the food web.

Various authors have studied the feeding of capelin in the Barents Sea (Panasenko & Sobolova 1980; Lund 1981; Panasenko 1981, 1984; Panasenko & Nesterova 1983; Hassel 1984; Hassel & al. 1991, Ajiad &

Pushchaeva 1992). Three groups of planktonic crustaceans are important in the diet of capelin: copepods, euphausiids and amphipods (Table 5). Their relative importance varies with season, area, predator size and year. Other important food items are *Chaetognatha*, *Limacina* and *Oikopleura*.

The most intensive feeding takes place during the period July to October. Young capelin do not feed during the winter but, among capelin larger than 15 cm, more than 50 % were found to have food in their stomachs. The feeding activity increases during a short period prior to spawning, but decreases again among that part of the stock which actually spawns (Lund 1981).

The relative importance of different kinds of prey varies with the length of the capelin. The importance of copepods decreases with increasing capelin length, while euphausiids and amphipods are most important for adult capelin (Table 6).

Among the copepods, the most important species are *Calanus finmarchicus*, *Pseudocalanus elongatus*, *Euchaeta norvegica* and *Metridia longa*, which contribute to the diet throughout the year, while *Calanus hyperboreus*, *Microcalanus pusillus*, *Oithona similis* and *Oncaea borealis* may play an important role during one or more quarters of the year.

Two species of Euphausiids, *Thysanoessa inermis* and *T. raschii* and two amphipods, *Themisto libellula* and *T. abyssorum*, play important roles in the diet of capelin. The Euphausiids are mostly found in the southern parts of the Barents Sea and are mainly eaten in spring and summer, while the two Amphipods are associated with arctic waters in the north-eastern parts and are mainly preyed upon during autumn, when the capelin stock is distributed farthest to the north (Table 5).

There is a considerable variation in feeding intensity with season (Panasenko 1984). There are two annual peaks in stomach fullness (Table 7), one in February and one in July-October. The first peak is associated with the onset of krill predation in coastal areas, but the second with predation on *Calanus*, krill and *Amphipoda* during the main feeding season in the northern areas.

There seems to be no prominent daily variation in food consumption. Ajiad & Pushchaeva (1992) showed that feeding peaked in the evening and a minimum occurred around noon among all length groups, while Lund (1981) found that during autumn, with limited light at night, feeding was most intensive during the day. In summer, when there is sufficient light both during day and night at these high latitudes, feeding seemed to continue also at night. Panasenko (1981) found that in the second half of August 1980, capelin fed intensively on concentrations of large plankton (*Euphausiacea*, *Copepoda*, *Amphipoda*) which at that time kept mainly to the near-bottom layers during the twenty-four hours. The capelin

Table 5. Relative importance (% energy contribution) of prey for 13-16 cm capelin sampled during the four quarters of a year. After Lund (1981).

	Spring	Summer	Autumn	Winter
Copepods	0.6	8.9	28.5	24.2
Euphausiids	98.4	88.3	27.6	62.8
Amphipods	0.8	2.1	41.8	11.2
Others	0.2	0.7	2.1	1.8

Table 6. Relative importance (% of weight) of the three main prey groups for Barents Sea capelin, for two length groups and two seasons. After Panasenko (1984).

	Capelin below 13 cm length		Capelin above 13 cm length	
Food components	February-May	July-October	February-May	July-October
Copepods	7.2	64.9	3.9	41.0
Euphausiids	87.1	22.7	89.7	43.3
Amphipods	2.1	7.0	4.0	12.4

Table 7. Seasonal variation of the index of stomach fullness (in ‰ of body weight), based on data from 1976-1982. After Panasenko (1984).

Month:	1	2	3	4	5	6	7	8	9	10	11	12
Length (cm)												
9-10	-	2.97	-	-	-	-	-	2.83	9.76	15.97	-	-
10-11	-	5.85	-	-	-	-	-	9.74	34.70	33.65	-	-
11-12	-	16.46	-	-	16.00	-	-	12.38	29.36	29.57	-	-
12-13	18.16	24.88	9.60	15.29	29.68	4.82	12.71	19.97	32.17	58.47	-	-
13-14	11.21	14.18	10.48	8.41	17.19	11.95	24.81	21.78	26.36	11.35	-	-
14-15	7.46	23.09	74.9	3.29	19.43	15.42	22.42	22.69	31.88	22.52	1.90	-
15-16	10.85	23.82	5.27	1.07	21.84	13.73	22.56	20.93	24.08	25.19	2.21	-
16-17	4.98	18.19	2.39	2.63	8.65	19.43	26.95	17.72	14.57	14.00	2.62	-
17-18	6.99	6.54	3.14	-	-	3.97	-	18.74	22.80	19.70	1.06	-
18-19	2.60	1.16	-	-	-	-	-	14.00	2.13	-	-	-

performed diurnal vertical migrations; descending during daytime to the plankton rich water near bottom depth. The stomach fullness increased during that period, and was at a maximum between 04 PM and 08 PM. At night the capelin ascended to midwater and scattered. During this period, the stomach fullness decreased. The main food objects were Euphausiids and Amphipods. There are reasons to believe that the feeding behaviour of capelin depends on the behaviour of the available prey. In August 1981, another three sets of twenty-four hour stations were worked, and reported on by Panasenko (1984). In this case, a decline in the stomach fullness at night could be seen at two of the stations, while the opposite was true in one case (Fig. 12). The diet consisted of 50-70 % *Copepoda* and 30-40 % *Euphausiacea* and *Amphipoda*, but it is not clear at what depths the main food concentrations were found in this case.

Hassel (1984) compared capelin prey selection to the available zooplankton in May and August 1981, collecting samples along north-south transects. In May, food supplies for the capelin seemed restricted, since only 1 g per m^2 was recorded in the upper 200 m. Of the capelin stomachs investigated 30 % were empty and the mean stomach fullness was 0.18 %. Euphausiids were the most important food item, constituting 40 % by weight, while the copepods ranged next with a contribution of about 32 %. In August, the stomach fullness had changed drastically from May. At the northernmost station the mean fullness index exceeded 8 %. The biomass of plankton was also much higher in August than earlier, and was increasing from south to north and reached about 20 g m^{-2} at the northern limit of the capelin distribution area.

Comparison between stomach contents and plankton composition in the sea indicated that capelin feed on the available food without a strong selection of any particular food item. There was, however, a selection of prey item by size. Small capelin preferred small copepods, while larger fishes selected larger copepods.

Ajiad & Pushchaeva (1992) studied capelin feeding in the Goose Bank area in August 1989 and estimated the daily ration during that period to be between 1.3 and 2.2 % of fish body weight.

5.2 FEEDBACK FROM CAPELIN FEEDING ON THE ZOOPLANKTON COMMUNITY

The capelin stock is the key link between zooplankton and higher trophic levels in the Barents Sea and the predation pressure from capelin seems to affect the biomass of zooplankton in the feeding area (Skjoldal & al. 1992). Dalpadado & Skjoldal (1996) found that following the large reduction of the capelin stock between 1984 and 1987, there was a subsequent increase in the abundance and biomass of the two euphausiid species *Thysanoessa inermis* and *T. longicaudata*, while a decrease in krill abundance and biomass was observed to follow the rapid recovery and growth of the capelin stock from then until 1991. This suggests a predator-prey interrelationship between capelin and krill and that the krill populations are controlled by predation. In August 1985, the impact of grazing from capelin on zooplankton was studied by Hassel & al. (1991). They found that the biomass of zooplankton in the uppermost 100 m was much lower in areas where capelin were present as compared to areas without capelin, suggesting rapid depletion of the major prey items by feeding capelin. The investigation showed that when the capelin moved northwards during the summer feeding migration (cf. section 4.2.1.5) the 'capelin front' had a capelin biomass more than three times that of zooplankton in areas without capelin, and would have the potential to graze down the available prey in 3-4 days.

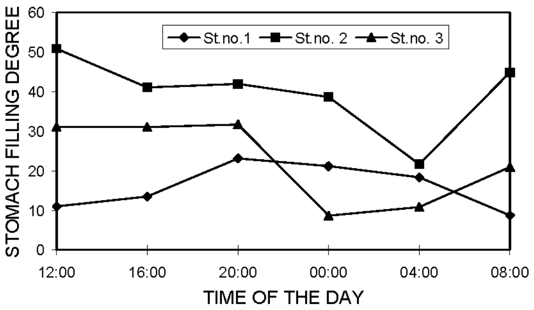

Fig. 12. Daily variations of capelin stomach filling degree (stomach weight in ‰ of fish weight) at three stations sampled every fourth hour in August 1981. Based on data in Panasenko (1984).

Another feedback mechanism was discussed by Timofeev (1988). He found that organic substances of sperm and seminal fluid, ejaculated by capelin males into the water, could influence plankton productivity in the spawning areas. His calculations showed that the increased production of phyto- and zooplankton caused by these substances, constituted from 0.3-3 % of the actual productivity of coastal Barents Sea waters.

5.3 PRODUCTION

The stock size estimates, obtained during the various surveys, do not give any direct information on the biomass production of the capelin stock. The annual production may be estimated as the weight of the catch taken during the year, the weight of the remaining spawning stock (which is lost through the spawning mortality), and the output due to natural mortality other than spawning mortality. Gjøsæter (1996) gave estimates for this quantity for the period 1973-1996, calculated by using the model 'Capstock' (cf. section 10.1). As shown in Fig. 13, the annual biomass production is generally higher than the

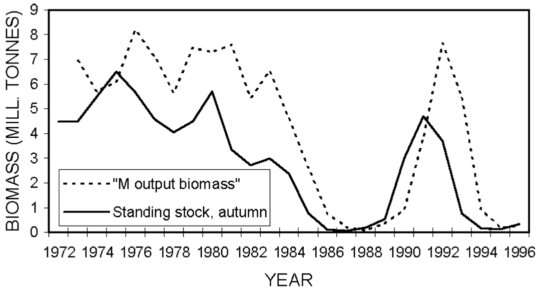

Fig. 13. Stock and production in the Barents Sea capelin stock. From Gjøsæter (1996).

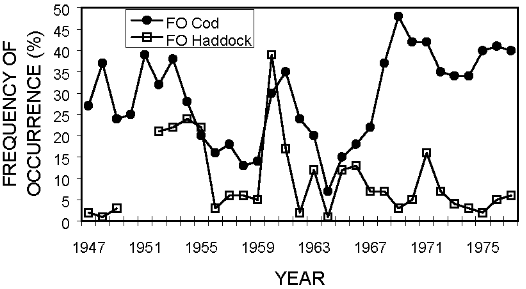

Fig. 14. Frequency of occurrence (FO) of capelin in cod and haddock stomachs during the period 1947-1977. Data from Ponomarenko & Yaragina (1984).

standing stock as measured during the autumn surveys. In periods with a high natural mortality, the removal from the stock is larger than the production, and the stock size decreases, while the stock size increases when natural mortality is low and production exceeds the losses.

5.4 PREDATION

The capelin may be classified as a forage fish (Gjøsæter 1996) with a key ecological role as an intermediary between the zooplankton level and higher trophic levels. Its important role as prey for numerous predators, e.g. other fish, seals, whales and birds has been known for centuries (Sars 1879; Hjort 1914). The consumption of capelin by some of these predators has been quantified, while the knowledge of the consumption by others is purely qualitative.

5.4.1 Fish predators

Cod (*Gadus morhua* L.) is the main predator of capelin. The Polar Research Institute of Marine Fisheries and Oceanography in Murmansk, Russia (PINRO) has run a stomach sampling program on cod, dating back to the beginning of this century (Ponomarenko & Ponomarenko 1975; Ponomarenko, Ponomarenko & Yaragina 1978; Ponomarenko & Yaragina 1978; Ponomarenko & Yaragina 1984). The reports on the results of this sampling program are mainly concerned with qualitative aspects, while consumption estimates are presented for the period 1971-1973 and 1975-1981. The frequency of occurrence (the number of cod stomachs with capelin as percent of the total number of analysed stomachs) is presented in Fig. 14 for the period 1947-1977. The observed variation is considerable; the lowest value of 7 is recorded in 1964 and the highest of 48 in 1969. The frequency of occurrence varies in a cyclic fashion, with approximately 10 years between each peak. In addition to the frequency of occurrence of various prey organisms, a degree of stomach fullness on a 1-5 scale (prior to 1958 1-4) is recorded (Ponomarenko & Yaragina 1978). The estimates of capelin consumed by cod (Ponomarenko & Ponomarenko 1975; Ponomarenko & Yaragina 1984) are based on a daily ration estimated by Novikova (1962) for a period of intensive feeding on capelin. Recalculated for age groups of cod (Ponomarenko & Yaragina 1984), this daily ration was 5.4 % of predator body weight for 3-4 year old cod, 3.4 % for 5-8 year old cod, and 1.7 % for age groups 9-15 years. The results of these calculations are given in Table 8. These results are based on the assumption that the daily rations cited above were applicable during two months of intensive feeding (in spring), while these rations were halved during the other 10 months of the year. Cod biomass was obtained from Virtual population analyses (VPA) runs made by Arctic Fisheries Working Group of ICES (ICES 1982a).

In 1984, the Institute of Marine Research in Bergen, Norway launched a program to monitor the consumption of various prey by cod. From 1987 the stomach sampling program has been carried out in co-operation with the Polar Research Institute of Marine Fisheries and Oceanography in Murmansk, Russia, and in the period 1984-1995 nearly 79000 cod stomachs have been analysed. This analysis is quantitative, i.e. the weight of each prey type in individual cod stomachs is recorded (Mehl & Yaragina 1992). Bogstad & Mehl (1997) presented estimates of capelin consumption by cod, based on this joint database for the period 1984-1995 (Table 8).

Larval capelin have been found in the stomachs of 0-group cod (Beltestad & al. 1975; Gjøsæter 1995). The extent of this predation, and whether it is of any significance for capelin recruitment is unknown.

Haddock (*Melanogrammus aeglefinus* L.) is a predator on capelin during parts of the year, mainly during the capelin spawning period, when both the capelin and their eggs are consumed by haddock (Collett 1903; Zenkevitzh 1963; Sætre & Gjøsæter 1975; Antipova & al. 1980; Kovtsova 1988). The frequency of occurrence (FO) of capelin in haddock stomachs over the period

1947 to 1977 is shown in Fig. 14. The FO is generally smaller for haddock than for cod, but shows a similar cyclic variation with maxima in the early 1950s, 1960s, and 1970s. Although haddock was regularly observed to feed on capelin eggs during the period 1971-1973, when extensive investigations on the spawning grounds of capelin were undertaken (Sætre & Gjøsæter 1975), it was not possible to assess the quanta of capelin eggs consumed by haddock. However, these authors stated that a significant part of the eggs spawned at depths exceeding 100-150 m may be consumed.

The herring (*Clupea harengus*) occur as juveniles in the Barents Sea, and while there, consume considerable amounts of capelin larvae (Huse & Toresen 1995). The resulting mortality of capelin larvae is thought to be a major cause of the recruitment failure of capelin associated with years when abundant herring year classes are growing up in the area (Hamre 1988, 1991; Huse 1994; Gjøsæter 1995; Gjøsæter & Bogstad 1998). Based on the contents of herring stomachs, sampled in the field in 1992 and 1993, and a simple predation model, Huse & Toresen (1995) estimated the number of larvae consumed by herring in the period 1984-1993 and the resulting impact on capelin recruitment (Table 9). In 1992, the frequency of occurrence of capelin larvae in herring stomachs was 5.6, while in 1993 it was 3.0. The average numbers of larvae per stomach were 3.1 and 1.8, respectively. The length of the ingested larvae ranged from 8 to 25 mm. In both years there was a large horizontal and vertical overlap between the juvenile herring and capelin larvae. Applying the average frequency of occurrence found in 1992 and 1993, the same model parameters, and available abundance estimates of herring and capelin larvae, the model was run for each year in the period 1984-1993 (Table 9).

Even if some of the underlying assumptions , as well as the abundance estimates of herring and capelin larvae, may be questioned, these results show that a substantial part of the capelin larvae that survive until June-July, may be removed by herring predation during the summer. This is in good agreement with the observations in the period 1983-1985 (Fossum 1992) and 1991-1993 (Gjøsæter 1995), i.e. that in spite of the large amount of capelin larvae recorded in early summer in these years, few larvae survived until the 0-group investigations in August, and the acoustic estimate of the one-year-olds in autumn og the following year. The consequences of these mechanisms for the recruitment of capelin are discussed in section 6.1.

Other fish predators include Greenland shark (*Somniosus microcephalus*) (Collett 1903), Greenland halibut (*Reinhardtius hippoglossoides*) (Collett 1903), Esmarks eelpout (*Lycodes esmarki*) (Collett 1903), Thorny skate (*Raja radiata*) (Antipova & Nikiforova 1990), Long rough dab (*Hippoglossoides platessoides*) (Berestovski 1989), Deep sea Redfish (*Sebastes mentella*) (Dolgov & Drevetnyak 1993) and various rockfishes (*Anarchicadidae*) (Collett 1903). These are

Table 8. Consumption of Barents Sea capelin by cod (million tonnes). Data sources: 1971-1973; Ponomarenko & Ponomarenko (1975). 1975-1981; Ponomarenko & Yaragina (1984). 1984-1995; Bogstad & Mehl (1996).

	Capelin consumed by cod (million tonnes)			
Year	3-4 years	5-8 years	9-15 years	Total
1971				4.76
1972				4.22
1973				5.44
1974				No data
1975	2.508	3.901	0.127	6.536
1976	3.087	3.432	0.125	6.644
1977	1.753	2.362	0.097	4.212
1978	2.138	1.816	0.116	4.070
1979	2.608	1.343	0.170	4.121
1980	1.515	2.577	0.148	4.240
1981	0.788	3.228	0.161	4.177
1982-1983				No data
1984	0.505	0.216	0.014	0.734
1985	1.179	0.423	0.017	1.618
1986	0.577	0.246	0.005	0.828
1987	0.183	0.043	0.000	0.225
1988	0.101	0.233	0.003	0.336
1989	0.169	0.422	0.001	0.593
1990	0.750	0.919	0.010	1.679
1991	1.879	1.163	0.053	3.093
1992	2.191	0.516	0.142	2.849
1993	2.434	1.058	0.151	3.644
1994	0.796	0.569	0.025	1.390
1995	0.470	0.330	0.003	0.801

Table 9. Estimated number of capelin larvae (10^{12}) consumed in the years 1984-1993 in three scenarios of different time-length of predation (TP80 = 80, TP100 = 100, TP120 = 120 days). Proportion of estimated capelin larval abundance removed by herring in the same number of days is also given. After Huse & Toresen (1995)

	Numbers			Percentage		
Year	TP80	TP100	TP120	TP80	TP100	TP120
1984	0.53	0.67	0.85	7	8	10
1985	0.35	0.45	0.54	4	5	6
1986	0.10	0.12	0.15	-	-	-
1987	-	-	-	0	0	0
1988	-	-	-	0	0	0
1989	0.06	0.07	0.08	1	1	1
1990	0.12	0.14	0.17	1	1	1
1991	0.74	0.93	1.11	25	31	37
1992	2.16	2.70	3.24	30	37	44
1993	1.47	1.83	2.20	44	56	67

mostly deep water fishes feeding on capelin when found at near bottom depths, or following the capelin to the coast during the spawning migration.

5.4.2 Seal predators

Among the seals, the main capelin predator is the harp seal (*Phoca groenlandica*). NORDØY & al. (1995a) give an estimate of the harp seal stock's food consumption, based on an analysis of stomach contents in 1993 and the observed food intake of captive seals. Of a total annual food consumption of 1 million tonnes, about 700 000 tonnes consisted of various fish species, of which about 250 000 tonnes consisted of capelin. This estimate is based on a Barents Sea harp seal population of 600 000 individuals. The authors argue that the results may be biased in that the proportion of fish in the diet is underestimated, because most of the stomach material was collected from seals caught in the pack ice where amphipods dominated the diet.

The dependence of the harp seal upon capelin as food was demonstrated during the capelin collapse in 1986-1989 (see section 11). During those years, the harp seal population invaded the coast of Northern Norway and more than 100 000 seals drowned in gill nets during 1987 and 1988 (HAUG & NILSSEN 1995). Food shortage in the traditional wintering areas was probably the main reason for these invasions.

The ringed seals (*Phoca hispida*) may feed on capelin during the autumn when capelin is distributed near ice in the northern Barents Sea. However, there is evidence that these seals mainly eat pelagic crustacean and polar cod (HANSEN & al. 1996).

5.4.3 Whale predators

The minke whale is the main whale predator on capelin (NORDØY & al. 1995b; HAUG & al. 1995a, 1995b). Based on calculated energy requirements of growing and adult animals, estimates of the diet composition in 1992 (HAUG & al. 1995a), and a minke whale estimate of 87 000 animals, NORDØY & al. 1995b estimated a total consumption of 355 000 tonnes of capelin. Since parts of the Northeast-Atlantic minke whale stock do not enter the Barents Sea, the use of the food composition data from the Barents Sea on the whole stock may lead to an overestimate of capelin consumption. On the other hand, the estimated number of whales in this stock based on sighting surveys in 1995, is considerably higher, 112 000 animals (TORESEN 1997).

Other whale species living in the area or visiting the area during feeding migrations, like the blue whale (*Balaenoptera musculus*), fin whale (*Balaenoptera physalus*), sei whale (*Balaenoptera borealis*), humpback whale (*Megaptera novaeangliae*), harbour porpoise (*Phocoena phocoena*), killer whale (*Orcinus orca*), narwhale (*Monodon monoceros*), white whale (*Delphinapterus leucas*) and white-beaked dolphin (*Lagenorhynchus albirostris*) may consume some capelin (COLLETT 1903; HANSEN & al. 1996), but no quantitative information is available.

5.4.4 Bird predators

The main fish feeding birds are the alcids, of which the common guillemot (*Uria aalge*), and the puffin (*Fratercula arctica*) have specialised in feeding on schooling pelagic fish, while the Brünnich's guillemot (*Uria lomvia*) feeds on zooplankton organisms in addition to capelin and polar cod (SAKSHAUG & al. 1992).

MEHLUM & GABRIELSEN (1995) estimated the food requirement of the total population of seabirds to be about 1.4 million tonnes annually in the Barents Sea, but the proportion of capelin of this total food base is not available. The common guillemot represents about 10 % of the total food requirement, and this species mostly eats capelin. The Brünnich's guillemot represents 55 %, but has a much lower proportion of capelin in its diet. A total mean capelin consumption in the order of 200 000-300 000 tonnes could be a fair guess (GJØSÆTER 1997).

GJØSÆTER & al. (1972) and GJØSÆTER & SÆTRE (1975) observed that diving ducks were feeding on capelin eggs at spawning beds shallower than 50 m. At one site, where dense concentrations of eggs (up to 200 eggs cm^{-2}) were found in a 600 000 m^2 area, a flock of about 1300 ducks (mostly king eider, *Somateria spectabilis,* together with common eider, *S. mollisima,* and long-tailed duck, *Clangula hyemalis*), were observed feeding during a period of 20 days. The stomachs of 12 out of 13 ducks that were shot were full of gravel and capelin eggs, and practically no other food remains were found in their stomachs. Although the ducks were quite numerous, calculations indicated that the quanta of eggs consumed were less than 2-3 % of the total egg production on the spawning ground (GJØSÆTER & SÆTRE 1975).

5.5 COMPETITION

Competition for food is most likely to take place between capelin and polar cod (*Boreogadus saida*), since both are opportunistic feeders on pelagic zooplankton (AJIAD & GJØSÆTER 1990), and there is a considerable overlap between their distribution areas (MONSTAD & GJØSÆTER 1987; GJØSÆTER & USHAKOV 1997). PANASENKO & SOBOLEVA (1980) calculated similarity indices between capelin and polar cod for different areas and seasons. They found that in the central areas the greatest similarity was observed in spring with respect to euphausiids, while in the north-eastern areas the greatest similarity was observed in summer with respect to copepods. If competition between these stocks was important, a consequence should be a rise in the polar cod stock size in periods when the capelin abundance was low. Although there was an increase in recruitment to the polar cod stock during the period of the first capelin stock collapse in 1985-1989 (ICES 1996c), the total stock of polar cod was not higher during this period than it was prior to or after that period, nor did polar cod abundance increase during the second capelin stock collapse in 1994-1996 (Gjøsæter & Ushakov 1997). Thus, it can be argued that a competition for food between these two stocks is probably not strong enough to affect the size of the stocks to any noticeable degree.

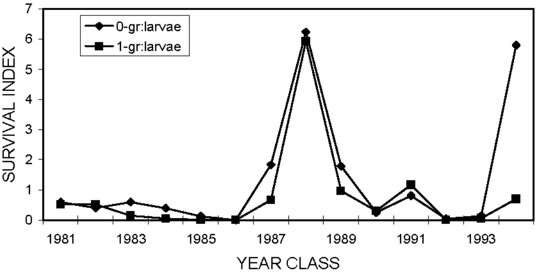

Fig. 15. Survival indices for capelin from the larval (June) stage to the 0-group (August) stage, and from the larval stage to the 1-group (October) stage. Data from ICES (1996a).

6 POPULATION DYNAMICS

6.1 RECRUITMENT

It is difficult to measure the recruitment to the capelin stock. A series of larval abundance estimates exists, based on annual surveys in June since 1981 (ICES 1997). A series of 0-group trawl indices (combined indices based on the area and density of the distribution), based on annual surveys in August, is available from 1965 (ICES 1996c). These two time series are given in Table 10. Gundersen & Gjøsæter (1998) compared these series to the series of acoustic abundance estimates of one-year-olds, and concluded that the larval estimates showed only weak correlation with the acoustic estimates. The 0-group index series was, however, highly correlated with the estimates of one-year-olds ($r^2 = 0.75$, $p < 0.0001$). The larval abundance estimates probably measure the number of larvae produced and, possibly, the spawning stock size, but a high and variable mortality during the first months of life renders them useless as measures of recruitment.

Based on data on larval abundance estimates, 0-group indices and 1-group abundance estimates (ICES 1996a) survival indices were calculated (Fig.15), showing that during the period 1984-1986 and 1992-1993, survival rates were low. The index series based on the 0-group estimates and that based on the 1-group estimate are quite consistent, apart from the years 1983-1985, when the survival until age 1 (1 ½ year time span) was seemingly much lower than until August in the first year of life, indicating additional high mortality during the second year of life. Furthermore, the indices for the year class of 1994 deviates considerably. However, almost no larvae were found in 1994, making the larval index uncertain and, consequently, the calculated survival indices as well.

6.1.1 Causes of variation in recruitment

Gjøsæter (1972) compared the observed recruitment with spawning area and spawning time, but found no significant correlation between either of these variables and recruitment. In the studied period, 1951-1971, there is only one example of a strong year class resulting from a westward spawning, otherwise recruitment was poor or medium. On the other hand, there was no example of a poor year class resulting from an eastern spawning, but several year classes at or above average strength. There was a connection between early and westerly spawning on the one hand, and late and easterly spawning on the other. According to Gjøsæter's data, it appeared that recruitment was favoured by a late easterly spawning. Olsen (1968) also suggested a connection between easterly spawning and strong year classes of capelin.

Bjørke & al. (1988) tested the hypothesis, that in years of westerly spawning the larvae will be partly dispersed in water masses carried to areas outside the Barents Sea, expatriated and lost from the Barents Sea capelin stock. They concluded that the hypothesis was probably too simplistic, but such a mechanism could not be ruled out as one of several factors controlling year class strength. Gundersen (1995) supported this hypothesis.

Table 10. Abundance (10^{12}) of capelin larvae in June (ICES 1997), and abundance indices of 0-group capelin in August (ICES 1996c).

Year	Larval abundance	0-group index	Year	Larval abundance	0-group index
1965		37	1981	9.7	570
1966		119	1982	9.9	393
1967		89	1983	9.9	589
1968		99	1984	8.2	320
1969		109	1985	8.6	110
1970		51	1986	-	125
1971		151	1987	0.3	55
1972		275	1988	0.3	187
1973		125	1989	7.3	1300
1974		359	1990	13.0	324
1975		320	1991	3.0	241
1976		281	1992	7.3	26
1977		194	1993	3.3	43
1978		40	1994	0.1	58
1979		660	1995	0.0	43
1980		502	1996	2.4	291

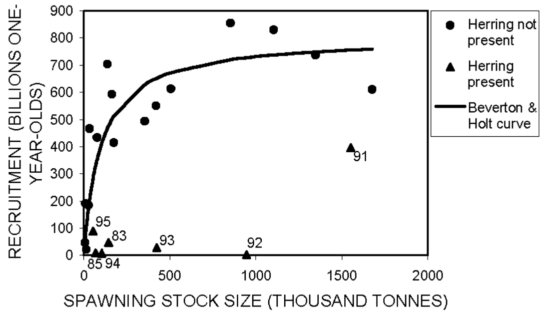

Fig. 16. Stock-recruitment relationship for Barents Sea capelin. Data from 1973 to 1996 are included. The years marked are years with young herring present in the Barents Sea. These years are excluded when the Beverton & Holt recruitment function shown was fitted to the data. From Gjøsæter & Bogstad (1998).

Gundersen (1993a) compared some environmental variables (temperature, salinity, inflow of Atlantic water to the Barents Sea), experienced by the larvae to the strength of the resulting year class. She found mainly weak correlation between these variables and larval abundance. Thus, larval abundance estimates were correlated with the volume of water flowing into the Barents Sea in June (r = 0.65, p = 0.08) and with the salinity in the western part of the Barents Sea in June (r = 0.61, p = 0.06), but not with the temperature.

The relationship between stock and recruitment is essential for all stock assessments on a time scale where recruitment affects the fishable stock. For the capelin, where most fish die after spawning and the main reason for regulating the fishery is to allow a sufficient amount of spawning to secure normal recruitment as far as possible, it is of vital importance.

Gjøsæter (1972) used catch per unit of effort data from the fishery in the spawning season as a measure of spawning stock abundance, and calculated recruitment at age 4 for the period 1951-1971. He found a positive relationship between stock and recruitment, but with considerable variation. Gjøsæter did not attempt to fit any recruitment model to the data, but concluded that both large and small spawning stocks appear to be able to yield both good and poor recruitment. On the average, small stocks seem to provide more recruits per parent than larger spawning stocks.

Hamre & Tjelmeland (1982) studied the stock-recruitment relationship in the period 1974-1979, on the basis of acoustic stock size estimates, using the number of two-year-olds as a measure of recruitment. They fitted the Beverton & Holt recruitment function $R = (S \cdot R_{max}) / (S + S_{1/2})$ to the data, and obtained estimates of $R_{max} = 44.5 \cdot 10^{10}$, and $S_{1/2} = 0.43$ million tonnes. All data points in this period fitted this function quite well.

Gjøsæter (1997b) investigated the stock-recruitment relationship on the basis of estimates of spawning stock and recruitment at age 1 in the period 1973-1995,using the spreadsheet model 'Capstock' (see section 10.1) (Fig. 16). Some years show a very different recruitment/parent stock ratio from the other years of the series. The most notable exceptions are the years 1984, 1985, 1992, 1993, and 1994. In all of these years, young herring where present in large numbers in the Barents Sea. Herring is known to reduce the survival of capelin larvae (cf. section 11) and, therefore, all years with more than 200 000-300 000 tonnes of herring present in the Barents Sea were marked on the stock-recruitment plot (Fig. 16). These included 1991 and 1995 in addition to those mentioned above. A Beverton & Holt function was fitted to the data when the herring years were excluded. The obtained estimate of R_{max} was $804 \cdot 10^{12}$, and of $S_{1/2}$ 98 700 tonnes. The values of R_{max} cannot be directly compared in the above estimations because the difference in age at recruitment, but the half-value of the function, $S_{1/2}$, shows that when this larger span of years is included the function rises much more sharply than it does when based on the data from 1974-1979. It seems reasonable to conclude that the stock-recruitment relationship for capelin, without herring in the Barents Sea, follows a Beverton & Holt function reasonably well, while in years when young herring are present recruitment fails completely. The two years, 1991 and 1995 seem to contradict this hypothesis. Gjøsæter & Bogstad (1998) explain these seemingly contradicting data points as being due to a small geographic overlap between young herring and capelin larvae in these years.

Serebryakov & al. (1985) approached the stock-recruitment problem in a slightly different way. Instead of using the biomass of the spawning stock, they calculated what they defined as the population fecundity (PF). The PF was estimated on the basis of individual fecundity by age (section 6.1.3), total number of fish, the maturity ogive and sex ratio in the spawning stock. As an index of recruitment, they used the number in each year class at an age of three years. In the study period, 1972-1981, the PF varied from $1.05 \cdot 10^{15}$ (1974) to $3.18 \cdot 10^{15}$ (1976), and the recruitment from $0.18 \cdot 10^{12}$ (1975) to $0.55 \cdot 10^{12}$ (1972). The authors calculated survival rates SR (the ratio between number of eggs and number of three-year-olds) which varied from 0.008 % (1975) to 0.029 % (1972), and defined three categories of survival conditions; favourable (SR > 0.020), average (0.014 < SR < 0.020), and unfavourable (SR < 0.014). This approach to stock-recruitment studies, taking into consideration not only the total biomass of the spawners but the actual number of eggs spawned, is interesting for two reasons. First, it may reveal some of the mechanisms regulating the stock recruitment relationship and, second, it could give a better fit to the data points and thereby improve the models where this relationship is used. However, the period available to the authors was probably characterised by more or less average survival conditions. In the following period, the capelin larvae have probably experienced better survival conditions (e.g. in 1988), as well as considerably worse conditions (years with young herring in the Barents Sea). Therefore, the different PF levels (sufficient PF to produce an average year class under unfavourable conditions, the critical PF which will not produce an average year class even under favourable conditions etc. as defined by Serebryakov & al. (1985) cannot be readily used in management for establishing a target spawning stock level.

6.1.2 Fecundity

The fecundity of Barents Sea capelin was studied by Pozdnjakov (1957), Gjøsæter & Monstad (1973), Galkin & Kovalev (1975), and Huse & Gjøsæter (1997). Fig. 17 summarises the results from these studies. There is an approximately linear increase in fecundity with increasing length. Most female spawners are in the length interval 14 to 18 cm, and the fecundity in this length range will vary from 6 000-10 000 to 14 000-18 000. Whether the differences in fecundity by length, shown in Fig. 17, are real differences between years and/or areas, or artefacts caused by methodological differences, is unknown.

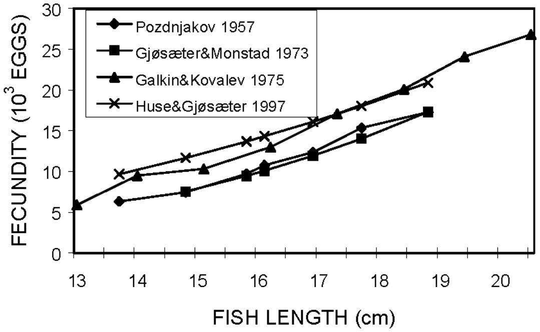

Fig. 17. Fecundity by length for Barents Sea capelin. Data from Pozdnjakov (1957), Gjøsæter & Monstad (1973), Galkin & Kovalev (1975) and Huse & Gjøsæter (1997).

6.2 AGE DETERMINATION

Scales do not develop in capelin during the first year of life, and otoliths (sagittae) have been preferred for age readings (Hamre 1977). The annual growth zones or annuli in capelin otoliths are relatively well pronounced, except for the first one which may be difficult to detect, particularly in older specimens. Prokhorov (1963, 1965, 1968) claimed that even very small first rings should be counted as the first winter ring because such otoliths mainly stem from summer spawned capelin with a short growth season before the first winter. However, some earlier Russian authors (cited by Prokhorov 1968) and Pitt (1958) omitted the central zone when counting annuli in capelin. Growth studies were used to assess the validity of ageing of capelin by Bailey & al. (1977) in Canadian waters and by Hamre (1977) for the Barents Sea stock.

By back-calculating lengths at deposition of the first ring and comparing them with lengths from sampling, Bailey & al. (1977) reached the conclusion that the first ring was a true winter-ring, but a second ring was found to be deposited during the process of metamorphosis, which normally occurred during its second year of life. This 'metamorphic check' was found in 77 % of one and two years old fish and in 44 % of adults, this decrease being interpreted as an obfuscation of the check by the increasing opacity observed in older otoliths. The absence of the metamorphic check in some otoliths could result from its deposition simultaneously with the first or second annulus.

Hamre (1977), working with Barents Sea capelin, studied this problem during the summer of 1976. Both 0- and 1-group capelin were sampled and length at deposition of the first ring was back-calculated. He found that even the smallest fish with one ring, a modal length of 5.8 cm in early July and a mean length at deposition of the first ring of 4.2 cm, were far too large to be the offspring of that year's spawning. It was found that even at the border of the larval drift towards the north and east, the mean length of the larvae was less than 2 cm. He concluded that the first ring, even with a radius as small as 0.05 mm, reflects the first year's growth and should be counted as the first winter ring. Otoliths from Barents Sea capelin interpreted at the IMR, Bergen have, since then, been aged according to these findings, and otoliths sampled previously and interpreted differently have been reread. The age reading method at PINRO, Murmansk also complies with this interpretation, and there is a high correlation between the interpretation of capelin otoliths at these two institutes (Gjøsæter 1985a).

Gjøsæter (1985b) identified two main problems in the age determination of capelin. The 'first ring problem', i.e. the thickening of the otolith which causes the first ring to disappear in older otoliths and the 'false ring problem', false rings which may be present quite frequently and are most pronounced in otoliths from capelin more than three years old. He concluded that although some individuals are probably assigned a false age by the current method of age determination, the practical consequences are small. He found no evidence of a metamorphic check like that described for the capelin in Newfoundland waters (Bailey & al. 1977).

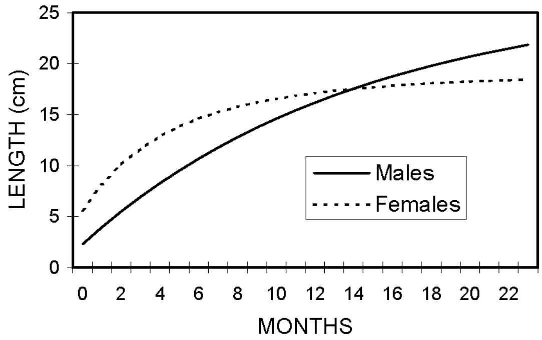

Fig. 18. vonBertalanffy growth curves for male and female capelin. From Monstad 1971.

Tereshchenko (1996) studied the capelin otolith structure with the aim to validate the age determination. She confirmed that the hyaline winter ring is formed during the winter cessation of growth from November to March-April. In 9 % of the otoliths, the hyaline ring was present already in September. The opaque summer zone is formed during the period of intensive feeding and growth, from May to September. There was evidence that in immature fish the opaque zone begins to form earlier in spring than it did in older fish. She also claimed that it is possible to identify individuals which have spawned from those that have not, based on the appearance of the otoliths. The criteria for discrimination is a thickening of the hyaline zone, increased contrast between hyaline and opaque material, and a sharp reduction in fish growth rate among those fish which have taken part in spawning. Based on these criteria she found that in 1993, 10 % of the capelin spawning stock were spawning for the second time (see also section 6.5.2).

Gjøsæter & Monstad (1982) studied the formation of primary growth increments in the otoliths of capelin from the Barents Sea. Otoliths from individuals with known age, reared in a basin, as well as otoliths from field samples were analysed. They concluded that primary growth increments do not form daily in adult capelin, but that they probably do in capelin up to the age of about one year. There was, however, evidence that fast-growing specimens form more rings per unit time than do slow-growing ones. The validation experiment was conducted in a basin located in southern Norway, and the temperature in the basin reached 20 °C during the experiment. This is much higher than the temperature experienced in the natural habitat and the validity of the experiment is, therefore, questionable.

6.3 GROWTH MODELS

Based on observed mean length-at-age, growth appears to be fast until an age of three years, and then stops almost completely. Monstad (1971) fitted von Bertalanffy growth curves to such data and found the growth to be described by the curves: $L_t = 26.72 \cdot [1 - e^{-0.07(t + 1.29)}]$ for males and $L_t = 19.80 \cdot [1 - e^{-0.12(t + 0.48)}]$ for females (Fig. 18). However, the rapid decline in growth rate for older fish is partly an artefact caused by the length dependent maturation and high spawning mortality among capelin. Individuals, surviving to an age of four or five years, experienced the slowest growth rate and did not mature and spawn at a younger age. The maturation length represents a kind of upper limit of the observed length in the stock (Gjøsæter 1985c, 1986). By back-calculating length from otolith growth zones, Monstad & Gjøsæter (1977) and Gjøsæter (1985c, 1986) found that the capelin continues to grow at a relatively fast rate during the whole of its life.

6.4 CONDITION

Monstad (1971) studied the length-weight relationship for males, females, immatures and maturing fish separately during the four quarters of the year in 1968-70. He calculated the parameters a and b in the equation $W = a \cdot l^b$, which are shown in Table 11. Maturing capelin exhibit the largest weight for a given length in spring, and this is most notable among the males. Among immature capelin there are small differences between the sexes. In autumn the curves for immature males and females are approximately equal.

Table 11. The parameters a and b in the equation $W = a \cdot l^b$ calculated for immature and maturing males and females during the four quarters of the year, based on data from 1968-1970. From Monstad (1971).

		Winter		Spring		Summer		Autumn	
		Male	Female	Male	Female	Male	Female	Male	Female
Immatures	*a*	0.00041	0.00029	0.01623	0.03072	0.00177	0.00248	0.00154	0.00182
Immatures	*b*	3.85	4.00	2.40	2.17	3.32	3.19	3.35	3.29
Maturing	*a*	0.00240	0.00036	0.00011	0.00037	0.01411	0.00093	0.00038	0.00259
Maturing	*b*	3.25	3.89	4.33	3.88	2.64	3.61	3.89	3.17

6.5 MORTALITY

6.5.1 Mortality of immatures

The mortality of larvae is probably mainly caused by predation, which is dealt with in section 5.4.1. The natural mortality of age one year and older capelin has been studied by Dommasnes (1981), Tjelmeland (1987b), Tjelmeland & Bogstad (1993) and Ices (1997). Dommasnes (1981) found annual instantaneous natural mortality coefficients (M) ranging from 0.35 to 1.03 for age 2-3 fish, 0.37 to 1.80 for age 3-4, and 1.16 to 2.66 for age 4-5 fish, when the year classes 1971 to 1977 were analysed. His estimates include spawning mortality, which explains the high M for older age groups. An M of 2.66 will remove 93 % of a year class during one year. Tjelmeland (1987b) attempted to analyse the mortality of mature capelin, caused by predation by cod, using cod stomach data and abundance as well as distribution of cod and capelin during the winter months (January to April). He derived mortality coefficients of 0.65 ± 0.05 and 0.95 ± 0.10 for the years 1985 and 1986 respectively, where the confidence intervals represent approximately 90 % probability. By using the acoustic estimates of each age group from the annual autumn surveys carried out jointly by PINRO, Murmansk and IMR, Bergen in the period 1973 to 1996, taking account of catches and assuming total spawning mortality, monthly natural mortality coefficients have been calculated for the immature part of each age group (Ices 1997). The results for the age groups 1-2, 2-3 and average for all age groups are shown in Fig. 19. Until around 1983, the natural mortality was stable at about 0.05 month^{-1}. From then on, M increased sharply to 0.2-0.3 per month, corresponding to a 20-25 % removal of the individuals from the stock each month. This was one of the main causes for the stock collapse in 1984-1987. The mortality decreased sharply during the period 1987-1990, and was estimated at an unrealistically low level in 1990. The same pattern was iterated in 1990-1996; the natural mortality increased to very high levels (partly causing the stock collapse in 1993-1995) once more to return to values observed in the 1970s.

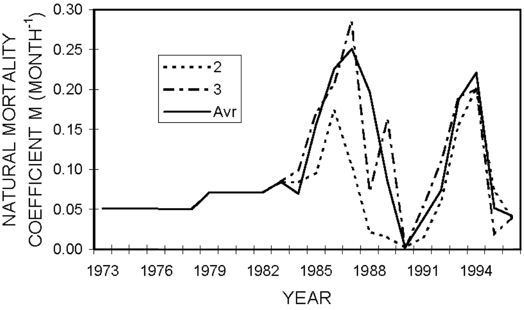

Fig. 19. Estimated instantaneous natural mortality coefficients M for the immature fish of age 2-3, 3-4 and average for all age groups of capelin, based on annual acoustic abundance estimates. Before 1983, the natural mortality was estimated only as average values for all age groups. Data from ICES (1997).

6.5.2 Spawning mortality

The question whether the Barents Sea capelin is semelparous or iteroparous has been discussed by several authors, i.e. Prokhorov (1960, 1965, 1968), Migalowskiy (1967), Monstad (1971), Forberg (1982), Borisov & Dvinin (1986), Oganesyan (1988). Furthermore, the question has been in focus in the ICES assessment working group dealing with capelin assessment (ICES 1991a).The main evidence for the capelin being semelparous are that large quantities of dead capelin near the spawning places in the spawning season is a common phenomenon (Rass 1933; Prokhorov 1960; Monstad 1971), that the spawning stock each year is totally dominated by 3 or 4 years old capelin (Prokhorov 1965, 1968; Monstad 1971; Dommasnes 1985; ICES 1991a), and that capelin older than 5 years are seldom found (ICES 1991a). There seems to be a consensus that most of the males die after spawning. The evidence for regarding the female capelin as iteroparous is that not all the oocytes mature when the capelin spawn for the first time, rendering them physiologically capable of spawning for a second time (Forberg 1982). Finally, the physiological state of the females after spawning shows that they are capable of surviving (Oganesyan 1988), and schools consisting of mostly spent females of which a large proportion had begun feeding have been detected several times just after spawning (Prokhorov 1960; Gjøsæter 1989, 1990). However, a skewed proportion of the sexes in favour of females among older fish, which would be anticipated if males die while females survive spawning, has not been detected. Thus, in the period 1969-1982 the average proportion of males among 4- and 5-year-olds was 50.7 % and 52.6 % respectively (ICES 1991a). Even if a certain proportion of fish survives the spawning process, the predation from cod and other predators is intensive in the spawning areas, and the chances of surviving a migration back to the feeding areas are probably low (Gjøsæter 1995). Disregarding the fact that some females may survive spawning, it may be concluded that only negligible amounts of fish in the Barents Sea capelin stock will survive the first spawning and live long enough to take part in a second spawning. For stock assessment purposes the capelin may, therefore, be regarded as semelparous (ICES 1991a).

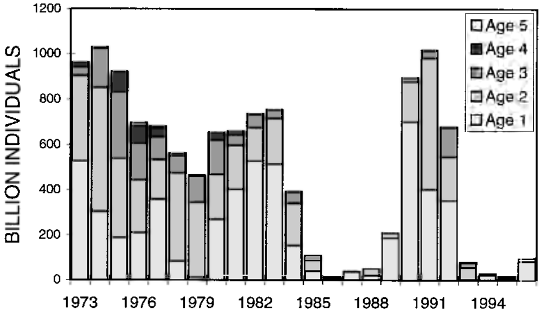

Fig. 20. Acoustic estimates (billion individuals) of capelin from 1973 to 1996.

7 ABUNDANCE

7.1 LONG TERM TRENDS

Estimates of capelin stock abundance before the 1970s are mostly based on the success of the capelin fishery or the fishery on young cod (called *loddetorsk* in Norwegian, i.e. 'capelin cod') following the capelin to the coast in spring, and are partly of anecdotal character. The capelin spawning migration to the coast seems to have been quite regular, but periods in which capelin failed to approach the coast for spawning seem to have occurred now and then. The earliest information describing such periods dates back to 1799, when Sommerfelt (cited by Stergiou 1984) wrote: 'They have the experience here that it has abandoned the coast of Finnmark for many years up to 16 or 20 in succession.' The next official record of such a period is a fishery report, according to which there was no capelin fishery at all on the Finnmark coast during the 1830-1840 period (Stergiou 1984). Collett (1903) mentions a longer period, 1819-1838, but from 1840 until 1938 the capelin seem to have visited the Norwegian coast regularly. There was, however, a period around the turn of this century when 'the mass approaches of capelin would seemingly not reach the coast as before: The spawning these days is often taking place so far from the coast that it is difficult for the fishermen to find the capelin, and thereby to get enough bait for the cod fishery' (Collett 1903). From about 1868 there are annual records of the first date on which the capelin appeared at the coast (Møller & Olsen 1962a, 1962b). This record is continuos from 1868 to 1937, but from 1938 to 1942 no capelin appeared at the coast of Finnmark. In 1962 this happened once again (Olsen 1965), and was caused by a serious decline in the abundance of the year classes 1958-1960. This temporary disappearance of capelin coincided with the recruitment of two extraordinarily strong herring year classes (1959 and 1960). It is likely, that the feeding area of young herring in those years overlapped with the distribution area of juvenile capelin and could be the reason for the disappearance of the capelin in the early 1960s (Hamre 1985). However, after 1962 the capelin have visited the coast every year, although the abundance has fluctuated, from almost zero to millions of tonnes.

7.2 ESTIMATES OF STOCK SIZE

Absolute estimates of stock size by acoustic methods are available from 1972 onwards. A comprehensive review of the time series of acoustic stock size estimates is contained in articles by Gjøsæter & al. 1998a & b. That time series of stock size estimates are shown in Fig. 20.

Other kinds of stock size estimates include estimation of spawning stock size from egg abundance (Gjøsæter & Sætre 1973b; Dragesund & al. 1973), from larval abundance (Dragesund & al. 1973; Salvanes 1984), from tagging experiments (Dragesund & al. 1973; Dommasnes 1978a), from catch per unit of effort (Gjøsæter 1972), and from age material alone (Olsen 1965). The abundance of larvae in June has been estimated since 1981 and an abundance index at the 0-group stage in August is available from 1965 to present (cf. section 6.1).

The first attempt to estimate the relative size of the spawning stock over a time period was made by Olsen (1965). He realised that the spawning stock size had fluctuated widely, but because of the effects of changes in availability, weather conditions, market demands and other variables, catch per unit of effort estimates would not give realistic indices of stock abundance. Consequently, he developed a method, using the proportions of spawners in different age groups in consecutive years to directly estimate relative spawning stock size. For the period 1959-1964, Olsen found that the relative strength of age groups ranged from 0.1 to 2.2 (Table 12), with a maximum in 1961 and a minimum in 1963-1964. He also found a correlation between the relative spawning stock size and the landings in the Norwegian fishery, and concluded that the size of the catch was largely governed by the size of the stock. In an attempt to analyse the stock-recruitment relationship of capelin, Gjøsæter (1972) used catch per unit of effort in the Norwegian fishery to assess the size of the spawning stock in the period 1954 to 1964. He also provided a 3-scale classification of spawning stock, i.e. poor, medium or strong in the period 1954-1971 (Table 12). Dragesund & al. (1973) estimated the spawning stock size on the basis of tagging experiments, egg- and larval surveys, and acoustics in the years 1970-1972 and Dommasnes (1978a) estimated spawning stock size on the basis of tagging experiments in 1973, 1974 and 1975 (Table 12).

Salvanes (1984) analysed the abundance of capelin larvae in the period 1972-1976, and estimated larval mortality at the yolk sac stage and, finally, spawning stock size. She used estimates of the age of the yolk sac larvae from measurements of the length of the yolk sac made by Helgesen (1977). Salvanes's estimates of spawning stock size are somewhat lower than those derived from the tagging data (Table 12). After this period, acoustic methods represent the sole technique for stock size estimation of adult Barents Sea capelin.

8 EXPLOITATION

The Norwegian capelin fishery has a long history. The capelin were fished with beach seines at the coast of Finnmark during the spawning season, and mainly used as bait, fertiliser or animal food (Sars 1879; Collett 1903; Nitter-Egenæs 1967). From 1916 capelin were used for meal and oil production in Finnmark, but it was not until in the 1930s that a fishery for industrial purposes became important (Møller & Olsen 1962a). From the late 1950s following the decline in abundance of the stock of Norwegian spring spawning herring, the fleet of purse seiners increasingly focused their effort on the capelin, and by 1957 purse-seiners had totally replaced the beach-seines (Stergiou 1984). From 1961 pelagic trawls were also employed in the fishery, which at that time took place in the spawning season only. Beginning in 1968, a summer fishery rapidly developed in the open sea (Monstad & Gjøsæter 1972; ICES 1997).

The Russian (former Soviet) capelin fishery also has long traditions, and was carried out with beach seines and nets along the Kola coast during the spawning season (Prokhorov 1965). From the early 1960s, purse seines and pelagic trawls replaced the beach seines and the fishing was expanded into the open areas of the Barents Sea in the 1970s (Stergiou 1984; ICES 1997).

In the 1970s, the fishery for capelin became of prime importance to Norwegian and Russian fleets, with nearly 3 million tonnes landed in 1977. Since then, two stock collapses have resulted in the fishing for capelin to become more variable. Furthermore, the capelin fishery was

Table 12. Various estimates of spawning stock size during the period 1951-1976. Investigation no. 1 and 2: Gjøsæter (1972) from catch-per-unit-of-effort (million tonnes) and from various subjective estimations respectively, no. 3: Olsen (1965) from age-distribution (relative numbers), no. 4: Dragesund & al. (1973) from tagging data (million tonnes), no. 5: Dragesund & al. (1973) from egg and larval survey (million tonnes), no. 6: Dommasnes (1978) from tagging data (million tonnes), and no. 7: Salvanes (1984) from egg and larval surveys (million tonnes).

	Investigation number						
Year	1	2	3	4	5	6	7
1951	2.76	small					
1952	1.24	small					
1953	3.13	small					
1954	6.34	medium					
1955	4.75	medium					
1956	9.74	strong					
1957	7.08	medium					
1958	5.96	medium					
1959	8.48	strong	0.48				
1960	6.64	medium	1.725				
1961	13.17	strong	2.217				
1962		small	0.46				
1963		small	0.115				
1964		small	0.09				
1965		small					
1966		strong					
1967		strong					
1968		strong					
1969		strong					
1970		strong					
1971		very strong		5.8	3.2		
1972				4.8			1.38
1973						2.2, 4.1	1.13
1974						1.1, 2.0	0.78
1975						1.1, 1.1	0.56
1976							1.11

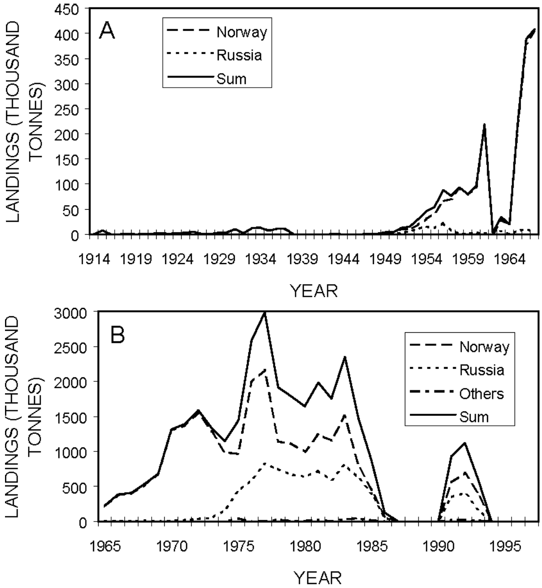

Fig. 21. Landings of Barents Sea capelin during the period 1914-1967 (A, see text for data sources), and during the period 1965-1997 (B, ICES (1997)).

closed from 1987-1990 and again from 1994 to the present time (Gjøsæter 1995; ICES 1997). In Fig. 21A and B, catch statistics are presented for the period 1914 to 1967 and for the period 1965 to 1997, respectively. The landings increased sharply in the 1950s, but declined almost to zero in 1962-1964. From 1965 the increase in catch continued until the early 1970s. From 1972 to 1983 Norwegian landings fluctuated around 1.5 million tonnes, while in this period the Russian landings increased sharply and brought the total annual landings up to 2-3 million tonnes. From 1984 catches decreased, partly because of quota restrictions, but primarily because the stock collapsed. The fishery was closed from autumn 1986 until autumn 1990, and the catches taken from the recovered stock in 1991-1993 were relatively small compared to the period 1970-1985. The fishery was closed again in spring 1994 when a new stock collapse was evident.

9 STOCK ASSESSMENT AND MANAGEMENT

Contrary to most fish stocks which are handled by assessment working groups within the ICES system, the capelin stock is not assessed by sequential population analysis (SPA) (Mohn & Cook 1993). The main reason is that most capelin spawn only once, and then die. The VPA and other SPA techniques rely on records of catch-at-age and measures or assumptions of natural mortality to reconstruct the initial number of fish in each year class. A useful estimate of the number of fish in a cohort at the time when it was recruited can only be obtained if the terminal size of the cohort is known (either if a long time has passed since it was recruited to the fishery and it can be assumed to be removed from the stock, or if the terminal cohort size can be assessed by other means). Another problem is that the capelin, being a forage fish, is subjected to a very high natural mortality, as compared to the fishing mortality, and SPA would, if only for that reason, not give very accurate results. On the other hand, the Barents Sea capelin stock is one of the few fish stocks where direct absolute estimates of its size can be obtained annually (Gjøsæter & al. 1998a, b), and the need for a survey-independent method (like SPA) for assessment purposes is less pressing.

Various ad hoc methods have replaced SPA in the stock assessment of capelin (Tjelmeland 1985, 1996; Bogstad 1997). These methods project the stock from the stock estimate, obtained during the annual acoustic survey in September-October forward in time until spawning in March-April, taking into consideration natural mortality, maturation and growth. It is then possible to analyse the effect of a fishery on the spawning stock.

A catch quota regulation of the capelin fishery was introduced in the winter season of 1974, when the Norwegian quota was set at 720 000 tonnes. In spring 1978, a Norwegian catch quota was set at 1 150 000 tonnes, and in the autumn of that year at 350 000 tonnes. These catch quotas were not based on an evaluation of the stock situation under different management regimes, but were rather acts of precaution because the acoustic stock size estimates showed that the maturing part of the population was small and could be endangered by a free fishery.

In 1978, the USSR/Norwegian Fisheries Commission agreed to regulate the Barents Sea capelin fishery bilaterally (Hamre 1985). It was agreed that a TAC assessment should be based on acoustic stock measurements carried out jointly in the autumn, and that the assessment should aim at a minimum remaining spawning stock of 500 000 tonnes (Anon 1978a, 1978b). A rule of a closed season, lasting from 1 May to 14 August was introduced, and the catch of juvenile capelin below 11 cm was limited to 15 % by weight. In 1981, the proportion of allowed catch of fish below 11 cm was reduced to 10 %, and in 1984 the opening date of the autumn fishery was postponed to 1 September. In 1981, a minimum mesh size of 16 mm in capelin nets (both trawls and purse seines) was introduced.

Hamre & Tjelmeland (1982) estimated sustainable yield of the Barents Sea capelin stock, using the model ‘Capelin’ (Tjelmeland 1985). Due to the mass mortality of post-spawners, the stock-recruitment relationship of capelin is a matter of great importance in determining the maximum sustainable yield (MSY), see section 6.1.1 for a discussion of stock-recruitment relationships. Hamre & Tjelmeland (1982) calculated equilibrium sustainable yield estimates under different fishing strategies, and found that with no fishing the stock would stabilise at about 5.5 million tonnes, of which about 1.8 million tonnes would spawn. When fished only during the winter, the maximum yield was 1.6 million tonnes for a parent stock of 0.33 million tonnes, and when fished only during autumn MSY was 1.7 million tonnes, achieved at an equilibrium state of spawners of 0.45 million tonnes. When fished both during autumn and winter, which usually has been done, a MSY of 1.65 million tonnes is obtained for a spawning stock of 0.4 million tonnes.

In the paper by Hamre & Tjelmeland (1982), ecological considerations were also discussed in connection with the yield estimates, a rather novel approach at that time. Together with the yield, they calculated the 'M-output biomass', the annual biomass output removed through natural mortality. This is a rough estimate of that proportion of the total production of capelin which is available to capelin predators. This quantity increased steadily for increasing spawning stock sizes, and is considerably reduced when the yield is at its maximum (Fig. 22). The authors concluded that, irrespective of fishing strategy, the yield curve was fairly flat near its maximum, and consequently there was not much difference in yield for spawning stock sizes in the range 0.3 to 0.5 million tonnes. The M-output biomass, however, increased by 0.5 million tonnes for this increase in spawning stock size. The authors also addressed the question of when capelin should be harvested. They stated that by managing an exclusive autumn fishery with an MSY-strategy, about 2 million tonnes of capelin remain as food for other stocks, excluding the biomass of postspawners. However, when the catch is taken during the winter, the importance of the capelin as a forage fish increases and the M-output biomass becomes some 2.5 million tonnes, based on the same criteria. Consequently, taking into consideration the ecological importance of the capelin stock, this fact justified, in the authors' opinion, an exploitation strategy which aims at an equilibrium state of spawning stock of 0.5 million tonnes, and a harvesting strategy where all, or at least the main part, of the catch is taken during winter.

The strategy of leaving 0.5 million tonnes to spawn was established in 1978 (Anon 1978a, 1978b) and has been followed in the management of the capelin stock since. The ICES working group dealing with capelin adopted this strategy, as well as the recommendation, originally given by a Soviet-Norwegian assessment working group (Anon 1983), that most of the quota should be taken during winter (ICES 1984b). Little is lost in yield by that strategy, while much is gained by a larger M-output biomass and also through reduced uncertainty in the stock assessment. A catch quota for an autumn fishery has to be recommended on the basis of a stock prognosis, made one year earlier and projected one and a half year ahead of time. This implies a lot more uncertainty than the procedure involved when recommending a quota for the winter fishery, based on an autumn assessment in the year before, i.e. 3-4 months before the fishery begins.

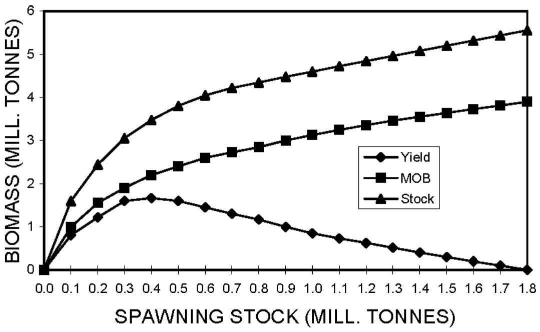

Fig. 22. Relationship between yield and spawning stock size and between M output biomass and spawning stock size.

When the capelin stock declined severely during the period 1983 to 1986, it was realised that the rationale and the model underlying the management of the capelin in the years prior to that period was inadequate (ICES 1995b; Tjelmeland & Bogstad 1993). It worked well during the 1970s, when there were no herring in the Barents Sea, and the recruitment to the cod stock was moderate. The management in the years 1991 and 1993 introduced a new element, i.e. the role of the cod as predator on capelin was taken into consideration when modelling the spawning stock size (Bogstad 1997). However, the management objective from the pre-decline period, to aim at a spawning stock level of capelin of about 0.5 million tonnes, remained unchanged. The method developed by Bogstad & Gjøsæter (1994) and used during this period, was fairly simple and can only be applied when the abundance of capelin is high. During the last few years, more sophisticated models taking into consideration both the mortality induced by cod on immature and maturing capelin and the changes in capelin recruitment when herring is present in the Barents Sea, have been developed (Tjelmeland 1996; Bogstad 1997). Because of the new collapse of the capelin stock in 1994 and subsequent years, new tools for the assessment of the Barents Sea capelin stock will be introduced, where both multispecies and environmental effects will be taken into account. However, the basic rationale behind the capelin fishery management; a constant escapement strategy for spawners, will not be abandoned. The size of the target spawning stock will probably not change much either, but it may change as a consequence of changes in recruitment perspectives. It remains to be seen whether these new models will enable managers to reach the ultimate goal, *i.e.* to keep the capelin stock (and the other exploited fish stocks in the area) at a level where a sustainable production to the benefit of the whole ecosystem, including man, is achieved.

10 MODELLING

Because of the complicated nature of an ecosystem, various kinds of mathematical simplifications of the reality are needed, both for the purpose of understanding the processes taking place in the system, and to enable construction of workable models for use in management of human exploitation of the stocks. Many different kinds of models exist, but the aim of the models mentioned here is to aid in the assessment and management of stocks. Some models are directly built as a tool to calculate fish quotas, while others are built with the aim to increase the general understanding of the ecosystem which, in the long run, will aid in the management of the system. Since capelin is one of the main components of the Barents Sea ecosystem, it plays an important role, even in multispecies and system models. I will not go into modelling detail here, but point the way for further reading.

10.1 SINGLE-SPECIES MODELS

At least two different types of single-species models have been built, i.e. analytical population dynamics models empirically tuned to fit the observed situation and theoretical models involving dynamic optimisation of behaviour. Examples of the former type is the model ‘capelin’, formerly used in conjunction with management of the capelin stock (TJELMELAND 1985) and in part ‘Capstock’, a model resembling a VPA type of model but based on annual stock size estimates (ICES 1991a). These models are based on an annual stock size estimate, the former predicts the future state of the stock as a function of future catches, while the latter keeps track of the stock history, giving estimates of stock abundance and production through the year as well as of fishing and natural mortality. Both of these models include a length based maturation model and an empirical growth model. Examples of theoretical models are a multi-dimensional continuum model (REED & BALCHEN 1982), and a fitness-based model of capelin distribution and migrations (GISKE & al. 1992; FIKSEN & al. 1995). The former models the distribution and migration of capelin on the basis of a ‘comfort function’ depending on temperature, food density, light, ocean currents and capelin density, assuming that the capelin will migrate in the direction where the comfort function has the steepest gradient. The latter predicts growth and distribution, assuming that the capelin will always behave in a way that maximises the ecological fitness. Although there currently are problems in fitting spatial distributions, obtained from these models, to observed distributions, this approach seems interesting (BOGSTAD 1997).

10.2 MULTISPECIES MODELS

In the early 1980s an initiative was taken at the Institute of Marine Research, Bergen to model stock interactions in order to improve the scientific basis for management. This initiative has resulted in the model MULTSPEC and a family of related models (MEHL & al. 1986; TJELMELAND 1987a, 1987b, 1992; BOGSTAD & TJELMELAND 1992; TJELMELAND & BOGSTAD 1993; ULLTANG 1995; TJELMELAND 1996; BOGSTAD 1997; BOGSTAD & al. 1997; TJELMELAND & BOGSTAD 1998), which are extensions to a Beverton & Holt type of model (BEVERTON & HOLT 1957). Output from these models is currently used by ICES in the management of the Barents Sea capelin stock (cf. section 9).

While these models are built on fundamental biological and oceanographic explanatory variables using a ‘bottom-up’ approach, a ‘top-down’ approach is used in a model called ‘Systmod’, which considers the system on a superior level, and models the most essential components of the system from the top of the food-chain and downwards (HAMRE & HATLEBAKK 1998). This model only takes into consideration the most vital dynamics of the key stocks, the interaction between them and the influence of the environment, and may prove suitable in fishing strategy analysis and for forecasts of catch and stock developments.

Other types of multispecies models, involving capelin, also exist. The model presented by REED & BALCHEN (1992) is a component of a larger system of physical and biological dynamic models describing the Barents Sea ecosystem (BALCHEN 1976). Multispecies VPA or MSVPA (POPE 1979; HELGASON & GISLASON 1979) has also been tried for ecosystems of the Barents Sea (ICES 1996d, USHAKOV & al. 1992).

11 A BRIEF HISTORY OF STOCK AND FISHERY

Gjøsæter (1995) gave a short summary of the development of the capelin stock, with emphasis on the question of whether the fishery or other causes were the main reasons for the large stock fluctuations observed in the 1980s and 1990s. As mentioned previously, little is known about the size of the stock prior to 1973. But from then on the stock size, distribution and composition have been monitored during annual surveys in the autumn, in the beginning by the IMR in Bergen, but later through the joint effort of IMR and PINRO, Murmansk. The stock size increased from 1973 to 1975 (Fig. 20), due to the recruitment of the three large but slow-growing year classes of 1971-1973. Since individual growth was slow, these year classes matured at a relatively old age and, consequently, a large number of immature fish was accumulated in the stock (Hamre 1991). When the bulk of this accumulated stock spawned and died in 1975-1977, the stock size decreased sharply. The next peak in the stock size in 1980 was caused by high individual growth rate in year classes of intermediate size. But once again the stock declined when a large portion of it spawned during 1980-1981. From 1984 to 1986, the stock was reduced from about four million tonnes to 100 000 tonnes (Fig. 20), and the possible causes of this will be discussed below. From 1988, the stock size increased sharply to reach six to seven million tonnes in 1990 and 1991. This was due to a very large year class in 1989, high individual growth and low natural (and no fishing) mortality. In 1993 a new stock collapse was evident, and at present (spring 1997) the stock is still at a low level, although there are signs of a new stock recovery.

Various explanations of the stock collapse(s) have been suggested. Hopkins & Nilssen (1991) argued that the first decline began as early as 1975 and that fishing was an important contributory factor during the whole period. Hamre (1991), Tjelmeland & Bogstad (1993) and Gjøsæter (1995) all agree that a too high exploitation pressure played a role in the two last fishing seasons (autumn 1995 and winter 1996), but maintain that the decreasing stock size prior to 1982-1983 can be explained by a natural response to changes in recruitment, growth, and maturation. Gjøsæter (1995) argues that since the impact of fishing will mainly be on reduced recruitment caused by a too small spawning stock, and since the production of larvae was at the same high level up to 1985, when the dwindling of the adult stock was already evident, fishing could not be the main cause of the stock collapse. This argument is supported by the stock development in 1991-1994, when the catches were low and the fishery was banned when the first signs of stock collapse was evident.

The explanation of the collapses should rather be sought in recruitment failure, not because of shortage of spawners but due to low survival of the larvae. This hypothesis, now frequently called 'Hamre's hypothesis' because it was first suggested and later on elaborated by him (Hamre 1985, 1988, 1991, 1994), is that the young herring, when they appear in the Barents Sea, will graze down the capelin larvae and thereby cause failure of recruitment to the capelin stock. This hypothesis has gained general acceptance after the mechanism behind this hypothesis was verified in the field (Huse 1994; Huse & Toresen 1995), and it was shown that even though the production of capelin larvae was 'normal' in years when herring were abundant, these capelin year classes never recruited to the stock, as measured by acoustic methods, as one year and older fish (Gjøsæter 1995). Based on tank experiments Moksness & Øiestad (1987) found that 0-group herring could also be responsible for mass mortality of capelin larvae. However, the survival of the capelin year classes 1983 and 1989, born in the same years as strong herring year classes, suggests that the predation on capelin larvae by 0-group herring is not as important as that by age one to age four herring.

The following scenario for the major perturbations of the capelin stock in the Barents Sea may then be outlined: A long period of cold ocean climate from 1977 to 1981, during which the capelin stock was large and stable, ended with a major inflow event of Atlantic water during 1982 and early 1983 (Skjoldal & al. 1992). Despite the fact that this inflow, ending in winter 1983, left the south-western Barents Sea filled with water containing low abundance of zooplankton, it probably enhanced the survival conditions for herring and cod larvae, spawned along the west coast of Norway, but growing up in the Barents Sea. For the first time in 20 years, a strong year class of herring grew up in the Barents Sea, but left the area in May-June 1986. In 1984 and 1985, this herring caused failure of recruitment to the capelin stock. Concurrently, the mortality of older capelin was increasing caused by enlarged food demand from a growing cod stock (Mehl 1991). Tjelmeland & Bogstad (1993) estimated that the natural mortality of capelin had increased from 0.04-0.09 month^{-1} in the period 1979-1983, to 0.18-0.26 month^{-1} in the period 1985-1987. An instantaneous mortality coefficient of 0.26 month^{-1} means that 96 % of the stock will die per year. At the same time, the fishing pressure lead to increased fishing mortality when the stock decreased in size (Gjøsæter 1995). Since the plankton biomass was low in 1984, the individual growth of capelin decreased (Skjoldal & al. 1992). These mechanisms, working together, caused the first stock collapse. When the herring left the Barents Sea in spring 1986, the survival rate of capelin larvae increased dramatically, but a small spawning stock size probably impeded the production of a large year class before 1989. Coinciding with the decline in the capelin stock in 1985-1986, there was an increase in zooplankton biomass to a maximum around 1987 (SKJOLDAL & al. 1992; DALPADADO & SKJOLDAL 1996). Reduced predation pressure by capelin was probably a major cause of this increase in zooplankton biomass, particularly in the case of larger species such as krill and amphipods. This high abundance of food for the capelin was probably the main reason for an observed increase in individual capelin growth, even when the capelin stock was rapidly increasing. Another reason for the rapid recovery of the capelin stock was that the natural mortality of capelin was drastically reduced (ICES 1997). This was probably a result of a reduction in some major stocks of predators, i.e. cod (MEHL 1991) and harp seals (HAUG & NILSSEN 1995; WIIG 1988).

A new major inflow event occurred in 1989 and 1990, the cod and herring stocks recruited large numbers of young fish to the Barents Sea, and a repetition of the events described above was evident from 1992.

The decisive role, given to the herring in this scenario, implies that the capelin stock should also have fluctuated widely prior to the period of heavy exploitation of the stock. Unfortunately, proofs of such events are lacking, since the capelin was only observed when it approached the coast for spawning, and an absence of capelin reported in one area could be caused by variations in migration routes and spawning areas. However, there is at least one example of a capelin stock collapse, prior to the ones discussed above, i.e. that in 1962-1964. At that time, the yield of the capelin fishery, which had been steadily increasing from the early 1950s (Fig. 21A) suddenly decreased and a rising trend was not re-established until 1966. In 1962 the capelin did not approach the Norwegian coast at all during the spring season (OLSEN 1965, 1968) and the spawning stock was small in the period 1962-1965 (Table 11). The 1959 year class of herring, which probably stayed in the Barents Sea in the period 1960-1963, is known to be one of the most numerous year classes in this century (HAMRE 1991).

Whether the absence of capelin from the coast, reported to have occurred intermittently in previous times (SARS 1879; HJORT 1914; STERGIOU 1984; MØLLER & OLSEN 1962a) occurred simultaneously with the presence of herring in the Barents Sea is unknown. However, it is known that good recruitment to the herring stock is a cyclic event. It is also known from Russian investigations of cod stomachs, dating back to the turn of this century, that herring and capelin have replaced each other in a cyclic manner as the main prey for cod (PONOMARENKO & PONOMARENKO 1975). This may be taken as supporting evidence for the stock of capelin being small when the herring were abundant and vice versa.

The antagonistic roles of herring and capelin in the Barents Sea also suggest that the main reason why the capelin stock was large and relatively stable and was able to withstand a high fishing pressure from about 1965 to 1983, was the absence of herring during that period. When the herring stock is at a ‘normal’ level, the chances that no recruiting year classes will be rich and enter the Barents Sea are probably low. It is possible and even likely, that a situation with large perturbations of the capelin stock, as witnessed during the last 15 years, is the rule and that the large and stable capelin stock, seen in previous years, is the exception rather than the other way round.

Only continued effort of investigations of the Barents Sea, to obtain direct evidence of the interactions between fish stocks and between those fish stocks and their biological and physical environment, together with further effort in modelling these processes, will throw more light on the population biology of capelin and its place in the ecosystem. We have learned much from previous investigations, modelling activity and the experience gained by observing the development of the fishery during this century. But a lot more remains to be learned in the future.

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