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Hjálmar Vilhjálmsson

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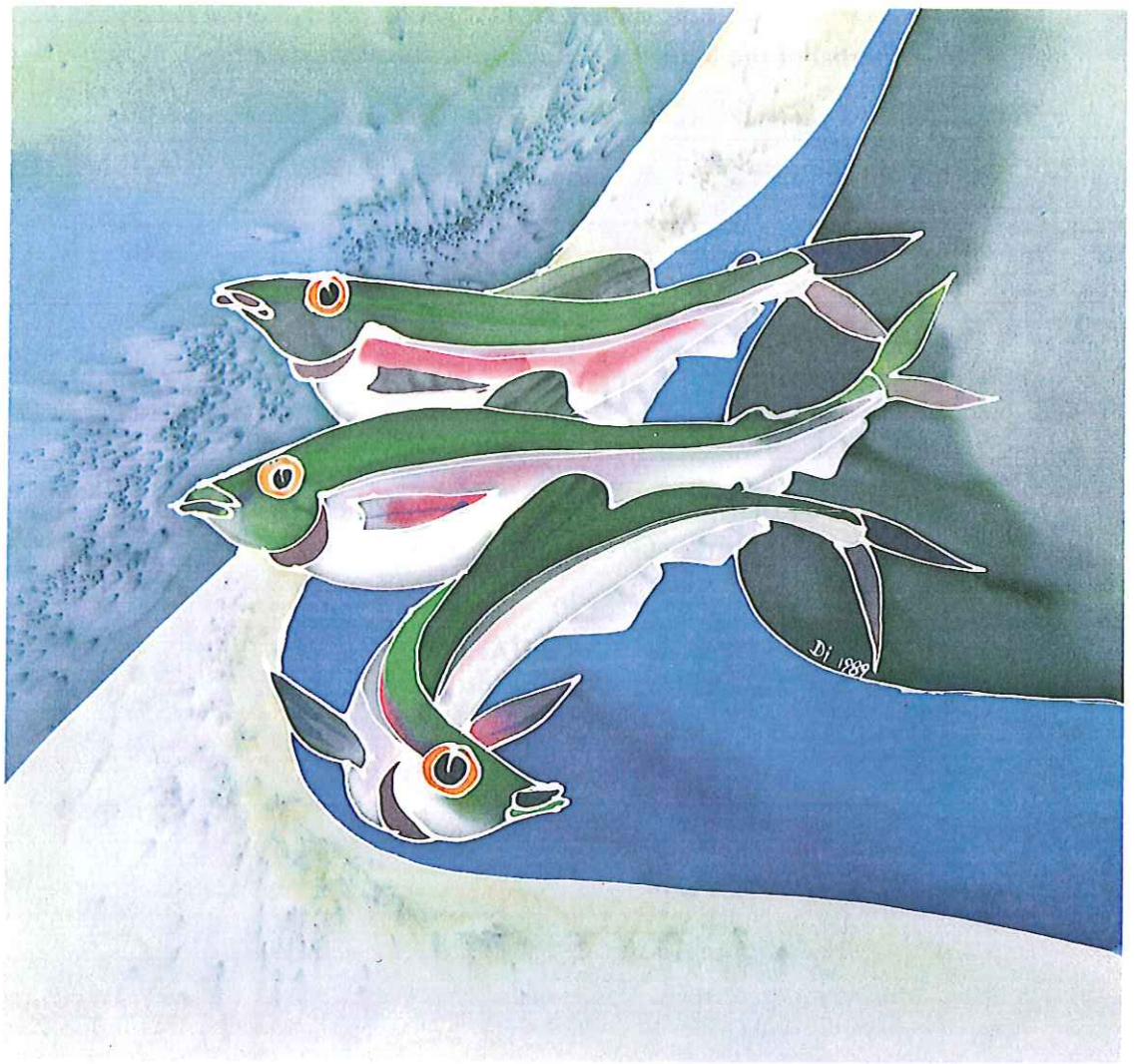
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by

HJÁLMAR VILHJÁLMSSON
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Reykjavík

CAPELIN. Painted on silk by Di Dabinett, Newfoundland.

DEDICATED TO *KOLBRÚN*
WHO IS STILL MARRIED TO ME

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1. INTRODUCTION

The capelin *(Mallotus villosus)* is a small pelagic, schooling fish, native to the northern hemisphere. The species is well known to inhabitants of arctic and subarctic regions where capelin may, in places, be extremely numerous and conspicuous. Depending on location and society capelin have been eaten by man, fed to domestic animals and used as bait or even as fertilizer.

However, in the last two or three decades the species has become the target of rapidly developed multi-national, major fisheries which, in turn, temporarily resulted in stock collapses, due to over-exploitation and/or natural causes. Cases in point are the Iceland – Greenland – Jan Mayen stock (Anon. 1982, 1982a), the Barents Sea stock (Anon. 1987a, 1988) and the stocks off eastern Newfoundland and Labrador (Carscadden *et al.* 1982). Although probably accelerated by the intense fishing effort these stock collapses were in all cases primarily due to naturally occurring recruitment failure (Leggett *et al.* 1984; Hamre 1988, 1989; Vilhjálmsson 1983, 1983a). Fortunately, all these stocks recovered (Vilhjálmsson 1985; Carscadden *et al.* 1988a; Anon. 1989, 1990, 1991) but lately all of them have again either gone through or are showing signs of recurring recruitment failures (Anon. 1990, 1991, 1992, 1992a, 1993; Vilhjálmsson 1991; Miller 1992).

Today capelin have acquired at least a good deal of the attention they deserve. The species is not only recognized as a valuable source of income in itself but also as an extremely important part in the diet of many and more valuable commercial species such as the cod. And finally, capelin have a unique position in the food web of at least part of the northern oceans where they transfer large amounts of energy from arctic to more temperate, boreal regions. This is done through extensive summer feeding migrations to more northern and colder areas which are retraced in the fall to the more southern overwintering grounds.

Because of the naturally occurring large fluctuations in stock abundance and the pelagic schooling nature of capelin, they are extremely sensitive to overfishing when pursued with modern techniques of finding and catching. High catch rates can be maintained until little is left resulting in recruitment failure, at least in part, and/or delayed recovery. Therefore, stock abundance, recruitment and migrations of exploited capelin stocks are now commonly monitored, biological and physiological studies are carried out and the position of the capelin in the food web of the northern oceans is being investigated in increasing detail and modelled by scientists at various research institutes.

In the area between Iceland, East-Greenland and the island of Jan Mayen capelin is one of the most common fish species. Magnússon (1966, 1968) found that in Icelandic waters 0-group capelin greatly outnumbered the combined abundance of the 0-group stage of all other fish species in the area. And in 0-group surveys in the last two decades, the total number of capelin in the catches has always been 2–3 orders of magnitude greater than that of any other species. In spite of this, Icelandic research projects centering around capelin were, for a long time, few and far apart and provided only a general picture of its life history. Prior to 1965 capelin were of little direct economic importance and, as a result, not considered a particularly feasible subject for research by disponents of financial resources. It was not until in 1965, at the beginning of a large scale capelin fishery, that continuous systematic research on this capelin stock began. At first research was conducted on and near the spawning grounds at South and West Iceland, but later it was extended to include other areas of adult capelin distribution as well as that of the younger components of the stock.

The main purpose of this monograph is twofold: First, to review the information that has been gathered on the capelin in the area between

Iceland, East-Greenland and Jan Mayen over the last 25 years or so and, in certain instances, compare these results to those of capelin in other parts of the world. Second, to clarify which areas of research have been neglected and to suggest research for improving our knowledge of this stock. The available information has never before been brought together for a coherent overview describing the present knowledge about the ways and nature of capelin in the Iceland – Greenland – Jan Mayen area and where our knowledge is incomplete.

For the purpose of orientation, a section summarizing briefly the general distribution, biology and taxonomy of the species, has been compiled. Moreover, it seems both appropriate and necessary to give an overview of the pioneering research, carried out in Iceland from the late nineteenth century until the mid-1960s. An attempt will be made to describe some of the ideas people had about the capelin in this part of the world in ages past.

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2. GENERAL OVERVIEW OF THE SPECIES

2.1. World distribution of capelin

The distribution of capelin is wide (Fig. 2.1). In the eastern Northeast Atlantic there are individual records as far south as Oslo (Hjort 1914; Sæmundsson 1926). Capelin are, however, usually not registered until north of Vesteraalen in Northwest Norway from where they are common north- and eastwards along the coasts of Troms and Finmark in northern Norway as well as off the north coast of the Kola Peninsula in Russia and, occasionally, in the White Sea (Prokhorov 1967). The eastern limit of capelin distribution in this region is generally said to be the island of Novaya Zemlya, but capelin sporadically enter the Kara Sea (Prokhorov 1967) and have been taken on the coasts of the Yamal and Tamyr peninsulas as well as in the region of the Lena River delta (McAllister 1963; Andriashev 1964; Winters 1966, 1969). Due to the extremely low temperatures in the northernmost Barents Sea, capelin seldom reach as far north as Franz Josef Land. In warm years, however, when capelin in the Barents Sea have a northeasterly distribution, they are regularly found along the northwestern coast of Novaya Zemlya (Loeng 1989; Dommasnes, personal communication). In the west they are common near Bear Island and sometimes migrate north to the west of Spitsbergen to 78°N, where some catches were for example taken near 5°E by an Icelandic vessel in the late 1960s. For most of the year the bulk of the capelin biomass in this part of the Northeast Atlantic is, however, generally located in the central Barents Sea.

Capelin have been recorded at the Faroes on rare occasions (Jespersen 1920; Sæmundsson 1926). They are abundant around Iceland, on the Iceland-Greenland Ridge as well as in the oceanic area between Iceland, Greenland and Jan Mayen where they have been recorded as far north as 74°N and as far east as 5°W (Anon. 1987). Capelin may be seasonally plentiful over the East Greenland shelf, particularly between Iceland and Greenland and off Scoresby Sound. They are also common farther west and south, often found to be conspicuous locally in inshore areas, and have indeed lent their name to a small community, Ammassalik (65°49′N, 37°20′W), on the east coast of Greenland.

Off the west coast of Greenland the main distribution area is from the southernmost promontory, Cape Farewell (59°50′N), to the Disko area (Upernavik, 73°N) and appears to be limited to the fjord systems and the banks just outside them (Kanneworff 1967, 1968; Jákupsstovu and Røttingen 1975; Friis-Sørensen 1985). At West-Greenland capelin have, however, been reported as far north as Thule at about 76°N (Jensen 1939, 1948; Hansen and Hermann 1953).

Off eastern North America the main capelin distribution area extends south from Saglek on the northern coast of Labrador and around the eastern and southeastern coasts of Newfoundland as well as on the Grand Bank off Newfoundland, St. Pierre Bank, Green Bank and the banks of the Labrador shelf (Jeffers 1931; Pitt 1958a; Winters 1966, 1969; Templeman 1968; Jangaard 1974). In the Gulf of St. Lawrence capelin are most common on the northern shore and at Anticosti Island, but in cold years they also occur in numbers around the Gaspé peninsula. On occasion, capelin have been reported as far south as Halifax, the Bay of Fundy and the Gulf of Maine (Jeffers 1931; Tibbo and Humphreys 1966; Winters 1966, 1969; Templeman 1968). In the north, capelin have neither been recorded at Baffin Island nor in the western part of the Hudson Strait. They are, on the other hand, periodically reported from Ungava Bay and are commonly met with in the southern and western parts of Hudson Bay, where surface temperatures are higher than in other parts of the bay (Winters 1969; Dunbar 1983). Occurrences of capelin have been recorded from the Coronation Gulf, Bathurst Inlet
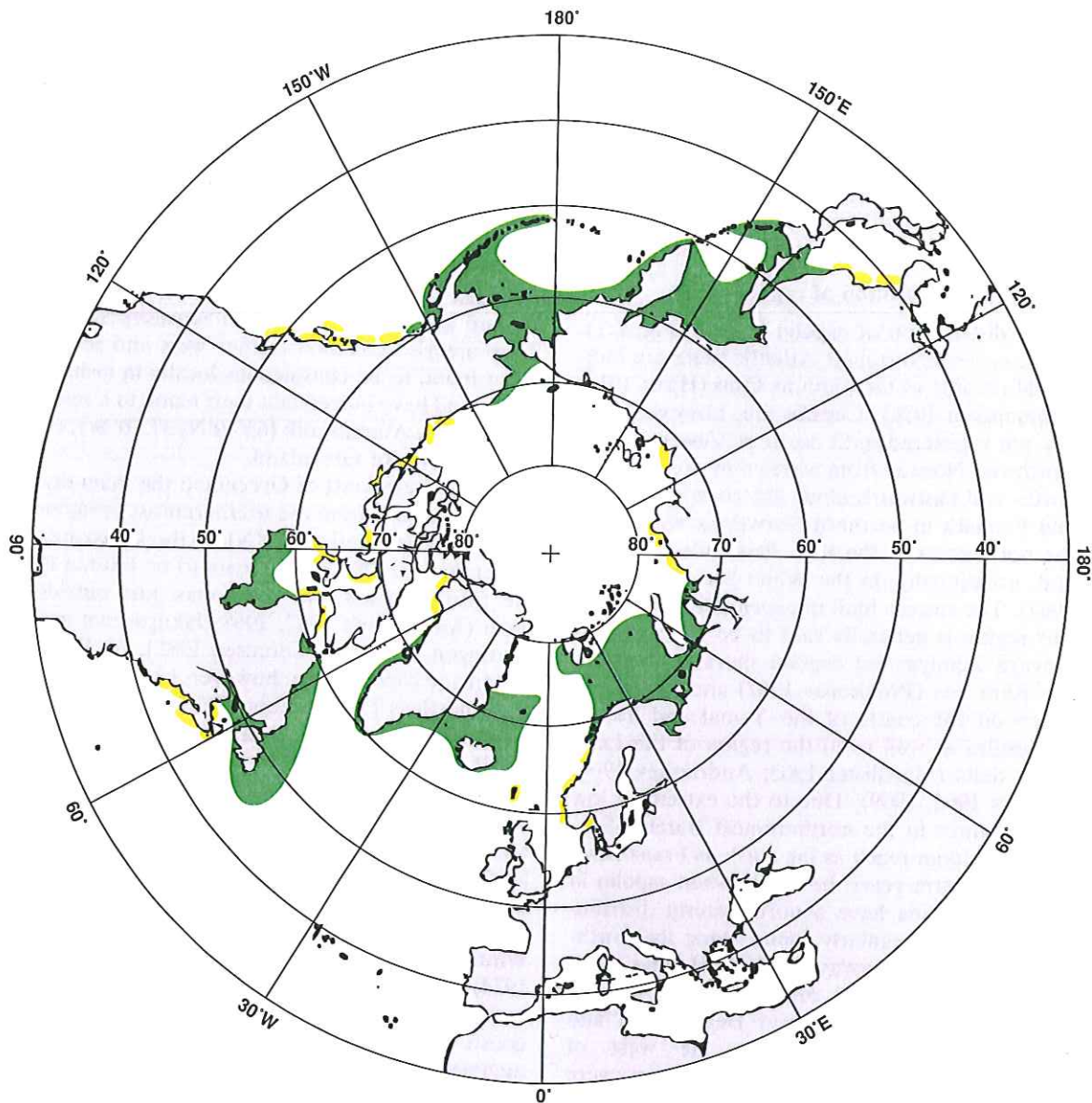
Figure 2.1. The world distribution of capelin. Green: Common occurrence. Yellow: Sporadic or rare records.

and Great Fish River of the Canadian Arctic (Jeffers 1931; Ellis 1962; Winters 1966, 1969; Templeman 1968).

In the Pacific capelin have been recorded along the entire Alaskan coastline, at least from Point Barrow in the north and including the Alaska Peninsula as well as the Aleutian Islands. They are common around Kodiak Island and in the northern and western Gulf of Alaska, but may be found off the coast of British Columbia as far south as the Strait of Juan de Fuca in the state of Washington. On the Asiatic side capelin have been recorded from south of Cape Lisburn, along the shores of the Kamchatka Peninsula as well as the island of Sakhalin to Hokkaido in Japan and the Tumen river in Korea (Winters 1966, 1969; Prokhorov 1967; Jangaard 1974; Pahlke 1985). Although said to be common in the Sea of

Okhotsk and the Sea of Japan (Velikanov 1984) the centre of capelin distribution in the Pacific is in all probability the Bering Sea proper (Hart and McHugh 1944). However, recent information (Vespestad 1987, and personal communication) indicates that, for the Bering Sea, the main capelin distribution is in the region of the Bering Sea shelf while they have occurred intermittently in the northern Gulf of Alaska, on both sides of the Alaska Peninsula and at the Aleutian Islands. In the last 25 years there have been no records of capelin in the area of the Bering Sea Basin.

Counting all occurrences, the distribution of capelin is practically circumpolar as shown in Figure 2.1. Records are fairly continuous across the Canadian Arctic but are more scanty in the Siberian Arctic, particularly in the far eastern part of it, where capelin have not been found from the Lena river delta to the Bering Strait. This may, however, be an artifact due to incomplete knowledge of that area (McAllister 1963; Andriyashev 1964).

2.2. Capelin stocks

Within the area of distribution it is customary to refer to several separate, self contained stocks or population complexes of capelin that generally do not mix (Fig. 2.2).

The largest known stock of capelin inhabits the Barents Sea and adjacent waters. The Barents Sea capelin spawn in March and April at depths of up to 150 m off the shores of Murman, Finmark and Troms (Bakke and Bjørke 1973; Sætre and Gjøsæter 1975). Their main feeding area is in the central and western Barents Sea (Prokhorov 1967, 1968; Monstad 1971). Since the mid-1960s this stock has sustained a large scale fishery for the production of fishmeal and oil. In the 11 year period 1972–82 the exploitable biomass, consisting of age groups 2 and older, was estimated to have totalled between 4 and 8 million tonnes and yielded annual catches of 1.2 – 2.9 million tonnes. In spite of regulatory measures, for reducing the catch of juveniles and the introduction of catch quotas, the Barents Sea capelin stock collapsed in the mid-1980s and the total stock abundance is estimated to have reached an all time low of 100 – 120 thous. tonnes in 1986 and 1987 (Dragesund et al. 1973; Hamre 1985, 1988, 1989; Anon. 1987, 1989). The Barents Sea stock has made a dramatic recovery, the total abundance estimate amounting to about 5.8 million tonnes in the fall of 1990 (Anon. 1991) but has since declined again, apparently due to predation by cod and, possibly, by herring (Anon. 1993).

In addition, several small, secluded fjordic populations are found in northern Norway. The best known example of these is the Balsfjord capelin which recently has been subjected to intensive study (cf. Friis-Sørensen 1983; Davenport and Steene 1986; Nyholmen and Hopkins 1988). The Balsfjord stock feeds in the outer reaches of the fjord and migrates to spawn intertidally on suitable beaches at the head of the fjord in May. These capelin mature and spawn younger and smaller than the Barents Sea stock. This, together with evidence from parasitological tags and the beach spawning habit, indicates that they are indeed isolated and segregated from the main capelin population. Genetic differences have, however, not been found (Mork and Friis-Sørensen 1983).

The capelin in the area between Iceland, Greenland and Jan Mayen will hereafter be referred to as the Icelandic stock. They spawn offshore, mainly at South and Southwest Iceland in March, and feed off North and Northwest Iceland as well as in the oceanic area farther north. As far as can be ascertained, there is no connection with the Barents Sea stock but some of the larvae often drift from spawning grounds at Iceland across the northern Irminger Sea to East Greenland and possibly around Cape Farewell to West Greenland (Vilhjálmsson 1983, 1983a). The Icelandic capelin have been fished for meal and oil production for almost two decades. The stock collapsed in the early 1980s but recovered again after a fishing ban of almost two years. The abundance of the fishable stock is estimated to have varied between 0.3 and 2.2 million tonnes in the period 1978–1991. Annual catches fell from nearly 1.3 million tonnes to practically zero from 1978 to 1982 but increased thereafter and stayed between 1.1 and 1.3 million tonnes in 1985–1988 (Vilhjálmsson 1983, 1985, 1986, 1987, 1987a, 1988, 1989). In the 1989–1991 period catches declined sharply but increased again to around the 1 million tonnes level in 1992 (Sveinbjörnsson 1991; Vilhjálmsson 1991; Anon. 1992, 1992a, 1993). There is some evidence for the existence of fjordic populations in Iceland but it is questionable whether these are self-sustained.

The West-Greenland capelin are a coastal
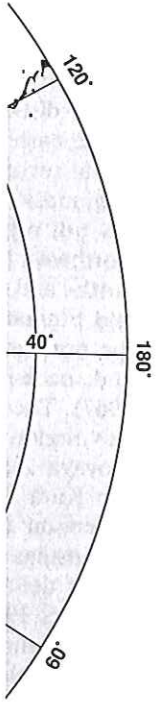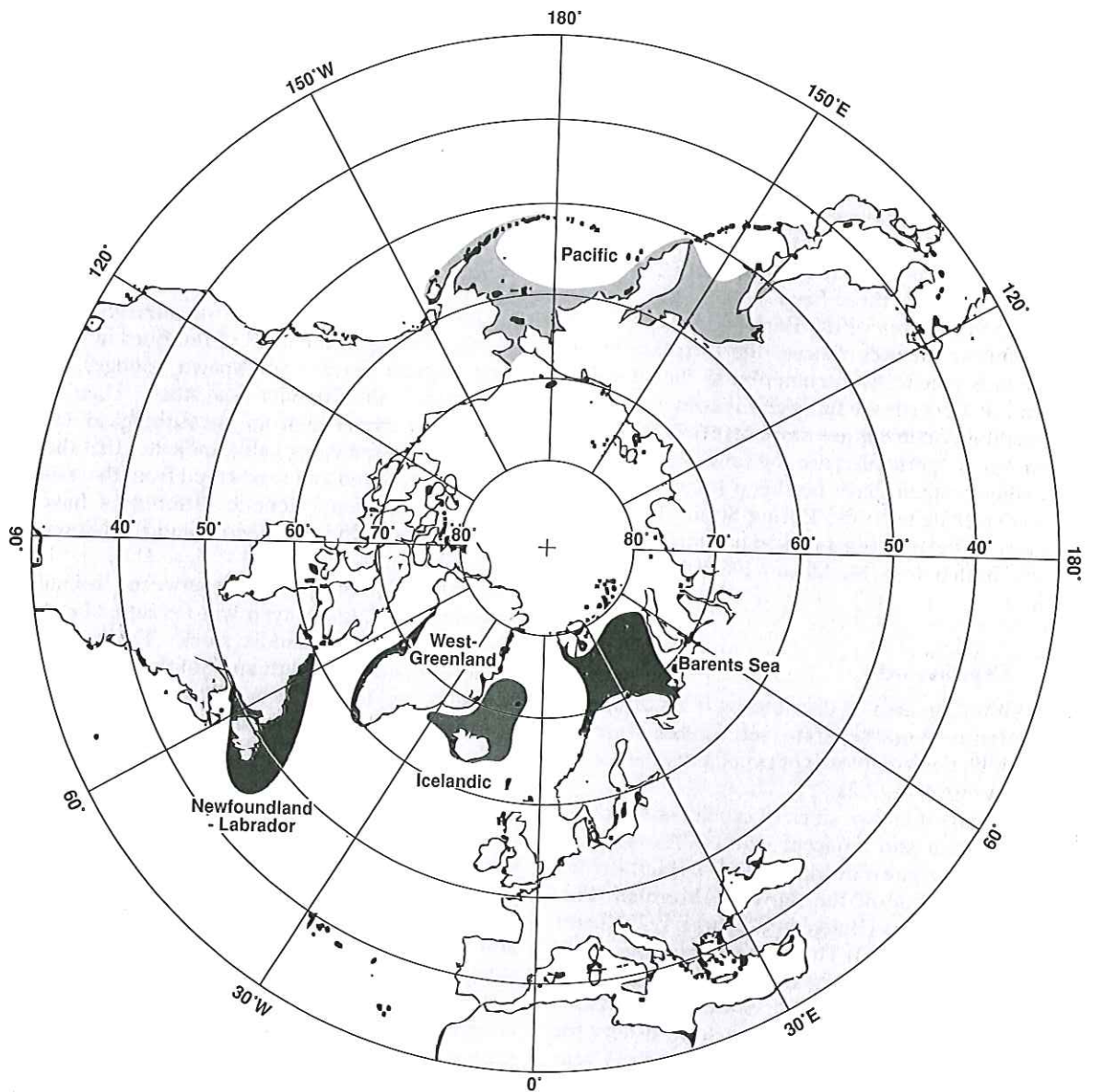
Figure 2.2. The location and names of major capelin stocks or stock complexes.

stock which may consist of several sub-populations that spawn on beaches in inlets and fjords in May–June and thereafter migrate out to the nearshore parts of the submarine terrace to feed in summer and autumn (Kanneworff 1967, 1968; Friis-Sørensen 1985). Although Greenland capelin have long been utilized locally for human consumption and dog feed, a large scale commercial fishery has never been attempted. The main distribution area is between Cape Farewell and Upernavik but may extend much farther north in warm periods (Jensen 1939). Local populations are also known from the east coast of Greenland, in particular the Ammasalik area (Hansen 1943). However, research in the East Greenland coastal region has been scanty and it is not clear whether

these populations are self contained or to some extent the result of larval drift from western Iceland.

The Newfoundland and Labrador areas are populated by several stocks of capelin with different spawning grounds and migration patterns (Campbell and Winters 1973; Carscadden and Misra 1980; Carscadden 1982; Misra and Carscadden 1983, 1984). These are the inshore or beach spawners of Labrador and Northeast Newfoundland, the Northern Grand Bank capelin that spawn on the shores of the Avalon peninsula of Southeast Newfoundland, the St. Pierre-Green Bank population spawning at southern Newfoundland, mainly in Placentia Bay, and the Gulf of St. Lawrence capelin spawning on the beaches of West Newfoundland as well as at Anticosti Island, on the northern shores of the Gulf and in the St. Lawrence River estuary (Bailey *et al.* 1977). The fifth main stock consists of the capelin which spawn on the Southeast Shoal of the Grand Bank and is the only stock in this area known to spawn demersally (Pitt 1958a; Carscadden 1978; Carscadden *et al.* 1989, 1989a).

Traditionally, the Newfoundland-Labrador capelin were subject to a small scale inshore fishery for local consumption and bait (*e.g.* Winters 1967). However, the largest of these stocks, those of the Labrador banks and the Grand Bank of Newfoundland, sustained an annual offshore fishery of 100–250 thousand metric tonnes in the 1972–1978 period. At that time the fishable part of these stocks is thought to have varied between 0.5 and 2.1 million tonnes. The abundance declined drastically in the late 1970s and the offshore fishery was largely discontinued (Carscadden *et al.* 1982). The fishable stock abundance was in 1989 estimated at about 3.3 million tonnes (Miller 1989; Miller and Carscadden 1989). In the 1980s the only offshore capelin fishery was conducted by a few USSR vessels working with pelagic trawls off the coasts of Labrador. Recognizing the importance of capelin as food for other marine species, a conservative exploitation policy has been adopted since 1979. Since then these capelin have only been fished in the spawning season for consumption and bait at a rate of less than 10% of the estimated exploitable biomass (Carscadden 1984; Anon. 1989a). However, during a stock abundance survey in autumn 1990 it was found that the Newfoundland and Labrador capelin stocks had suddenly collapsed and have not yet recovered (Miller and Carscadden 1990; Miller 1992). Recent tagging experiments carried out by Nakashima (1992) prompted him to suggest that capelin in NAFO divisions 2J3K and 3L were one stock complex. In fact, Canadian biologists have now recommended that these two stocks be combined into one for management purposes (Carscadden, personal communication).

In the Canadian Arctic there also exist beach spawning capelin populations that appear to be either isolated self-sufficient stocks or temporary seclusions, resulting from migrations during warm periods, in which case they will in all probability die out eventually. Cases in point are the Ungava Bay, Hudson Bay and Coronation Gulf-Bathurst Inlet capelin (Ellis 1962; Winters 1969; Dunbar 1983).

The Pacific capelin have in the past been referred to as if they were a single stock. Until very recently they have not received much attention by researchers or the commercial fishery community. So far as is known, the Pacific capelin are predominantly beach spawners and investigations conducted by Pahlke (1985) suggest the presence of several spawning groups or populations off the Alaskan coasts. By analogy, this should be the case on the Asiatic side also, where capelin are said to spawn in numerous, extensive and different locations (Velikanov 1984).

Although capelin are thus fairly common, particularly in the northern Bering and Okhotsk Seas, the abundance of Pacific capelin is in all likelihood much lower than that of the the stocks inhabiting the North Atlantic. Thus, Atlantic capelin have sustained large fisheries in the past while the recorded annual catch of Pacific capelin has never exceeded 5,000 tonnes (Vespestad 1987). Nevertheless, Pacific capelin are a common item in the diet of some sea birds and many species of marine mammals (Frost and Lowry 1987; Sanger 1987). The dynamics of Pacific capelin populations are as yet not well known. Vespestad (1987) has suggested that if the main feeding area of the Bering Sea capelin moves with the Polar Front, as is the case in the Barents Sea (see *e.g.* Hassel *et al.* 1990), the summer feeding migrations will place the bulk of the Bering Sea capelin resource beyond the northern Bering Sea, outside the area covered by groundfish surveys and the fishery.
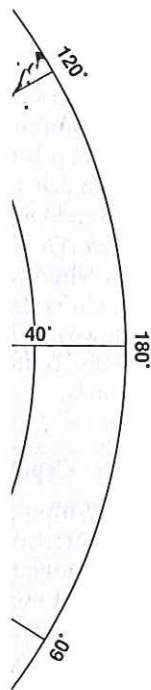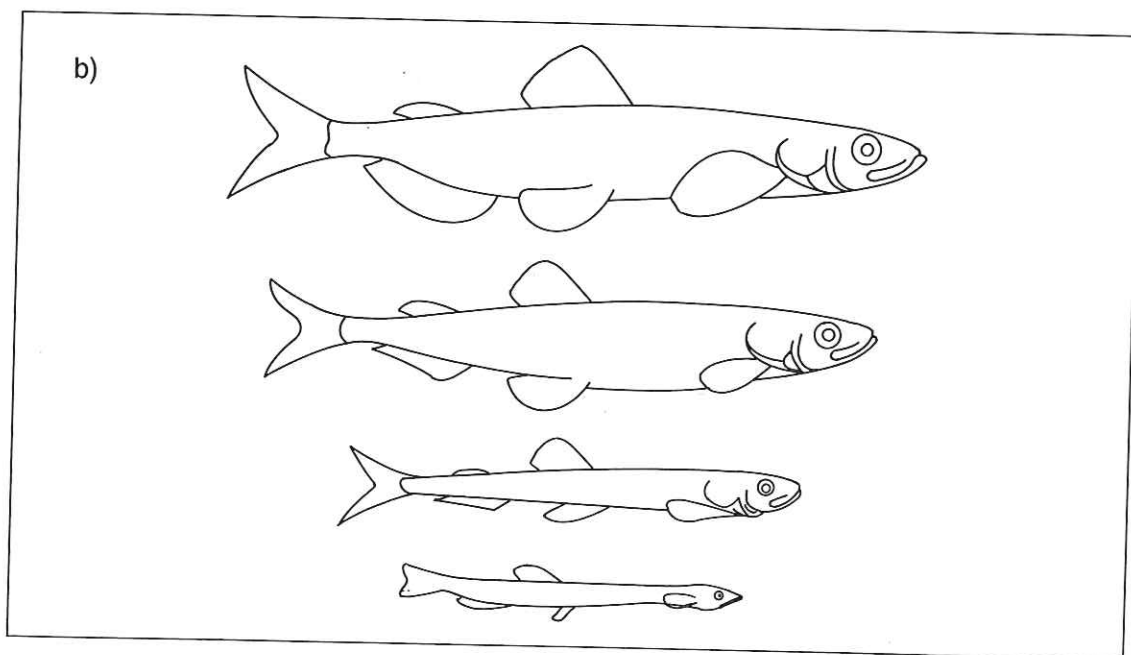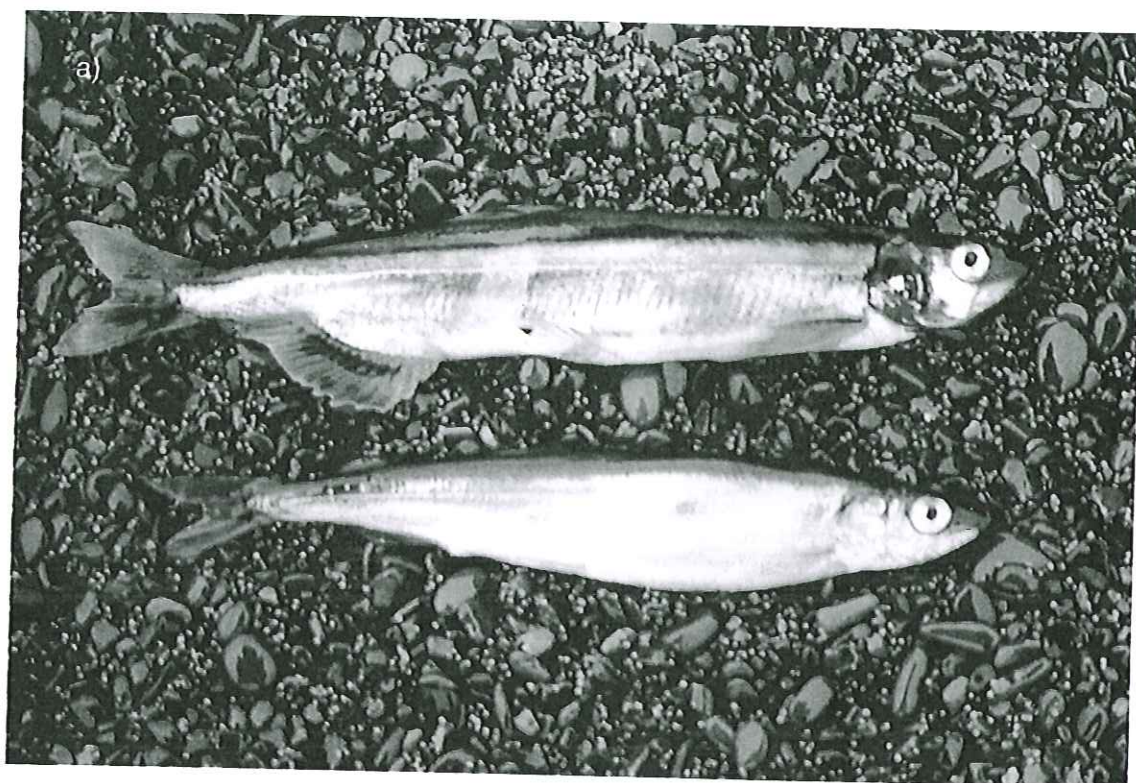
Figure 2.3. a) Age 4 male and female capelin at the height of the spawning season. Note the sex related difference in size and shape. b) A lateral view of mature male and female capelin. The figure also shows the outline of immature capelin in the 1- and 0-group stage on the same scale. – Photo: H. Vilhjálmsson.

2.3. Description and some distinctive features of capelin

The capelin are relatively small fish with mature individuals commonly ranging between 13 and 20 cm in length at ages of 2–5 years. Larger individuals are, however, not uncommon and the world record seems to be a 25.2 cm 10 year old female belonging to one of the Newfoundland stocks (Winters 1970a).

Above the lateral line the capelin appear dark-greenish in colour while below it the sides are silvery and the belly silvery white. The scale margins are dotted with small, dark specks and the gill covers have numerous black dots. In the breeding season dark colouring becomes much more pronounced in the male which may then appear almost black on the dorsal side of the body and on the head.

The mouth extends back below the large eyes and the lower jaw protrudes. The teeth on the jaws and tongue as well as on the roof of the mouth are small. Scales are small and soft and the lateral line is almost straight. At about the middle of the back is the fairly large dorsal fin and an adipose fin is situated just in front of the tail fin. There are well developed pectoral and pelvic as well as anal fins.

With the onset of sexual maturity the capelin begin to show sex-linked dimorphism in growth with mature males being 1–2 cm larger on the average than females of the same age. The immature as well as the female body in the early stages of maturity is elongate and slender but the females gradually increase in girth as the roe content increases.

The ripe or spawning male appears very different from the female. The fins are larger and both the pectoral and pelvic pairs project sideways from the body as well as curving slightly upwards at the ends. In the mature male the base of the anal fin becomes progressively more swollen as the time of spawning approaches. The most prominent difference, however, is the formation on the males of two pairs of "hairy" spawning ridges of longitudinally enlarged scales. The larger of the two is situated just above the lateral line extending along its entire length, and a smaller ventral pair runs from the pectoral to the pelvic fins. These spawning ridges begin to develop about 2–3 months before the spawning season, becoming progressively more distinct as the time

of breeding approaches. These physical changes play an essential role in the execution of the spawning act as will be explained later and give the transverse cross section of the male an almost angular shape as opposed to the round shape of the female. Outside the spawning period it is difficult to distinguish the sexes by external examination. Examples of male and female capelin in the spawning season are shown in Figure 2.3a and the difference between the body shape of mature and immature capelin is illustrated in Figure 2.3b.

On the Atlantic coast of Canada three other small, slender fishes of similar appearance may be mistaken for capelin. These are the rainbow smelt, *Osmerus mordax;* the Atlantic silverside, *Menidia menidia;* and the Atlantic argentine, *Argentina silus* (Jangaard 1974). The first two species are, together with the capelin, abundant in the Gulf of St. Lawrence while the argentine has a more oceanic distribution. All are easy to distinguish by consulting the appropriate literature except perhaps in the younger stages (McAllister 1963; Jangaard 1974).

On the Pacific side the following osmerids occur in the same areas as the capelin: Eulachon or candle fish, *Thaleichthys pacificus;* longfin smelt, *Spirinchus thaleichthys;* surf smelt, *Hypomesus pretiosus;* and toothed or rainbow smelt, *Osmerus mordax dentex* (Clemens and Wilby 1961; Hart 1973; Jangaard 1974).

In the Northeast Atlantic and at Greenland there are no species sharing the capelin distribution area which in their adult stage are even remotely similar to capelin.

For distinctive features and classification of the Osmeridae see McAllister (1963).

2.4. On the systematic position, origin and evolution of capelin

In the past, the capelin, *Mallotus villosus,* has been designated by several generic and specific names. Originally it was classified by Müller in 1776 under the genus of herring *(Clupea)* and it was not until 1829 that the present generic name, *Mallotus,* as well as the obvious salmonid appearance was first mentioned by Cuvier in his book on the animal kingdom and its organization. The specific name of *villosus* is, however, attributed to Müller who classified capelin as *Clupea villosa* in 1776 (Jeffers 1931; McAllister 1963; Winters

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1966; Jangaard 1974; Jónsson 1989). Both the generic and specific names (from Greek and Latin respectively) mean hairy and apparently refer to the appearance of the male in the breeding season.

The systematic position of the capelin is described by McAllister (1963) and has been summarized by many authors (cf. Winters 1966; Prokhorov 1967; Jangaard 1974). Capelin are classified in the suborder *Salmonoidei* or salmon-like fish. The northern salmonids are in turn classified into four main families, *i.e. Salmonidae* (salmon and trout species), *Osmeridae* (smelts and capelin), *Argentinidae* (argentines) and the *Bathylagidae* which are deep sea smelts.

The Atlantic and Pacific capelin were long considered to be separate species. Schultz (1937) established a morphometric character index (based on the number of fin rays, scales and gill rakers) by which he was able to separate Atlantic and Pacific capelin populations. The names *Mallotus villosus* (Müller) and *Mallotus catervarius* (Pennant) were consequently adopted for the Atlantic and Pacific forms respectively. However, some later authors (quoted in McAllister 1963) did not accept Schultz's distinction of separate species but usually recognized these forms at a subspecific level.

McAllister (1963) was of the opinion that further morphometric research and the continuity of records across the Canadian Arctic has provided evidence that *Mallotus* should be regarded as a monotypic genus. The continuity of records along the Russian Arctic admittedly leaves much to be desired, but is probably to some extent an artifact due to inadeqate knowledge of the area (Andriyashev 1964). In arctic specimens the character index is intermediate between those of Pacific and Atlantic populations. McAllister (1963) believed that the observed morphologic differences between Atlantic and Pacific capelin can be regarded as clinal, having arisen when the populations became separated by a southward shift of isotherms and/or the Bering land bridge during the Wisconsin glaciation. However, the debate over capelin taxonomy is far from over (cf. Kljukanov and McAllister 1973; Kljukanov 1979). In the literature Pacific and Atlantic capelin may thus still be referred to as *Mallotus villosus socialis* and *Mallotus villosus villosus* respectively.

There seems to be general consensus among researchers that the *Osmeridae* most likely originated in the Pacific. This is not only suggested by the predominance of the number of Pacific species over Atlantic ones but also by the presence in the Pacific of several pairs of endemic sub-species, presumably recently evolved, and the relative primitiveness of the Pacific forms (McAllister 1963; Kljukanov 1979). It can also be inferred from the literature that for colonization of the North Atlantic the capelin are thought to have migrated east along waterways in the Canadian Arctic as shown in Figure 2.4, rather than from the west along the north coast of Siberia (Schulz 1937; McAllister 1963; Stergiou 1989).

As mentioned in an earlier section, most capelin stocks spawn, as far as is known, intertidally or on the beach and not subtidally unless forced to by late season high temperature conditions (Templeman 1948). Exceptions are the Icelandic and Barents Sea stocks (NE-Atlantic) which spawn in deeper waters although near the coast, and the stock spawning on the Southeast Shoal of the Grand Bank southeast of Newfoundland (NW-Atlantic) at a depth of about 50 m, almost 200 nautical miles from the nearest beach (Pitt 1958, 1958a; Carscadden 1978). Accepting the view of McAllister and Kljukanov that the species originated in the Pacific and in view of the observed method of spawning in that region, there can be little doubt that beach or intertidal spawning is the original way of capelin egg deposition.

Stergiou (1989) suggested that during the last glaciation Pacific capelin were able to spawn in the original manner while there were few areas in the Atlantic suitable for beach or intertidal spawning. He theorized that spawning at depths was, therefore, evolved for the Atlantic capelin, which in the northeastern North Atlantic became highly successful indeed. Stergiou believed that capelin in the Northwest Atlantic area died off and were replaced by invading beach spawning Pacific capelin during the height of the holocene hypsithermal some 4500 to 6000 years ago. A single exception would then be the capelin stock which was able to survive by spawning demersally on the Southeast Shoal of the Grand Bank.

However, research carried out by Carscadden *et al.* (1989, 1989a) supplied convincing evidence that the capelin spawning demersally on the Southeast Shoal represented a stock that continued to spawn on the ancestral beach as it

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Figure 2.4. Possible distribution of capelin from the Pacific. The green arrows indicate the route considered the more likely, due to the continuity of records in the North American Arctic.

gradually became submerged during the glacial melt some 12,000 years ago. Although not directly stated, the implication is that other stocks in the area may have managed to adjust to the changes in sea level and found suitable beaches to spawn and survive or that they descended from the Southeast Shoal population.

When the available information on vertebral counts from various parts of the capelin distribution area is studied and corrections have been made for the inclusion or omission of the last segment, the urostyle, (cf. Table 14.12), an interesting fact comes to light. While information on the average number of vertebrae in the Barents Sea stock is somewhat contradictory (Prokhorov 1967), there seems little doubt that the Barents

Sea stock at large and the stock in the Iceland-East Greenland-Jan Mayen area are composed of fish with essentially the same average number of vertebrae (69.16–69.59). On the other hand, all stocks in the Labrador-Newfoundland-Gulf of St. Lawrence area, as well as in the eastern North Pacific, have vertebral averages generally ranging from 66.13 to 66.72. Such a difference of about 3 vertebrae is highly significant, and it seems only reasonable to assume that it must be genetically determined. Thus, the two major capelin stocks in the Northeast Atlantic proper must have been isolated from the rest of the capelin complex for long enough time to become distinct.

The evidence of vertebral numbers alone, strongly points to an early divergence and isolation of Northeast Atlantic capelin from other parts of the distribution of the species, as suggested by Stergiou. However, vertebral counts do not suggest different evolutional age groups in the Northwest Atlantic nor any such differences between capelin from that region and the eastern Pacific. This includes the capelin stock spawning at depth on the Grand Bank of Newfoundland and refutes the relationship between spawning mode and geographic location suggested by Stergiou (1989). Today, the Grand Bank capelin may simply be taking advantage of the marginal temperature conditions on this "ancestral beach" as sugggested by Carscadden *et al.* (1989, 1989a).

To the knowledge of this author no simple and plausible explanation has been given of the very successful spawning mode of the Barents Sea and Iceland stocks of capelin, both of which spawn at considerable depth. The basic requirements for the successful spawning of capelin are twofold, *i.e.* a suitable substrate and temperature between about 3° and 10°C. Many if not most capelin habitats are characterized by hydrographic conditions where polar waters and low temperatures prevail. Cases in point are capelin in the Northwest Atlantic and probably most of the stocks in the North Pacific area as well. In these locations temperature requirements for spawning can only be met in the summer period when solar warming of the top layer of the water column has taken place. From this it follows naturally that the only available spawning sites are beaches or very shallow areas. In the Northeast Atlantic, on the other hand, waters of polar origin dominate only in the more northern feeding areas. Both at Iceland and northern Norway, the coastal areas are bathed by waters of predominantly Atlantic origin with much higher temperatures. In these situations beach spawning is not necessary to meet temperature requirements and may indeed be much less effective. An exception is found in a local capelin stock occupying the long and narrow Balsfjord, cutting into the coast of northern Norway. However, due to the sequestered nature of this fjord system and the cold winter climate, temperature conditions in the Balsfjord are more like those at Newfoundland, Labrador and Greenland than conditions generally found off the coast of northern Norway.

In the case of the Icelandic stock, recent studies suggest that the success of cohorts is not only dependent on larval production but in most cases also to a very large degree upon survival through the first winter (Vilhjálmsson 1988). For a successful propagation, the Icelandic stock depends on early spawning producing large larvae in good physical condition in autumn. This can only be obtained through spawning in the relatively warm Atlantic waters at the south and west coasts of Iceland already in March. In that way the larval capelin is able to make use of the following spring and summer food supply. The southern and western parts of the Icelandic coastline are, however, almost entirely open to the heavy winter surf. In order to lessen mechanical damage to the spawning products, or simply to prevent them from being thrown high and dry, this in turn necessitates that most spawning takes place well below the low water mark. The spawning of capelin that takes place in the fjords and bays on the north and east coasts of Iceland later in the year, to some extent resembling the beach spawning habit, seems to contribute little to the total biomass of the Icelandic capelin stock.

Through time, the deep water spawning habit may have become genetically imprinted, making the propagation of the Icelandic and Barents Sea capelin stocks difficult under conditions resembling those found in other areas of capelin distribution. At present there is an ongoing genetic research for the purpose of seeking explanations for differences in various biological variables of capelin populations, occupying the Northwest Atlantic as well as other parts of the distribution area of the species. These studies of mitochondrial DNA (mtDNA) restriction fragment length

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polymorphism in capelin have clearly reflected a genetic separation of the bottom spawning Icelandic and Barents Sea capelin stocks from those of Labrador, Newfoundland, the Gulf of St. Lawrence and the Southeast Shoal, while no genetic heterogeneity was found among the latter group (Dodson *et al.* 1991). In fact, this research strongly indicates that the Northwest Atlantic capelin complex is comprised of groups of genetically similar beach spawners where it so happens that one of the spawning sites is presently at a depth of about 50 m. In that case there would seem to be little need for a relatively recent immigration from the Pacific to account for either of them.

In view of its range of distribution and variety of habitats, capelin have obviously been very successful in adapting to extremes in environmental conditions. The two different spawning modes are very striking examples of such an adaptation and the genetic studies by Dodson *et al.* (1991) suggest that the capelin populations, characteristic for the Northwest and Northeast Atlantic respectively, have been isolated from each other for a very long time. Due to the variety of capelin habitats and adaptations, the evolutionary aspect of capelin biology is most interesting. In the past, stock separation has been based mostly on the comparison of meristic and morphometric characteristics which are useful when determining the possible existence of local stock units and their rate of mixing, if any. Such data are, on the other hand, difficult to interpret in an evolutionary sense. The new methods of research, based on recently developed genetic techniques and knowledge of past geographic and climatological changes, might prove more informative regarding the ways in which the species developed and colonized the various ecological niches that capelin have occupied in the past as well as at present.

2.5. The general life history of capelin

Capelin spawn over a substrate of sand or gravel at depths that may range from zero (*i.e.* on the beach) down to 250 metres. However, even among populations spawning offshore, capelin spawning does in all probability mostly take place at depths not exceeding 100 metres (Sætre and Gjøsæter 1975; Thors 1981). About ⅓ of the capelin egg surface is covered by a thick coating

of glue-like material which becomes active when the egg is spawned and comes in contact with water. The glue-covered part is heavier than the rest of the eggs which ensures that they will stick to the particles composing the spawning bed substrate as the disturbance, caused by the spawning process or wave action, subsides (Friðgeirsson 1976).

It is reported that the preferred type of substrate may vary considerably from relatively fine sand or sandy gravel (grain size 0.1–4.0 mm) to coarse sand, gravel or pebbles (0.5–15.0 mm). As a rule, areas containing only mud or very fine sand seem to be avoided (Templeman 1948; Pitt 1958a; Sætre and Gjøsæter 1975; Thors 1981). Thors found that capelin spawning at Iceland and on the Southeast Shoal of the Grand Bank used similar types of substrate which was much finer than that apparently preferred by the Barents Sea capelin and those stocks spawning on beaches of the coasts of Newfoundland (Templeman 1948; Sætre and Gjøsæter 1975). Templeman suggested that within the observed range the apparent variations in the choice of substrate type for spawning may be governed by availability rather than anything else. However, recent studies indicate that the preferred grain size of the spawning substrate in the Newfoundland region is about 2 mm and the range of grain size is much narrower than previously thought (Nakashima and Taggart 1987).

Capelin are known to spawn within a wide range of temperatures or from as low as 0–2°C to as high as 10–12°C. The preferred temperature range, however, is probably narrower, or between 3° and 10°C. Temperature conditions may, nevertheless, be quite specific for each stock or group of stocks (Templeman 1948; Pitt 1958a; Vilhjálmsson 1968; Winters 1969; Bakke and Bjørke 1973; Sætre and Gjøsæter 1975; Frank and Leggett 1981; Thors 1981; Velikanov 1984; Pahlke 1985; Carscadden *et al.* 1988, 1989). When spawned on beaches, capelin eggs may become exposed and as a result be subjected to large fluctuations in temperatures. Davenport and Steene (1986) found that the eggs of the beach spawning capelin of the Balsfjord in northern Norway could survive at least to −5°C for likely periods of tidal exposure and were extremely euryhaline, developing and thriving in salinities between 3.4 and 34‰. Furthermore, Davenport (1989) has shown that the same holds
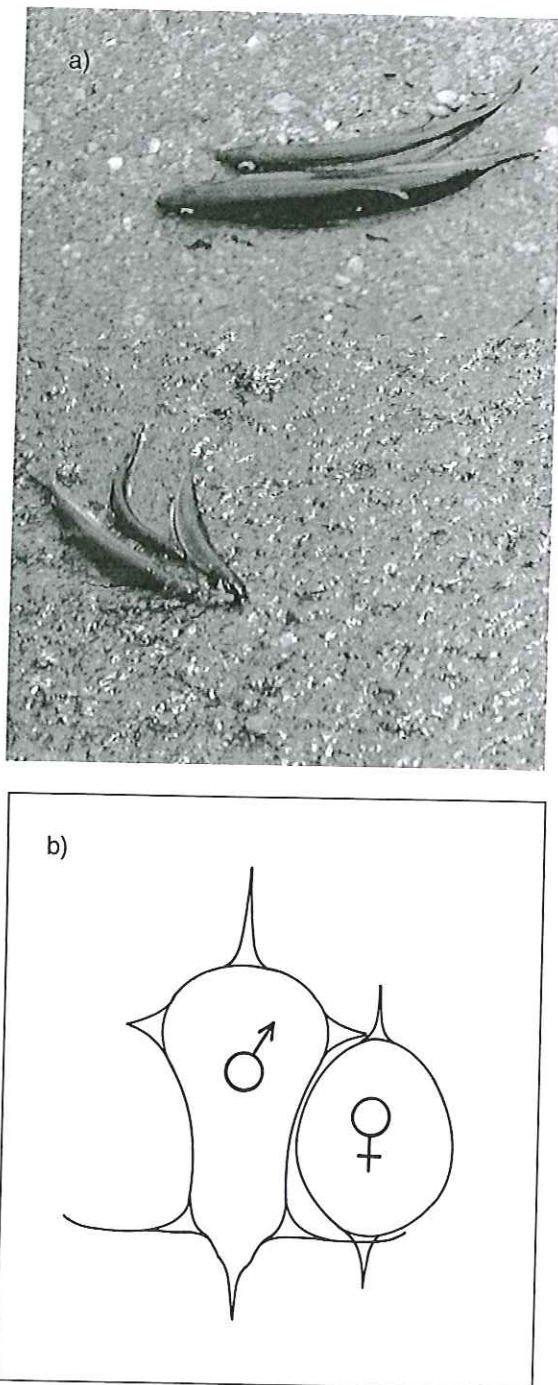
Figure 2.5. a) Female and male capelin (upper half) and a female with two attending males (lower half), spawning on a Newfoundland beach. b) A cross-section of male and female capelin in the spawning act, showing the special adaptations of the male body to ensure contact between the sexes during spawning. – Photo: H. Vilhjálmsson.

true for the Icelandic stock although the eggs of those capelin do not, as a rule, become exposed.

The act of spawning is very similar whether performed on the beach or at depth (cf. Templeman 1948; Friðgeirsson 1976). It is carried out in pairs or by three individuals where two males attend to the female (Fig. 2.5a). The execution is quite violent in that the capelin wriggle at a very fast tempo along the substrate whirling up grains of sand and small pebbles and spreading roe and milt over them. As indicated in Figure 2.5b, the spawning ridges on the males as well as the enlarged and upturned pelvic and pectoral fins are instrumental in keeping the fish together and thus ensuring fertilization of the eggs. The enlarged male anal fin serves to disturb the uppermost layer of the substrate and disperse the spawning products. Whether spawned on the beach or demersally at depths, the sticky eggs of the capelin adhere to the substrate or to other eggs and remain in place during incubation (Figure 2.6). The length of the incubation period varies with temperture within the extremes of 55 days at 0°C to 9 days at 12°C (Winters 1969).

Frank and Leggett (1981) have shown that for beach spawning sites on the beaches of eastern Newfoundland capelin larvae stay in the spawning substrate to emerge during periods of onshore winds. Since the late 1970s much research has been done on the early life history of beach-spawning capelin by personnel from McGill University, Montreal. For full details of this research, the reader is referred to a series of papers published mainly in Can. J. Fish. Aquat. Sci. and Mar. Ecol. Ser. beginning in the early 1980s. Thus Leggett et al. (1984) showed that for Newfoundland beach spawning capelin, larval survival is enhanced in years of frequent periods of onshore winds, apparently by ensuring good physical condition of the emerging larvae as well as favourable temperatures, food, drift and possibly reduced predation during their subsequent development. Frank and Carscadden (1989) found that among the bottom spawning Southeast Shoal capelin population, the size of larval cohorts also correlated positively with periods of strong winds and vertical mixing. No such mechanism has been demonstrated for the bottom spawning stocks at Iceland or in the Barents Sea. In these last mentioned areas the larvae are assumed to float to the surface layers upon hatching, where they can subsist on the

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Figure 2.6. Capelin eggs adhering to a sandy substrate of a spawning site off northern Norway (from Sætre and Gjøsæter 1975). This substrate looks like that found at the most important spawning sites at South and West Iceland.

nutrition in the yolk sac for about a week to ten days without external food supply (Friðgeirsson 1976).

The size at hatching is given by Pozdnjakov (quoted by Friðgeirsson 1976) to lie between 4.8 and 7.5 mm. The yolk sac will last for 8–10 days and failure to find suitable food before the end of that period will result in mass mortalities, while partial success will somewhat prolong the yolk sac period (Friðgeirsson 1976). Once in the surface waters, the capelin larvae may be said to be at the mercy of ocean currents and will gradually drift to their nursery areas. However, the larvae exhibit a diurnal, vertical migration pattern which may influence their drift path (Bailey *et al.* 1977; Fortier and Leggett 1983; Frank and Carscadden 1989). This mechanism is probably more effective in lower latitudes where such migrations seem to be more pronounced in summer due to larger differences in light intensity than farther north. It has also been pointed out that diurnal vertical migration may reduce predation (Beltestad *et al.* 1975).

In the second year of their life the young capelin will start showing a migration pattern of their own which, at least in the case of the more migratory stocks, frequently is a miniature of that of the older age groups (Vilhjálmsson 1983). Migrations are undertaken in response to seasonal changes in the physical environment and/or in search of food as well as finding or homing in on spawning areas.

As their anatomy implies, capelin are mainly filter feeders thriving on planktonic organisms that are filtered out on the gill rakers. In most areas euphausiids constitute the bulk of the food by weight of adult capelin, while copepods, especially of the Calanus species, are more important in the diet of the juveniles. Capelin also feed on amphipods and a variety of other small planktonic invertebrates. Larval capelin feed mainly on eggs and young stages of the above mentioned species. In general, there is a pronounced size-related shift towards larger food items in the diet of capelin, occurring at metamorphosis, and again as they grow beyond 12–14 cm in length (*e.g.* Sæmundsson 1926; Prokhorov 1967, 1968; Vesin *et al.* 1981; Panashenko 1981, 1984; Sigurðsson and Ástthórsson 1991).

Feeding activity is highly seasonal but also marked by the biological peculiarities of individual stocks. In spring-spawning populations the feeding season is continuous, usually lasting from April/May to October/November. The accumulated energy is then used for growth as well as for tiding the fish over the winter and, in case of maturing fish, to develop sexual products. Among summer spawners the feeding season may be said to be divided by the spawning season

among that part of the spawning stock which survives to spawn again (Prokhorov 1960; Winters 1970; Campbell and Winters 1973; Chan and Carscadden 1976; Friis-Sørensen 1983, 1985). In winter as well as during the spawning season, capelin do not seem to search for food. Nevertheless, they will take food, sometimes in large quantities, when they happen to migrate through abundant areas, *e.g.* in overwintering stocks of euphausiids (Vilhjálmsson 1974, Naumenko 1989).

The rate of growth is generally very high in the first 2–3 years but slower after that. Thus, it is not uncommon to find 3-group capelin measuring on average 18–20 g in weight, having grown at the rate of several hundred percent each year. The weight increment in the fourth year is normally much less and seldom exceeds 50%. In the case of second time or multiple spawners the growth rate tends to become much reduced (Friis-Sørensen 1985). It should be noted, however, that growth rates vary considerably between stocks as well as within areas inhabited by the same stock (*e.g.* Vilhjálmsson 1974; Winters 1982) and are dependent upon variations in the physical environment, food supply as well as the age and/or length at which maturity is reached.

Among the Atlantic capelin sexual maturity is usually reached in the third year with spawning taking place at the end of it. Depending on available food, temperature and other growth conditions, a varying proportion of each year class does not, however, mature to spawn until at the age of four or even five years and, consequently, the spawning population counts at least two year classes. A common age composition in the spawning part of the Icelandic capelin stock is 75% 3 year old and 25% 4 year old fish (Vilhjálmsson 1983) and similarly for the Gulf of St. Lawrence (Bailey *et al.* 1977). Among the Newfoundland/Labrador capelin stocks as well as among the Barents Sea stock, until its collapse in the mid-1980s, the contribution of 3 year old spawners generally amounts to less than 50% while age group 4 usually is the most prominent with 5 year olds as important contributors in some years (Carscadden 1978, 1984; Hamre 1985). In later years, however, age group 3 has been the most important contributor to the spawning stock of the Barents Sea capelin. In some of the West-Greenland populations 6 or even 7 year old fish may make important contributions to the spawning biomass (Kanneworff 1967, 1968; Friis-Sørensen 1985; Kleist 1988). The predominant year classes among Alaskan Pacific capelin spawners are, on the other hand, reported to be 2 and 3 year old fish (Pahlke 1985) and the same is true for the Balsfjord capelin in northern Norway (Friis-Sørensen 1983).

It has long been recognized that following spawning the capelin suffer mass mortality. That there may be some survival of spawners has, nevertheless, long been accepted but found difficult to quantify (*e.g.* Vilhjálmsson 1968). In present models of the exploitation of the capelin stocks in the Barents Sea and in the Iceland-East Greenland-Jan Mayen area it is assumed that only a small fraction survives to spawn again and, furthermore, that for all practical purposes the spawning mortality is total (Vilhjálmsson 1983; Tjelmeland 1985). On the other hand, several authors have shown that spawning survival may be of considerable importance for the propagation of other capelin stocks. Winters (1974) claimed to have observed spawning checks in otoliths from Newfoundland capelin, and a survival rate of about 25%, 18% and 9% among spawners of age groups 3, 4 and 5 respectively has been calculated and was incorporated in projections of stock abundance for the Newfoundland-Labrador capelin (Carscadden *et al.* 1985). Recently, Shacknell *et al.* (1993) have estimated age- and sex-specific survival rates in the northern Grand Bank capelin population using data from annual acoustic/trawl research surveys from 1982–1990. From these data it was concluded that the average annual contribution of surviving mature females to the total number of female spawners was in the range of 24–47%. The male spawning survival ratio appeared to be much lower, especially among the older age groups. However, Nakashima (1992) reported the return of several tags one year after tagging. These were mature fish on the spawning grounds when they were tagged, and they were recaptured on the spawning grounds one year later. Interestingly, about one half of the returned tags derived from surviving males.

Kanneworff (1967) suggested that female capelin at West-Greenland might spawn up to four times. This was corroborated by Friis-Sørensen's (1985) observation of more numerous age groups in the female part of the spawning population than in the male one. Winters (1971) supplied

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evidence of repeated spawning checks in female capelin otoliths from the Newfoundland area and. Kleist (1988) has observed spawning checks in otoliths from numerous female capelin at Greenland. Kleist also maintained that for mature capelin from the West-Greenland area it is fairly easy for an experienced worker to determine from which sex an otolith has been taken. And Forberg (1984) believed that multiple spawners may represent up to 50% of the female half of the spawning stock of the secluded Balsfjord capelin population in northern Norway.

It seems, in other words, to be the general consensus that spawning survival applies mostly if not only to females. This is explained both by the female usually becoming spent in one run while the male may repeat his overtures several times, as well as by the fact that the male is the much larger and more active partner (Templeman 1948; Friðgeirsson 1976). In consequence, the larger male capelin become much the worse for wear during spawning and tend to die of the lacerations they receive when wriggling along the substrate in the process, while the smaller females do not come in such direct contact with the spawning substrate. Males also stay longer near to beaches where surf may consequently do them more damage than the females which tend to leave the spawning site if they can. Dead males are indeed always more numerous than females on or near spawning sites, both beaches and at depth (Templeman 1948; Bakke and Bjørke 1973). Furthermore, masses of dead capelin, particularly males, are frequently reported in trawl catches of demersal species off the south and west coasts of Iceland in April and May (Vilhjálmsson 1983).

Capelin are an extremely important item in the diet of many species of fish, marine mammals and sea birds. The most important single predator in the North Atlantic seems, however, to be the cod. Thus, Campbell and Winters (1973) made a rough calculation of capelin removal by some of the more important predator species, both fish, mammals and birds, in the area east of Newfoundland and Labrador. Their conclusion was that some 2.2–3.7 million tonnes of capelin were probably removed annually by predators, ⅔ of which they attributed to the cod alone. This calculation was updated by Carscadden and Winters (1978) with similar results. A later study

(Akenhead *et al.* 1982) produced further corroborative evidence to the same effect.

The high ranking of capelin in the food of cod has been demonstrated for the Barents Sea and Icelandic waters as well as the Newfoundland and Labrador areas. In all cases capelin was found to represent about ⅓ of the cod's total food intake by volume on an annual basis (Akenhead *et al.* 1982; Pálsson 1983; Mehl 1987). Seasonally, in the months preceding and during the spawning of the capelin, they have been found to rank much higher on the menu of the cod, and on a monthly basis capelin may at times practically constitute the sole item of forage (Akenhead *et al.* 1982; Pálsson 1983; Mehl 1987; Lilly 1989). All recent studies indicate an even more vital role of capelin in the diet of cod than indicated by their percentage contribution alone. Thus, during periods of low capelin abundance, cod are only able to compensate in part (30% according to Magnússon and Pálsson 1989) for the loss of capelin by feeding more intensely on other prey (Mehl 1987; Lilly 1989; Magnússon and Pálsson 1989; 1989a).

Apart from the cod, capelin are the mainstay of the diet of many other fish species. As an example, capelin have been found to account for 45–100% of the food of adult salmon, depending on size, in Newfoundland waters where they are also preyed heavily upon by Greenland halibut and American plaice (Lear 1969, 1972; Pitt 1973). Furthermore, Bowering and Lilly (1992) found that off southern Labrador and northeastern Newfoundland, medium sized Greenland halibut preyed primarily on capelin, and a recent study in north Icelandic waters indicates that in the summer months between 30% and 70% by weight of the food of Greenland halibut may consist of capelin (Skúladóttir and Jónsson 1991). The extensive predation by haddock upon capelin eggs among those stocks spawning demersally at depths is also well known (Templeman 1968; Sætre and Gjøsæter 1975). And smaller fish, such as herring, may at times feed intensely on capelin larvae (Templeman 1948; Magnússon 1966; Hamre 1988, 1989).

Whales and seals are also known to follow and feed upon capelin schools. Thus, Sergeant (1973) estimated that at least 25% of the diet of Newfoundland and Labrador harp seals consisted of capelin, and Whitehead and Carscadden (1985) found that the abundance of humpback and fin-

back whales on the northeast coast of Newfoundland could be predicted at least 1 year in advance using knowledge of variations in year class strength of capelin. And in the Icelandic area, humpback whales have been observed following both the feeding and spawning migrations of capelin in such numbers that fishing operations became difficult and often resulted in severe gear damage when one or more humpbacks made their escape through the nets. Finally, numerous species of sea birds may obviously take their toll, especially from the younger stages of capelin and in the capelin spawning season. Thus, Brown and Nettleship (1984) estimated the annual capelin consumption by all seabirds in Newfoundland waters to be about 250 thous. tonnes and of the same order of magnitude as that consumed by seals and whales.

Capelin in the North Atlantic are hosts to helminth parasites of various descriptions. An investigation of the possible use of parasites in capelin stock identification demonstrated considerable differences in infestation rates by areas but added little to existing means of stock separation (Pálsson 1982, 1986; Pálsson and Beverley-Burton 1983, 1984). These studies did, however, reveal a much wider parasitic fauna than previously described. Thus, three species of gyrodactilid monogeneans were found on the gills of capelin, all new geographic records for Newfoundland and Icelandic waters. Of the three digenean species recorded, two were new host records and one seemed to be absent in the Barents Sea capelin and rare at Iceland. Mature specimen of one cestode species were found in limited numbers in capelin from Newfoundland waters and the Barents Sea, but not at Iceland.

It has long been known that capelin are also hosts to larval nematodes (cf. Templeman 1948,

1968; Winters 1967a). Pálsson's (1982) study identified three species, *Anisakis simplex, Contracaecum* species and *Thynnascaris adunca*. Considering the present market for fresh capelin, the first of these is of particular interest because of its potential to infect man and cause the so-called herring-worm disease. These nematodes are either found in the body cavity or on the viscera. The frequency of infestation seems to be higher among males than females and on the whole much higher for *Contracaecum* (about 30%) than *Anisakis* or *Thynnascaris* (around 9% each).

2.6. Common names

In the English language the species *Mallotus villosus* may originally have been referred to as *capeling* (Jangaard 1974). Nowadays it is always called *capelin* with the exception that in Newfoundland it used to be, and sometimes still is, spelled *caplin* with the letter e missing (Templemann 1948). The pronounciation, however, is the same. The French and Spanish version is *capelan*.

In Norwegian the capelin is called *lodde*. It is *lodda* in Swedish, *loðna* in Icelandic and *loðnasíld* in Faroese. In German and Dutch capelin are also called lodde, perhaps not surprisingly, considering the relation to Scandinavian languages and close trade ties of old. In all of these languages the meaning is the same as that of *villosus, i.e.* hairy.

In Russian the capelin is known as *mojva* but in the far east of Siberia they are called *uyok* (Prokhorov 1967). In Japanese capelin is *karafuto shisamo* and in Finnish *villakoure* (Jangaard 1974). As mentioned in a previous section the Greenlandic Innuit word for capelin is *ammasat* (Friis-Sørensen 1985).

3. HISTORIC RECORDS OF CAPELIN AT ICELAND

Contrary to the case of many other marine fish, mammals and sea birds, records of capelin at Iceland are both few and far between in centuries past. This is all the more surprising since capelin are both common and, in the spawning season, conspicuous in Icelandic waters. They should, moreover, have been a godsend to hungry people in times of need that all too often overtook much of the populace of the island in the fifteenth to nineteenth centuries.

There exist fairly comprehensive records for the time period 1400–1800. This is the so-called Íslenskir Annálar (Icelandic Annals), compiled by many authors. These annals contain not only "noteworthy" events such as the comings and goings of kings, lensmen, prelates and other dignitaries in Iceland and elsewhere in Europe, the marital exercises, partying and scandals pertaining mainly to the same but also records of the brighter and darker sides of the life of ordinary people in the country. The annals thus contain numerous references to major periods of famine as well as descriptions of how people's plights often were relieved by stranded whales, seals suddenly becoming available with the appearance of drift ice or by cod and other fish being washed ashore in storms.

Although the Icelandic capelin as a rule do not spawn on the beach as is common in many other localities, which worldwide seems indeed to be the rule rather than the exception, they are sometimes washed ashore at Iceland during the spawning season, even in large quantities. There are many records of this happening on the south coast in the last 150 years or so, when they were collected and happily consumed by man and livestock (Sæmundsson 1926; Kristjánsson 1980, 1985). It is almost inconceivable that similar occurrences did not take place in the period covered by the "Annals" and in times of famine, frequent as they were. Yet, capelin is mentioned only once where it is stated that much "herring" was washed ashore in Hrútafjörður on the western north coast in 1684. This "herring", it is said, was collected by many but "found bad for eating but good for oil". Although the name given for the fish in the old annals is somewhat ambiguous, there seems little doubt that this must have been capelin.

In other literature capelin is first mentioned in 1638 as loðnusýl (the hairy little fish) by bishop Gísli Oddsson in his work on the wonders of Iceland, *De Mirabilibus Islandiae*. Two years later (1640) Jón Guðmundsson, called the learned by his contemporaries, registered capelin in his "Natural History of Iceland" (Ein stutt undirrietting um Islands aðskiljanlegu náttúrur) under the name of loðnusijlld (hairy herring) and describing it as "short and thick and having a hairy ridge along the back . . . shaped as fingerling cod but somewhat longer".

In 1737 an Icelander by the name of Jón Ólafsson wrote his *Icthyographia Islandica,* a treatise on Icelandic fishes. Ólafsson was well educated by the standards of his time and the country of origin. Although he obviously repeated much uncritically after "sensible persons" and in spite of the fact that his writings were interspersed with myths and superstitions, Ólafsson's descriptions are much better than those of any of his predecessors, and he obviously made an effort to investigate for himself when possible. Thus, he gives a good description of capelin under the name loðnusíld (hairy herring).

However, true to his research methods that probably were commonly accepted in his day and age, Ólafsson also gives a description of a peculiar fish species that must have originated from descriptions by "sensible persons" and undoubtedly refers to male capelin. In Ólafssons *Ichthyographia* this description is contained under the section heading "On inedible trouts" and translates roughly as follows:

"The 'hairy trout' comes in different sizes as other trouts, but does not normally become larger than a small trout of the usual type and as a rule not larger than a man's finger; but it is narrower in the tail and thicker at the front than other trouts. The head is shorter and broader, broadest in the region of the cranium but behind that the fish tapers and tapers again towards the tail. The eyes are fairly large and inside the head, the skull behind them round as in a seal or king fish. The snout is short and broad and the lower jaw protrudes, the mouth is broad and the gullet wide; teeth as in the cod, continuous and many; in colour almost black all over. The hairs are invisible unless it is dead and yet not visible except while it is in the water and not on land; these hairs are white, in nature as eiderdown, but when the fish is taken out of the water they will fold along the skin and can not be seen; they cover all of it except the tail fin. The dorsal fin is lower than on normal trout and the adipose fin resembles a small wart. The hairy trout is thought inedible to any beast."

Although Ólafsson names his subject "hairy trout" there seems little doubt that he is describing the male capelin, which probably was commonly known as "hairy herring" at the time. With regard to the distinctive external features of male capelin the above description is in fact quite accurate. Otherwise, the description bears an amusing witness to Ólafsson's research methods which, as well as incorporating a good deal of the superstitions of his time, depended to a large degree on corroborative evidence of "sensible persons" that at the time was considered the equivalent of proof. In fact, one can not but wonder if in and before Ólafsson's time it may not have been generally believed to be outright dangerous to eat the male capelin, at least if it was found in or near river mouths or lagoons where it would probably have been recognized as a trout and yet obviously did not belong to any of the usual and edible types (Vilhjálmsson 1982b).

In the middle of the eighteenth century the Danish Science Society commisioned a lawyer by the name of Niels Horrebow to carry out research on the natural history of Iceland or to be *"scrutator rerum curiosarum"*, an observer of curiosities, as it was called. Horrebow was a lawyer by education and said to be well versed in other matters as well, whatever that may have meant. He had at any rate managed to mishandle his finances in such a way that he was available for investigating the curiosities of that frightful part of the Danish kingdom called Iceland, as the the general concencus seems to have had it in those years.

Horrebow came to Iceland in 1749 and returned to Denmark in 1751. He managed to cover a surprisingly wide ground in such a short space of time and wrote a report, "Tilforladelige Efterrettninger om Island" (Incidental Reports on Iceland), which was published in Copenhagen in 1752. Horrebow has left an excellent and a very picturesque description of the dramatic approach of the spawning migrations of the capelin which, according to him, are called loðsíld (hairy herring) by the natives. He described how this "herring" is pursued by the cod and the whales, sometimes until the latter get stranded and suffocate on the beach. He then finished his description as follows:

"It is a most interesting sight, which I have often seen, when schools of these small herrings approach the land in unbelievable numbers and the sea birds gather over them in the thousands and dive like arrows from the air upon the herring. When the birds dive into the sea the water splashes high into the air. They pursue the herring schools for long periods of time until the fish migrate into fjords and coves where they are completely at the mercy of the birds."

Horrebow stated quite categorically that Icelanders do not take capelin. He did not, however, mention any superstitions concerning their edibility but suggested that the reason was the complete lack of suitable fishing gear.

It was not until in the latter half of the eighteenth century that scientifically trained observers started to investigate the Icelandic marine fauna. The pioneer of these was the Icelander Eggert Ólafsson who, together with the physician Bjarni Pálsson, travelled the country extensively in the 1760s. The results of their observations were contained in Ólafsson's voluminous report Reise igiennem Island (A Journey through Iceland) published in 1772. Unfortunately, the fishes recorded are not treated in a systematic

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way but simply mentioned in descriptions of the different regions. On capelin Ólafsson and Pálsson reported that it is not eaten except in Eyjafjörður on the north coast where the inhabitants collect it on the beach, salt it in containers and keep it for later use. They noted that capelin also occur at the south coast but do not indicate whether any use is made of it there.

In the period 1775–1777 Ólafur "the secretary" Olavius studied the fish fauna of Iceland from an economic point of view. In his comprehensive report from 1777, "Ökonomisk Reise" (Economic Travels), he barely mentioned capelin. Earlier (1771) Olavius had, however, won a competition with an essay, "Avhandling om de Islanske Fiskerier", a treatise on the Icelandic fisheries, where he wrote on capelin as follows:

> "*Clupea vulgaris,* which Icelanders call loðna (the hairy) is worthy of much more attention although it is seldom fished except in Eyjafjord (central north coast) and Reydarfjörður (on the east coast) when the schools are so dense that it is possible to scoop the fish up in barrels and troughs. This happens mostly between Saint John Baptist Day (24 June) and Michaelmas (29 September)."

Jón Eiríksson, an Icelandic government employee in Copenhagen, wrote an essay on the fishing and curing of salmon, herrings and other seafood at Iceland which was published in 1782. Eiríksson stated that capelin are plentiful in many of the Icelandic fjords and that he himself remembers them running ashore in Hornafjörður on the southeast coast when he was young. At that time, Eiríksson states, the capelin had been lying almost 12 inches thick on the beach as far as the eye could see. He further goes on to state that many travellers in Iceland had reported similar occurrences in fjords elsewhere along the coast, especially in Eyjafjörður in the north. Finally, Eiríksson stated that to his knowledge capelin are only occasionally eaten in Iceland, where they are cooked when fresh, mostly in Eyjafjörður on the north coast.

Although several naturalists as well as other investigators studied the fish fauna at Iceland, both in the field as well as in museums in the next 100 years or so, their work revolved mainly around records and taxonomic descriptions of species. In that period little if any progress was made in learning about the ways of the capelin. At the time it was, however, certainly realized how important an item the capelin was in the diet of many birds and marine animals, not to mention such "favourite" fish as the cod, which in Iceland has long been the only fish species enjoying the distinction of being referred to as fiskur (fish) rather than being called by its proper name.

But from records of occupations and eating habits in Iceland in the nineteenth century (Kristjánsson 1980, 1985) it is clear that in many locations on the coast the population had by that time begun to make some use of capelin in order to supplement their meagre diet as well as for animal fodder and sometimes for bait or even as fertilizer.

4. RECORDS AND RESEARCH IN THE 1890–1965 PERIOD

It was not until in the 1890s that fisheries research in the Icelandic area took on new dimensions. In order to study the fish fauna the Danish government began sending students to Iceland on board patrol vessels and fishing boats in the summer. Soon thereafter Denmark joined the International Council for the Exploration of the Sea (ICES), and in that connection a small trawler, the *Thor,* was fitted out for research purposes in 1903 (Jónsson 1988). Since then it may be said that research vessels have operated in the Icelandic area on a regular basis.

As far as the capelin is concerned it was, however, only around the turn of the last century that real headway was made in learning about its specific ways of life. This came about through the works of Bjarni Sæmundsson, the first Icelandic fisheries scientist, as well as those of the Danish scientist Paul Jespersen. In spite of becoming the government's special advisor on marine resources, Sæmundsson was obliged to teach at the local grammar school in Reykjavík, to earn his living. Consequently, he could pursue his biological observations, which indeed did not only concern the marine environment, only during his summer vacations and other spare moments. In the first two decades of the 20th century these two scientists pieced together the main features of the life history of the capelin around Iceland, Jespersen concerning himself with the first year of its life and Sæmundsson studying the older age groups.

During several research cruises on the *Thor* in the spring and summer of 1904 and 1905, a fairly comprehensive sampling of larval and post larval stages of fish around Iceland was carried out. Considering the facilities at the time, this study was surprisingly detailed and complete. The collections, together with hydrographic data gathered at that time as well as later, enabled Jespersen to descibe correctly the progress of capelin spawning at the coasts of Iceland and the reasons for it (Jespersen 1920).

In short, Jespersen's findings were that spawning begins in the warmer waters (about 6°C) at the south and southwest coasts of Iceland in April, at the north coast in June (May), off the east coast in July (June) and may extend over several months, especially in the south. Jespersen stated that the reasons for this time difference are that the cold winter water in the northern and eastern areas (about 1.5°C) is gradually warmed up in a clockwise direction during the months of May, June and July. He described how the smallest larvae are always found in shallow waters, the size increasing with water depth or distance from the shore. Jespersen further commented on the apparently enormous size of the parent stock but found its sporadic occurrence very curious. However, the irregular appearences of capelin Jespersen related quite correctly to varying migrational patterns of the spawners.

As a guest on most of the Thor cruises, during his numerous trips on fishing vessels as well as through interviews with residents of local fishing communities and by his research in the laboratory, Bjarni Sæmundsson managed to piece together the remainder of the life history of the Icelandic capelin. Apart from his annual reports to the government, which describe his activities and findings in a general way, Sæmundsson's findings on capelin appeared first in Danish in "Oversigt over Islands Fiske" (1909) which was an overview of Icelandic fishes within the 400 m isobath. A more extensive and detailed Icelandic version, Íslenskir fiskar (Icelandic Fishes) was published later (1926).

Apart from providing an excellent anatomic and morphological description as well as giving the taxonomic position of the capelin, Sæmundsson gave a good, but admittedly very general, outline of its life history in the area. Thus, he remarked on the seasonal distribution of age groups in relation to geography and environmental variables, mainly temperature, as well as spawning times, areas and substrate,

where he of course had corroborative evidence supplied by his Danish colleague. He noted the spawning mortality of capelin, the main items of their diet and gave a rough outline of their growth. In addition, he most vividly described the obvious importance of capelin in the food chain of the sea. Like Jespersen, Sæmundsson stressed the large variations in capelin migrations which he apparently believed to be due to changes in food supply or in the general environment rather than changes in the abundance of the fish themselves. That capelin are abundant he did not leave in doubt but categorically stated that the pre-spawning schools "may reach across tens of kilometers in length" which in fact is quite correct.

During the first decates of this century and in particular in the 1920s a marked rise in sea surface temperatures was observed in large parts of the North Atlantic culminating in the mid-thirties. In the Icelandic area this anomaly was most pronounced off the northeast and east coasts (Stefánsson 1954). In this period Sæmundsson (1934) noted that capelin became scarce or totally absent on their main spawning grounds at South and Southwest Iceland while spawning migrations increased in the north and east and arrived earlier than before. A similar northward displacement was also noted at West-Greenland in this period (Hansen and Hermann 1953).

In his capelin studies Sæmundsson never succeeded in determining the age, neither from otoliths nor from scales or bones. In using the length distribution of samples collected at the same time of the year Sæmundsson saw but three distinct humps which led him to conclude that the Icelandic capelin only grew to three years of age. In comparing the overall length distribution to that of the spawning population Sæmundsson further concluded that the spawning stock consisted of one year class only, namely fish in their third year, which would then spawn and die at three years of age.

It was left to Sæmundsson's successor Árni Friðriksson to find that the age of the Icelandic capelin could easily be read from otoliths and to ascertain that although the maturing population consisted chiefly of three year olds, two and four year olds did also contribute to some extent. This discovery led Friðriksson to believe that in spite of the obvious mass mortality at spawning, a considerable number would survive to spawn in the following year (Friðriksson 1943).

In the 1950s and 1960s a large number of herring search surveys were carried out in the area around Iceland. The work included frequent sampling of plankton in the uppermost 50 m of the water column, both with Hensen nets and high speed samplers. In 1966 Mrs. J.V. Magnússon of the Marine Research Institute in Reykjavík published her work on capelin larvae that had been collected with high speed samplers in the months of May–September in the five year period 1960–1964.

The main points of Magnússon's (1966, 1968) findings were similar to Jespersen's (1920) earlier conclusions: As time advances in May and June and the sea temperature rises, spawning takes place in progressively more northerly areas. Magnússon also found that the overall abundance of larvae as well as the extent of their distribution correlated positively with temperature and that the size increased with distance from the shore. However, during the 1960–1964 period little spawning of capelin seemed to take place east of the central north coast of Iceland. Magnússon was aware of the limitations imposed on her interpretation by the data being collected for other purposes than to study the distribution and dispersion of capelin larvae. In retrospect, it seems that these data on the average size at age (month) became somewhat skewed in the latter half of summer due to the fact that the samplers which were used did not catch the larger capelin fry in the same proportions as the smaller individuals.

5. RESEARCH EFFORT IN THE 1966–1993 PERIOD

After some initial experimentation with gear and methods of processing (Thorbjarnarson 1961), a large scale capelin fishery for meal and oil was started on the spawning grounds at Southwest Iceland in 1965. Concurrent with this, a programme was set up for systematically sampling the commercial, and later research vessel catches and has continued since then. Shortly afterwards, a search system was initiated to study capelin migrations and thus assist the fishing fleet during the then short winter season (February/April). This kind of work was soon extended to cover the migrations in January and February from the wintering areas north of Iceland along the east coast to the spawning grounds at the south coast. It resulted in the winter season beginning in January as of 1972.

The early 1970s saw occasional capelin cruises for studying migrations and behaviour in feeding areas off North and Northwest Iceland in summer, autumn and early winter. A special survey to monitor the relative distribution and abundance of 0-group fish (including capelin) has continued in the month of August since 1970. In the mid 1970s there began a summer and autumn fishery which quickly became a success and was based on migrations of feeding capelin and later in the year on overwintering concentrations. This fishery soon took on international dimensions being pursued by vessels from Iceland, Norway, the Faroes, Denmark and even Britain in a large oceanic area, the Iceland Sea, delimited roughly by Iceland in the south, the east coast of Greenland in the west and the island of Jan Mayen and the Jan Mayen Ridge in the north and east.

Since 1978 the size of the fishable stock has been assessed by acoustic methods with surveys in autumn and winter, which in part were conducted in cooperation between Iceland and Norway. Similar surveys have been carried out for immature capelin in the month of August as well as in mid-winter when possible. Capelin have been tagged in order to record migrations, abundance and other projects of lesser dimensions have been undertaken for various purposes.

In addition, the marine environment around Iceland and of the Iceland Sea (cf. Fig. 6.1) has been monitored regularly for much of the 1966–1992 period. This is done both to record physical characteristics (temperature and salinity) as well as species composition and density of planktonic organisms.

All the data from the 1966–1993 period, whether gathered directly through research or from the fishery, have added greatly to our knowledge and understanding of the stock of capelin native to this area. As stated before, much has been written on these data sets in the form of progress reports or papers on specific topics. The following sections contain a review of the existing literature and an analysis as well as an evaluation of the present state of knowledge about the biology, abundance and exploitation of the Icelandic capelin stock.

SCOTLAND

FAROES

NORWEGIAN SEA

JAN MAYEN RIDGE

JAN MAYEN

ICELAND SEA

KOLBEINSEY RIDGE

ICELAND-GREENLAND CHANNEL

SCORESBY SOUND

GREENLAND

ICELAND-GREENLAND RIDGE

FAROE-ICELAND RIDGE

ICELAND

ICELAND BASIN

REYKJANES RIDGE

IRMINGER SEA
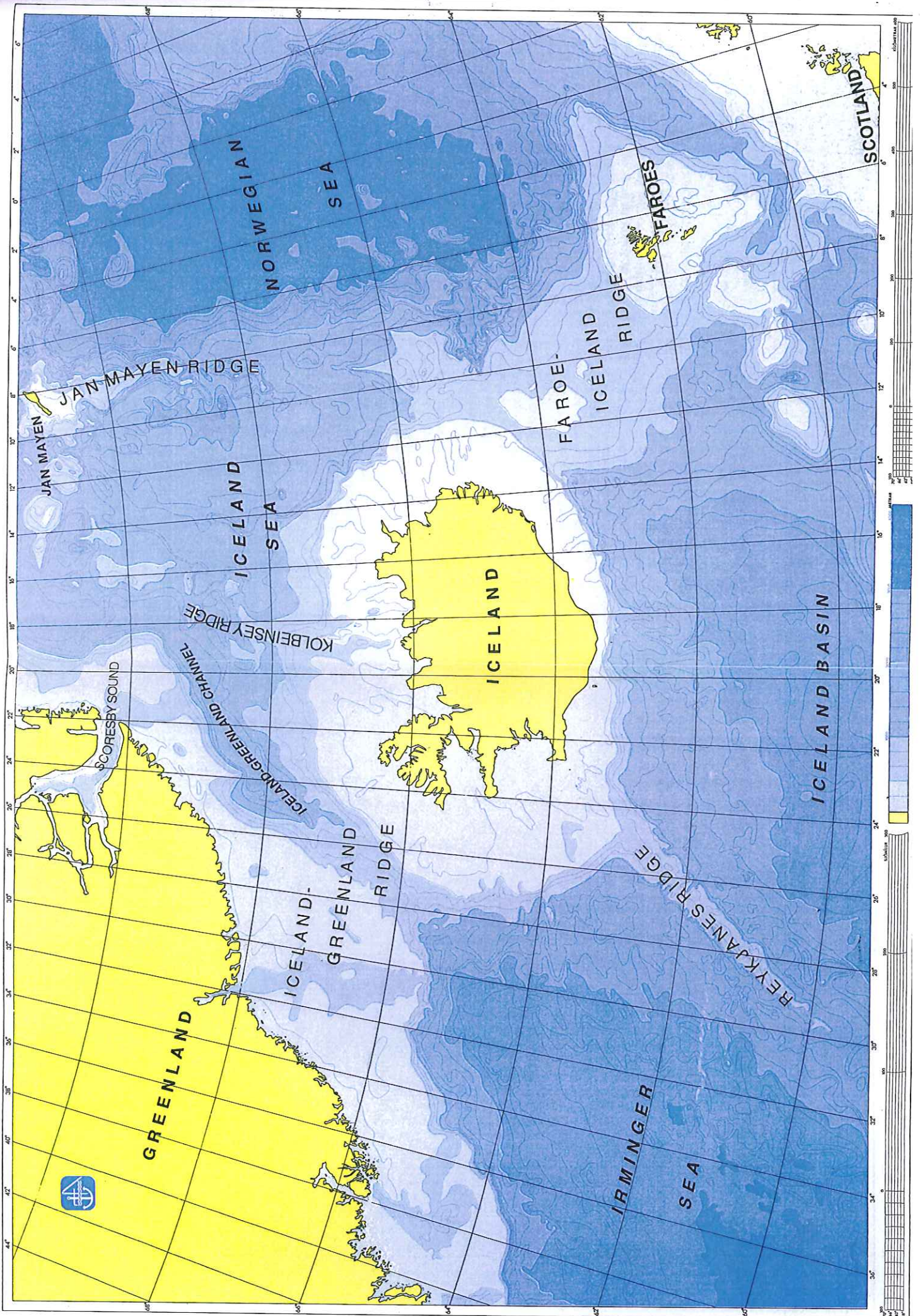
6. THE ENVIRONMENTAL CONDITIONS OF ICELANDIC WATERS

In this section a brief account will be given of the physical environment, nutrients, primary and secondary production of the waters surrounding Iceland as well as of the Iceland Sea. This description is essential since physical characteristics of the marine environment largely affect the general distribution, migrations and general biology of the capelin.

6.1. Bottom topography

Iceland rises from the crest of the Mid-Atlantic Ridge and is also a part of the system of transversal ridges extending from Scotland through the Faroes to Greenland (Fig. 6.1). The saddle depth of the Iceland-Greenland Ridge is about 600 metres, some 70 naut. miles off Northwest Iceland. On most parts of the ridge, however, depths range between 300 and 400 metres. On the Faroe-Iceland Ridge depths range mostly between 400 and 500 metres. These transversal ridges play an important role oceanographically, since they separate the relatively warm waters of the Northeast Atlantic from the cold arctic deep waters of the Iceland and the Norwegian Seas.

South of Iceland lies a deep basin, generally known as the Iceland Basin. In the west it is separated from the Irminger Sea by the Reykjanes Ridge, which is a part of the Mid-Atlantic Ridge, and in the east from the Norwegian Sea by the Faroe-Iceland Ridge.

The outer boundary of the continental shelf surrounding Iceland roughly follows the 400 m depth contour. The shelf is narrowest off the south coast where in places it extends only a few miles out. From there the continental slope descends steeply to depths exceeding 1500 metres.

◊ Figure 6.1. An overview of the topography of the sea area between the Faeroes, Iceland, East-Greenland and the island of Jan Mayen.

Off the west, north and east coasts, however, the shelf is relatively broad and generally extends for 60–90 naut. miles out from the coast. Cutting across the shelf are a number of submarine valleys or channels which generally are direct continuations of bays and fjords while the elevations between them lead off from mountain ridges and promontories on land. Off the northeast coast of Iceland there are steep descents but slightly farther to the south a relatively shallow area extends to the east and northeast. Still farther south the shelf area broadens and eventually connects to the Faroe-Iceland Ridge.

The width of the East-Greenland continental shelf is similar to that of the Icelandic submarine terrace. In the region of Scoresby Sound it is about 70 naut. miles wide with reference to the 400 m isobath, but appreciably narrower farther south. The most dominant features of the East-Greenland shelf are the large troughs extending out from the shoreline, believed to be erosional scars produced by the advancing glaciers coming down from the Greenland ice cap (Perry 1986). From the greatest depth of the Iceland-Greenland Ridge a channel or narrow basin extends towards the northeast between the continental shelves of Greenland and Iceland. This channel, the Iceland-Greenland Channel, widens somewhat as it continues to the north, west of the Kolbeinsey Ridge. The floor of the channel lies at depths between 1000 and 1500 metres.

Two submarine ridges extend south from the island of Jan Mayen. One is the Kolbeinsey Ridge just mentioned, which is a segment of the Mid-Atlantic Ridge. The second ridge is the Jan Mayen Ridge, extending due south from the island towards the continental shelf northeast of Iceland, and forming the eastern boundary of the Iceland Sea. A third ridge, the Mohn Ridge, extends to the northeast from Jan Mayen, separating the Greenland Sea from the Norwegian Sea

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(not shown in Fig. 6.1). In the central part of the Iceland Sea lies a basin between the continental terrace north of Iceland and the two ridges, the Kolbeinsey Ridge and the Jan Mayen Ridge, with depths ranging from 1500 to 2000 metres except for a small depression west of the Jan Mayen Ridge between 68°30′N and 69°30′N where depths exceed 2000 metres.

6.2. Water circulation

The main surface currents of the Iceland Sea and the waters southeast, south and west of Iceland are indicated in Figure 6.2 and described in the following text.

The south and west coasts of Iceland are bathed by relatively warm and saline water transported by a branch of the North Atlantic Drift. The Atlantic water flows northwards on both sides of the Reykjanes Ridge and continues clockwise along the south and west coasts. The north flowing water in the eastern part of the Irminger Sea is referred to as the Irminger Current. At the Iceland-Greenland Ridge this current splits in two. The larger branch swings towards the west to form a cyclonic eddy in the Irminger Sea. The other branch, usually smaller, is referred to as the North-Atlantic Irminger Current. It rounds the northwest peninsula of Iceland (Vestfirðir) and continues eastwards along the north coast. The proportion of Atlantic water in this east flowing current decreases in the direction of flow. Its last traces may be found in the shelf area east of Iceland.

The East-Greenland Current transports polar water to the south along the east coast of Greenland and crosses the northwestern part of the Iceland-Greenland Ridge. Velocities of this current are relatively high on the Greenland shelf, but they seem to reach a maximum near the continental slope (Malmberg *et al.* 1972). The easternmost portion of the East-Greenland Current is diverted towards the southeast as the current approaches the north Icelandic submarine terrace. This branch is normally much less polar in character than the main current and is referred to as the East-Icelandic Current. The main southward flow of polar water does, however, take place west of the Kolbeinsey Ridge. In the area south and southeast of Jan Mayen an appreciable current is directed to the north and northwest bringing relatively warm and saline water from

the Norwegian Sea. Between these two currents, in the central part of the region between Jan Mayen and Iceland, a weak cyclonic eddy is formed. This eddy feeds water to the East Icelandic Current which also receives water from the North Icelandic Irminger Current and a variable portion of East-Greenland Current waters. Off Northeast Iceland a small portion of the East Icelandic Current is deflected towards the north and thus contributes to the cyclonic eddy, whereas the major portion continues along the continental shelf of Iceland and dissipates into the Norwegian Sea.

This description applies to average conditions, but there may be large fluctuations from year to year, even within the same month. Thus, the influx of Atlantic water to the north Icelandic shelf area in spring and early summer is highly variable, depending upon weather conditions. In warm periods, when southerly winds predominate off the northwest coast, the influx is increased, but it is reduced or even stopped altogether when the prevailing wind is from the north (Stefánsson 1962; Stefánsson and Guðmundsson 1969). In periods with small amounts of drift ice east of Greenland, the central region between Iceland and Jan Mayen consists of arctic waters with practically no polar water from the East Greenland Current. On the other hand, during cold periods the Atlantic influx is nearly always weak, and at the same time cold, low salinity polar water may predominate in this area with large parts covered with sea ice (cf. Malmberg 1972; Stefánsson and Jakobsson 1989).

The water circulation around Iceland itself runs in a clockwise direction. Its main components are the coastal current, essentially driven by gravity forces due to water afflux from land, the Atlantic water running westward off the south coast and north to the west of Iceland from where its continuation, the North Icelandic Irminger Current, completes the circulation around the island. This circulation is further strengthened by the East Icelandic Current flowing in the same direction farther offshore to the north and east of Iceland.

There are, however, large seasonal variations in the coastal current. In winter, when fresh water on land is to a large extent bound as snow or ice, the runoff is markedly reduced. Furthermore, during winter the coastal water is cooled to
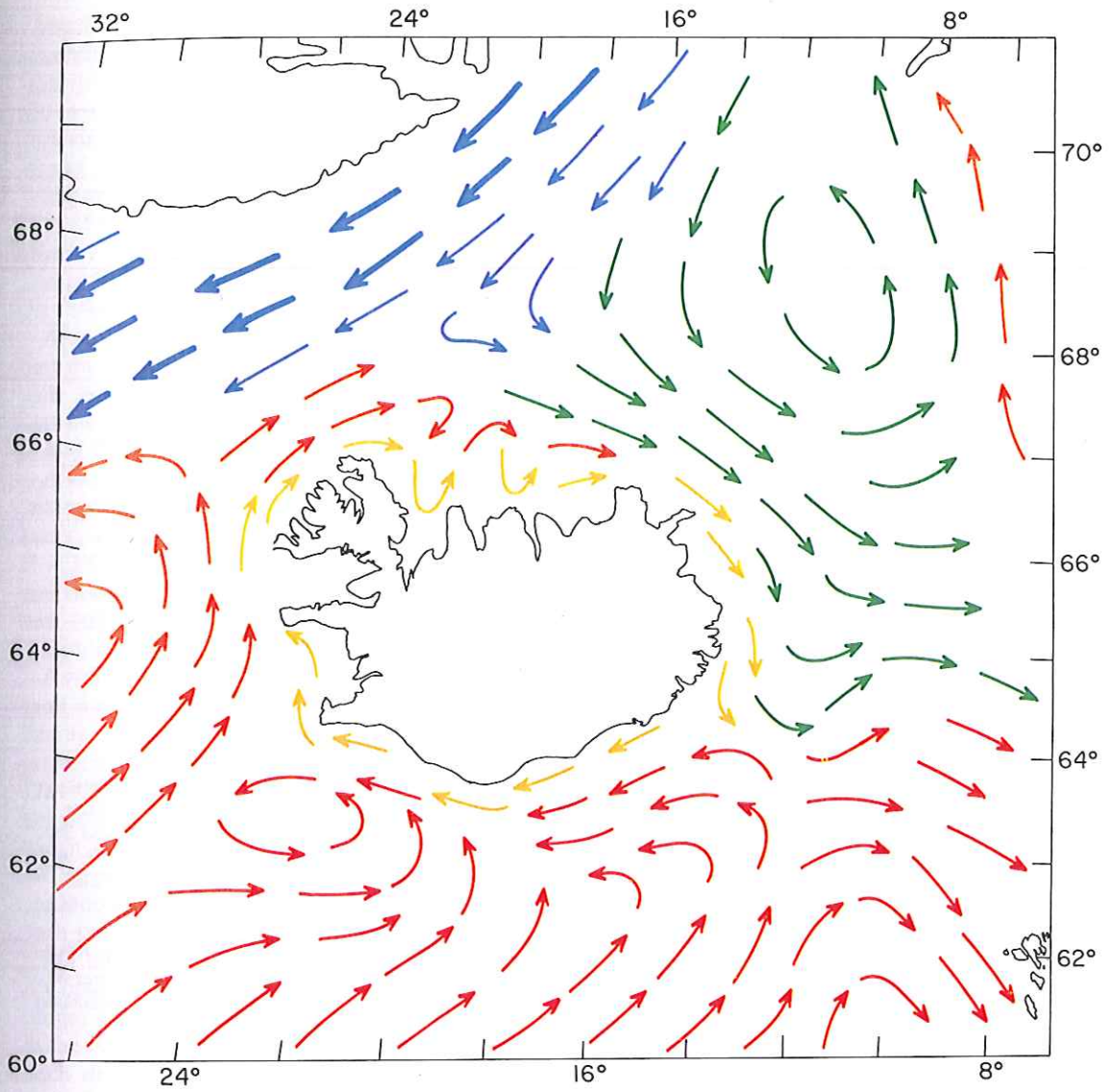
Figure 6.2. Ocean currents around Iceland. Red colour: Relatively warm and saline Atlantic water. Blue: cold and low salinity polar water. Green: Arctic water. Yellow: Icelandic coastal water (from Stefánsson and Ólafsson 1991).

a greater extent than the offshore water, the reverse taking place in summer. This causes a seasonal change in the horizontal pressure gradient of the coastal water and consequently increased coastal circulation in summer, but decreased circulation in winter (Stefánsson 1962; Stefánsson and Guðmundsson 1969). There are also considerable year to year variations, especially in the area north of Iceland, and in addition, short-periodic, irregular fluctuations due to changes in the wind regime.

6.3. Water masses

In the Iceland Sea water masses of highly different characteristics are found. These greatly affect living conditions of marine organisms, either directly or indirectly. The description of these water masses, which follows, is based on Stefánsson (1962) and Hopkins (1991). Three primary water masses can be identified. They are:

Atlantic water derived from the North Atlantic

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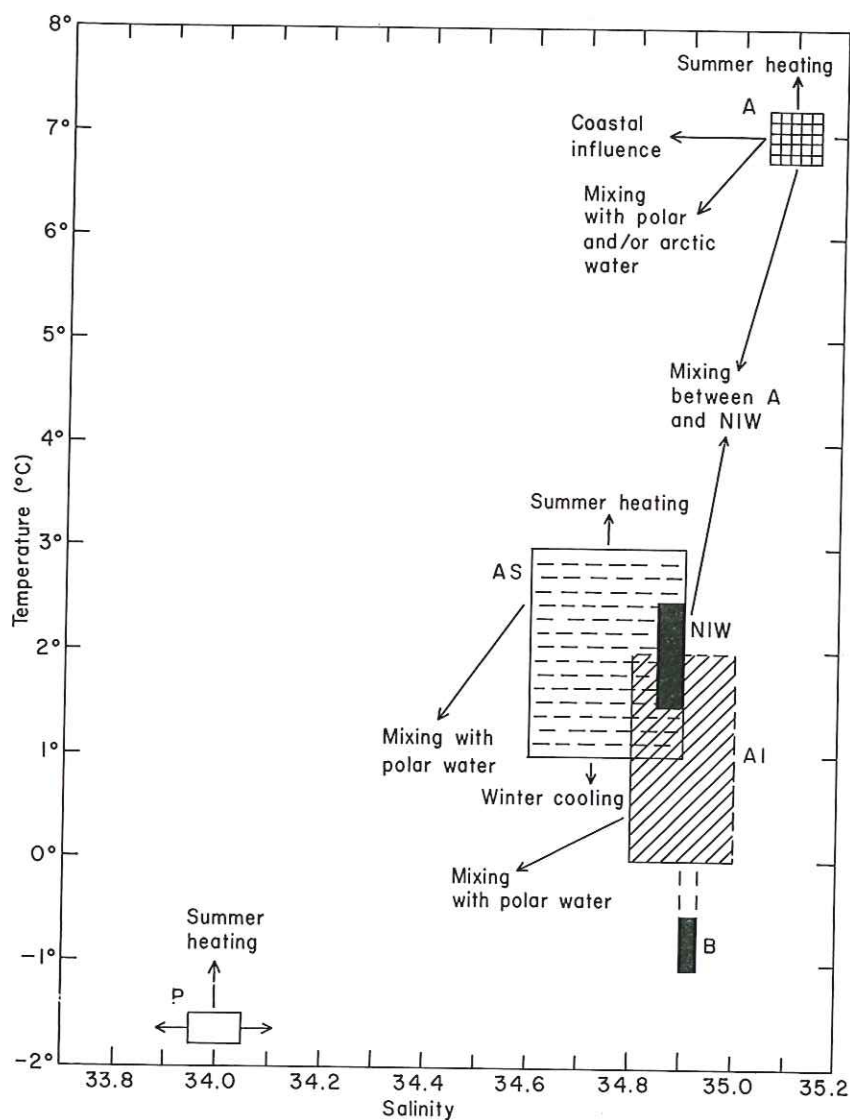
Figure 6.3. Schematic representation of water masses in the Iceland Sea. A: Atlantic water. B: Arctic bottom water. P: Polar water. AS: Arctic surface water. AI: Arctic intermediate water. NIW: North Icelandic winter water. (Modified from Stefánsson, p 128, 1962).

Drift and having a salinity above 35.0. It enters the Iceland Sea with the Irminger Current from the southwest where it has a temperature of around 7°C in late spring and a salinity of 35.05 – 35.15. Another much smaller contribution af Atlantic water, derived from the Norwegian Sea, enters the region south of Jan Mayen, as previously stated.

Polar water denotes the cold, low salinity upper layers of the East Greenland Current. It may to a variable degree mix into the surface layers of the Iceland Sea, in particular the area north of the Icelandic shelf. In heavy ice years it may also occupy large parts of the north Icelandic and even east Icelandic coastal areas. During warm periods, however, it has not to any appreciable degree been found to the east of the East Greenland Current. The polar water has a temperature of <0°C and a salinity of <34.5. However, during summer the temperature of the surface layer may rise considerably due to heating by the sun, and at the same time the salinity may be markedly lowered, even down to 30.0 units or less, because of ice melting. In winter the temperature will be close to the freezing point, −1.9°C and the salinity around 34.0.

Arctic bottom water occupies the deep waters, generally below 300–400 m, in the middle and eastern part of the Iceland Sea, but below about 600 m in the western part. It is characterized by a uniform salinity of 34.90–34.94 and a temperature of <0°C.

Important *secondary* water masses are also formed by various degrees of mixing between the primary water masses as well as by dilution due to runoff from land. The most important ones are the following:

Arctic intermediate water overlies the arctic bottom water and is formed by cooling of originally Atlantic water through mixing with arctic bottom water. It has a temperature between 0° and 2°C and salinity between 34.8 and 35.0.

Arctic surface water is formed by the mixing of polar water with water originating from Atlantic water. Its temperature is generally in the range 1° – 3°C, and the salinity 34.6–34.9. This water constitutes to a variable degree the surface and near-surface layers in the area north of the Icelandic shelf.

North Icelandic winter water is formed in the shelf area north of Iceland in winter by vertical mixing of Atlantic water with arctic and to a less extent polar water. In the relatively warm period 1924–1964 this homogenous water, usually with temperatures of 1.5° – 2.5°C and salinity between 34.85–34.90, occupied the uppermost 200–300 m on the shelf. During colder periods with appreciably greater admixture of polar water, both the temperature and the salinity values are lower and the thickness reduced.

Considerable modifications of the values or ranges of values for these water masses are found in the coastal area due to fresh water admixture. Such diluted water mixtures are referred to as *coastal water*. There will also be large seasonal changes in the water mass characteristics of the surface layers due to seasonal changes in temperature and salinity, and due to ice melting in years with appreciable admixture of polar water.

A schematic representation of water masses in the Iceland Sea is given in Figure 6.3.

6.4. Temperature-salinity variations

Due to its location near the boundary between warm and cold currents, *i.e.* at the oceanic Polar Front in the northern North Atlantic, hydrographic conditions in the sea area north of Iceland are highly variable. Consequently, changes in intensitiy of the influx of Atlantic water and/or variable admixture of polar water to the surface layers north of Iceland may lead to marked fluctuations in temperatures and salinities, both in space and time. Thus, time and again large displacements of the location of the Polar Front have been recorded and as a result, changes in the distribution of the various water masses (see *e.g.* Malmberg 1986). Off the south coast, however, where Atlantic water predominates, year to year fluctuations are normally much smaller (Stefánsson 1970).

It is well known that during the first decades of this century a marked temperature increase occurred in northern waters in general, leading to a retreat of the polar ice in the Iceland Sea. The period 1933–1964 was particularly warm in North Icelandic waters. Then a sharp downward trend in temperature and salinity, in both surface and intermediate layers, was observed in all of the years 1965–1971, due to a widening of the ice belt, increased admixture of low salinity polar water in the surface layers and, as a result, increased stratification in the southern and eastern Iceland Sea. In the period 1972–1992 cold and mild years have alternated and ice conditions generally improved from the preceding cold period (Stefánsson 1969; Malmberg 1984; Stefánsson and Jakobsson 1989; Anon. 1992).

As an index of the variability in the volume of Atlantic water flowing into the region north of Iceland, Ólafsson (1985) computed the deviations from the mean temperature and salinity of the uppermost 200 m for 5 stations on the section north of Siglunes (cf. Fig. 6.6). These results reveal large inter-annual variations in the shelf area (Fig. 6.4). The period 1965–1971 was characterized by negligible inflow of Atlantic water whereas polar influence was pronounced over the whole north Icelandic shelf area.

Fluctuations in the oceanic region between Northeast Iceland and the island of Jan Mayen in recent decades have been described by Stefánsson (1962), Malmberg (1984) and Malmberg and Kristmannsson (1992). Figure 6.5 shows the distribution of water colder than 0°C at 50 m depth in the 32 years period 1961–1992.

In general, the fluctuations described above can be related to large-scale changes in the atmospheric circulation in the arctic regions during the preceding decades (Rhodewald 1972;
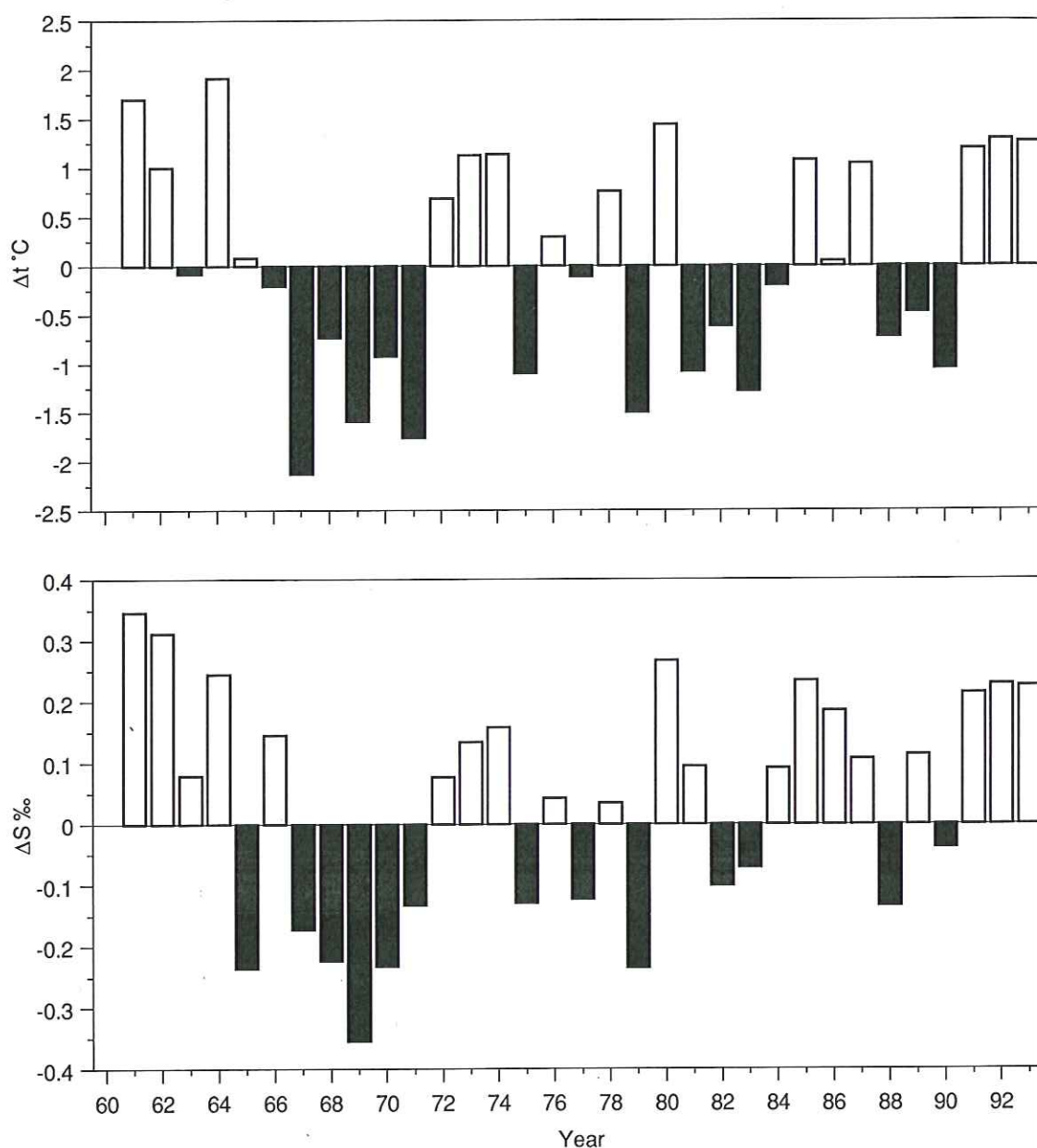
Figure 6.4. Temperature and salinity deviations in late spring from the 1961–1980 mean for stations 1–5 on the Siglunes section (see Fig. 6.6). The deviations were computed as mean values for 0–200 m at the stations between 2 and 46 naut. miles offshore. After Stefánsson and Ólafsson 1991. Based on Ólafsson 1985 with values added for 1986–1993).

Dickson *et al.* 1975; Malmberg and Svansson 1982). Local conditions at any given time, however, seem to depend on the prevailing meteorological conditions of a much more recent past. Thus, the oceanographic conditions of northeast Icelandic shelf waters at intermediate depths as well as in the surface layers, were found to be closely related to meteorological conditions a few months earlier off the west or northwest coast of Iceland which apparently control the inflow of Atlantic water to the north Icelandic shelf area (Stefánsson 1962; Stefánsson and Guð-
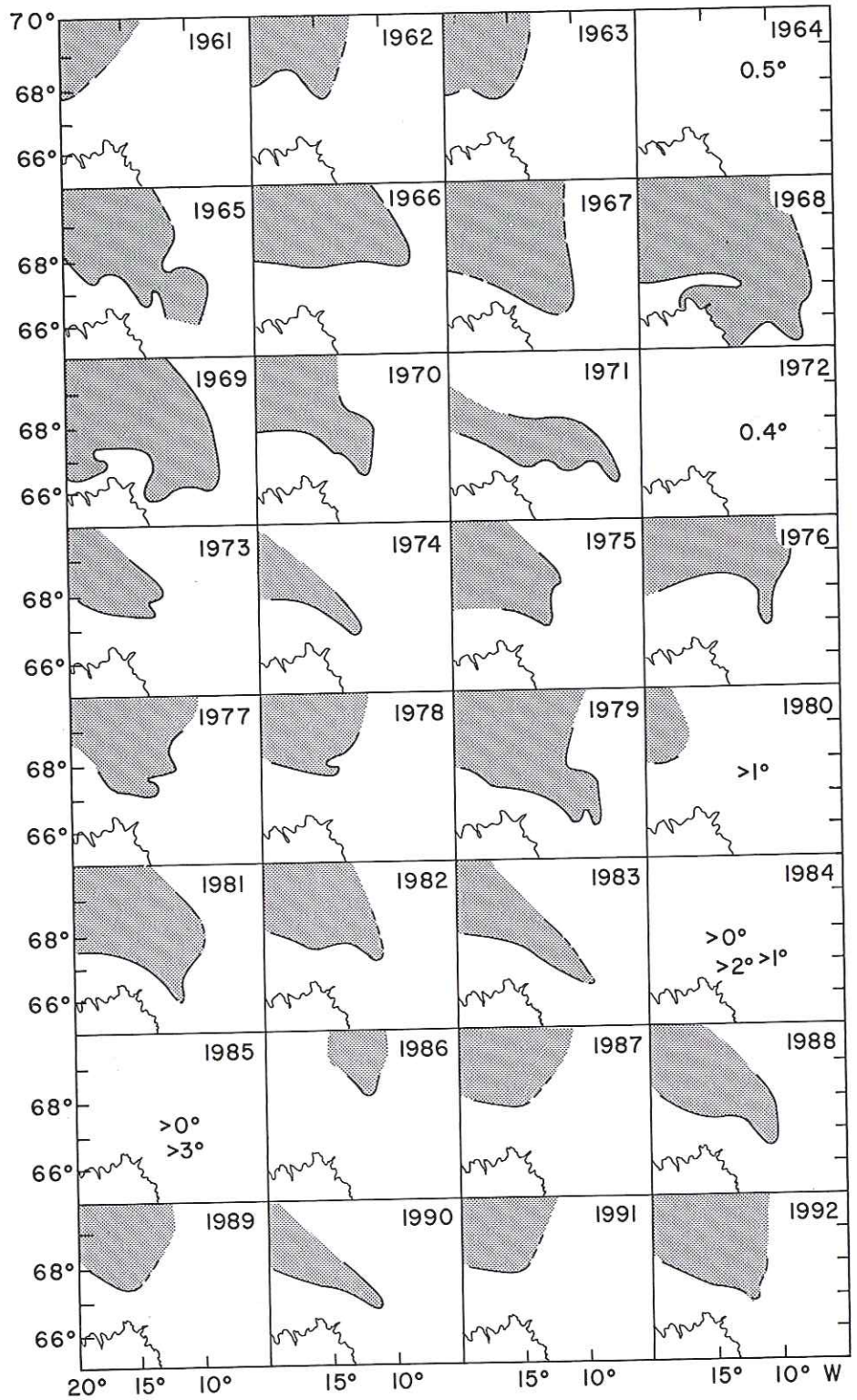
Figure 6.5. The 0° isotherm at 50 m depth in June 1961–1992. Within the shaded areas the temperature was below 0°C. (Redrawn after Malmberg 1984. The data for the years 1981–1992 were provided by Malmberg).

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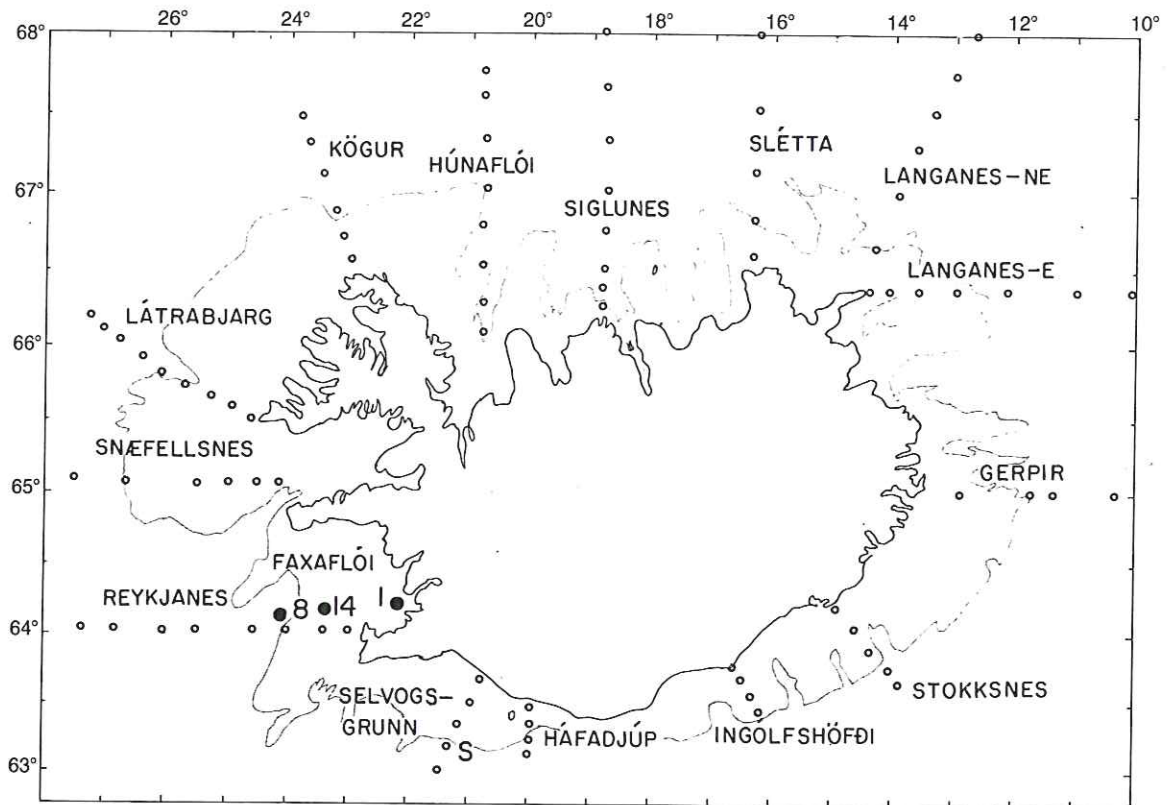
Figure 6.6. Sections and stations occupied during spring cruises in the years 1961–1992 (North and East Iceland) and in the years 1972–1992 (South Iceland). In 1983 the Reykjanes and Snæfellsnes sections were replaced by a single section running due west along 64°30′N. Locations of stations where seasonal studies were made in 1964–1965 (S) and in 1966–1967 (1, 14 and 8) are also shown.

mundsson 1969). With appreciable admixture of polar water into the north Icelandic area, as observed in many of the years after 1964, however, this simple relationship will be complicated.

6.5. Nutrients

Most of the hydrographical observations, nutrient and production measurements and collection of plankton samples have been carried out over the last 25–35 years during routine Icelandic late spring/early summer cruises. Sections and stations occupied are shown in Figure 6.6. In addition to these late spring cruises, considerable nutrient data are available from July–August and some limited data from the winter season. Furthermore, seasonal changes were studied at selective stations (see Fig. 6.6).

Besides nutrient data from the shelf waters around Iceland, Icelandic rivers have also been sampled for nutrient determinations. The results have shown that the effect of fresh water runoff on the nutrient content of the surface layers is insignificant with respect to phosphate and nitrate except close inshore. With regard to silicate, the effect is clearly much greater, so that in the near-shore region the high concentration of silicate, brought by the rivers, might prolong the growth of diatoms (Stefánsson and Ólafsson 1991). The fresh water afflux is important, however, for the development of stratification. Thus, in the Faxaflói region nutrient uptake in spring begins about two months earlier at near-shore stations than in the deeper region west of the bay and at the edge of the continental shelf south of Iceland.

Normally, there is a markedly stronger stratification and smaller nutrient concentrations in the north Icelandic shelf area than in the region of Atlantic water south and west of the country, the main reason for this difference being the admix-

ture of low salinity polar water in the northern region. A characteristic feature of the nutrient distribution in late May and early June (Fig. 6.7) is a tongue of relatively high concentrations in the outer part of the shelf region west of Iceland, extending northwards along the northwest peninsula of Iceland (Vestfirðir) into the western part of the north Icelandic region (Stefánsson and Ólafsson 1991). This tongue is associated with the influx of Atlantic water from the shelf area west of Iceland. In the eastern part of the north Icelandic region, however, nutrients are quite low on the average at this time of year, and the nutrient deficient area extends southwards along the east coast.

The Atlantic water thus provides an important nutrient source to the north Icelandic area, both directly due to relatively high nutrient concentrations, and indirectly because of much more efficient renewal in the surface layer by eddy diffusion in the Atlantic water than in the highly stratified arctic or polar waters. During warm periods with small extension of drift ice and consequently small or even negligible admixture of polar water to the surface layers, continued inflow of Atlantic water to the north Icelandic area should therefore maintain favourable mixing conditions and make a longer lasting plant production possible.

Year to year variations in nutrient concentrations and vertical mixing at St. 3 on the Siglunes section (some 20 naut. miles from the coast, see Fig. 6.6) are shown for most of the years in the period 1954–1988 in Figure 6.8. The observations were made in late spring. In the warm period up to 1964, nutrient concentrations at this locality, which is representative for the middle part of the north Icelandic area, were clearly relatively high, coinciding with strong influx of Atlantic water (cf. Fig. 6.4). In the very cold years 1965–1971 the nutrients were exceptionally low, whereas in the years 1972–1988 high and low values interchanged. Conspicuously high nutrient concentrations occurred in the years 1957, 1959, 1980
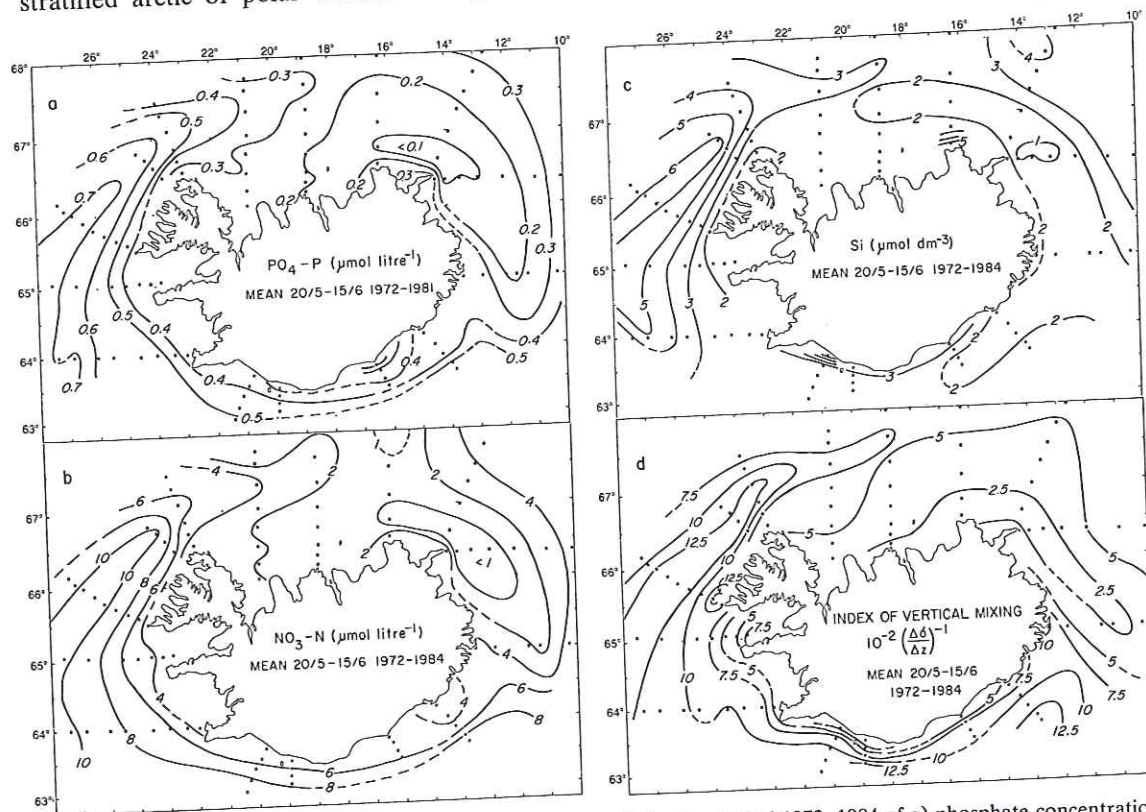

Figure 6.7. Mean near-surface values during May 20 – June 15 for the period 1972–1984 of a) phosphate concentration (μM), b) nitrate concentration (μM), c) silicate concentration (μM) and d) index of vertical mixing (10^{-2} $[\Delta\sigma_t/\Delta z]^{-1}$. (After Stefánsson and Ólafsson 1991).
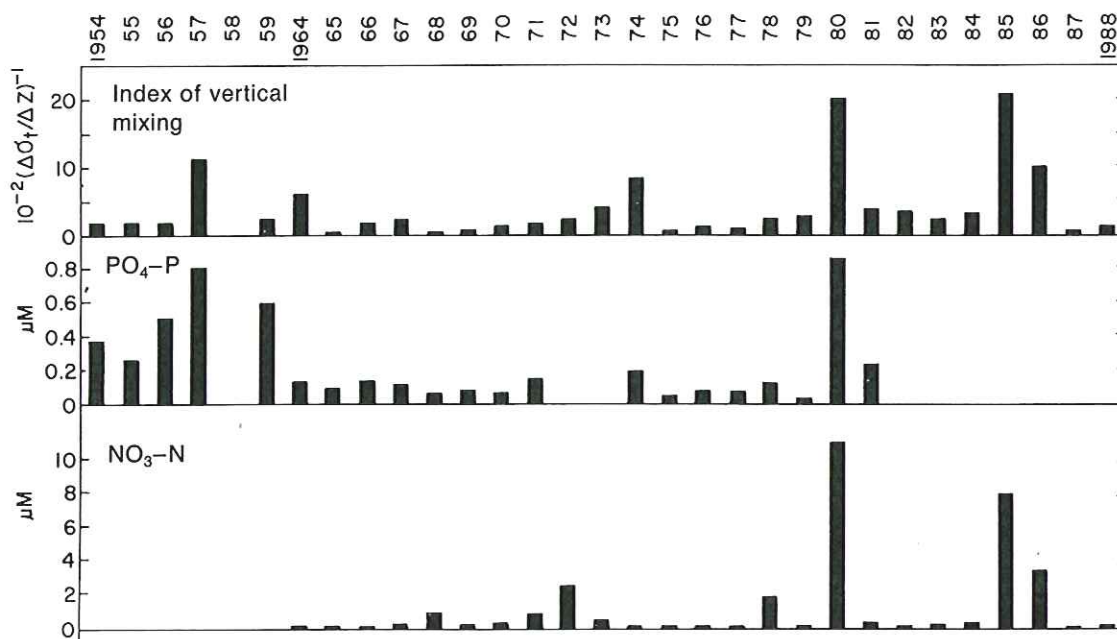
Figure 6.8.   Year to year variations at station 3 (counted from land) on the Siglunes section (for location see Fig. 6.6) in index of vertical mixing, near-surface phosphate and near surface nitrate. (After Stefánsson and Ólafsson 1991).

(phosphate) and 1985 (nitrate) with favourable mixing conditions (Stefánsson and Ólafsson 1991).

6.6. Primary production

Primary production in Icelandic waters has been measured since the late 1950s using the conventional C-14 method. Most of the observations have been made during the late spring cruises. Considerable data have also been acquired in late summer and to a lesser degree in winter. In addition, seasonal studies were made in the Faxaflói region in 1966–1967.

On the basis of these measurements, Thórdardóttir (1993, in press) has computed the average annual primary production in Icelandic waters for the period 1958–1982 (Fig. 6.9). Comparison with other sea areas, including satellite image data, indicates that Icelandic waters on the whole are relatively productive. There are, however, considerable year to year as well as regional variations within the Icelandic area. The average productivity map (Fig. 6.9) reveals that where Atlantic water predominates, i.e. off the south and west coasts, the values are relatively high, whereas in the arctic and mixed water areas north

and east of Iceland the average productivity is markedly lower. It will be noted that the values decrease from west to east in the north Icelandic area in the direction of diminishing admixture of Atlantic water. The very lowest average values, roughly 4 times lower than those over the shelf off the south and southwest coasts, are found in the deep, normally highly stratified areas northeast of Langanes.

Not only is the average production smaller in the areas north and east of Iceland, but the year to year variations are also much more conspicuous in the cold regions than in the warm areas in the south and west. Thórdardóttir (1977, 1984) has shown that in cold years with limited inflow of Atlantic water to the north Icelandic area, productivity was very small in the northern waters, whereas during warm years the values were many times greater. This is illustrated in Figure 6.10 where the primary production in late spring in the very cold years of 1965, 1967, 1968 and 1969 can be compared with that of the relatively warm years of 1974, 1976, 1978 and 1980.

These large productivity variations in the north Icelandic area, as well as the difference between the northern and southern areas, have very little to do with temperature as such, but can no doubt

be attributed to variations in the density stratification of the surface layers as the result of recent climatic changes. And as described in section 6.5, the main cause of the particularly strong stratification during cold years is the admixture of low salinity polar water to the surface layers north of Iceland leading quickly to nutrient deficiency. Furthermore, the difference between sea and air temperature north and northeast of Iceland in late spring is considerably greater in the warm water area south of Iceland than in the colder waters north of Iceland (Stefánsson 1969). Thus in June when the sea temperature at Vestmannaeyjar is higher than the air temperature and hence a heat loss from the water to the air, the opposite is true at Grímsey off the north coast. Therefore, heating of the sea water will be more rapid in the northern area, leading to a steeper temperature gradient which also serves to create

a stronger pycnocline (Stefánsson and Ólafsson 1991).

Seasonal studies have shown (Thórdardóttir and Stefánsson 1977; Thórdardóttir 1986; Stefánsson et al. 1987) that the phytoplankton blooming normally starts in the near-shore waters and is delayed with increasing distance from the coast. In the shallow part of the Faxaflói region the phytoplankton uptake starts in late March and the maximum productivity is attained around the beginning of May. In the deep area west of the Faxaflói, however, the uptake does not start until after the middle of May. The growth period is also of longest duration inside Faxaflói and west of Reykjanes.

The early beginning of primary production in the immediate coastal waters off Southwest Iceland is the result of an early development of stratification due to the fresh water afflux as
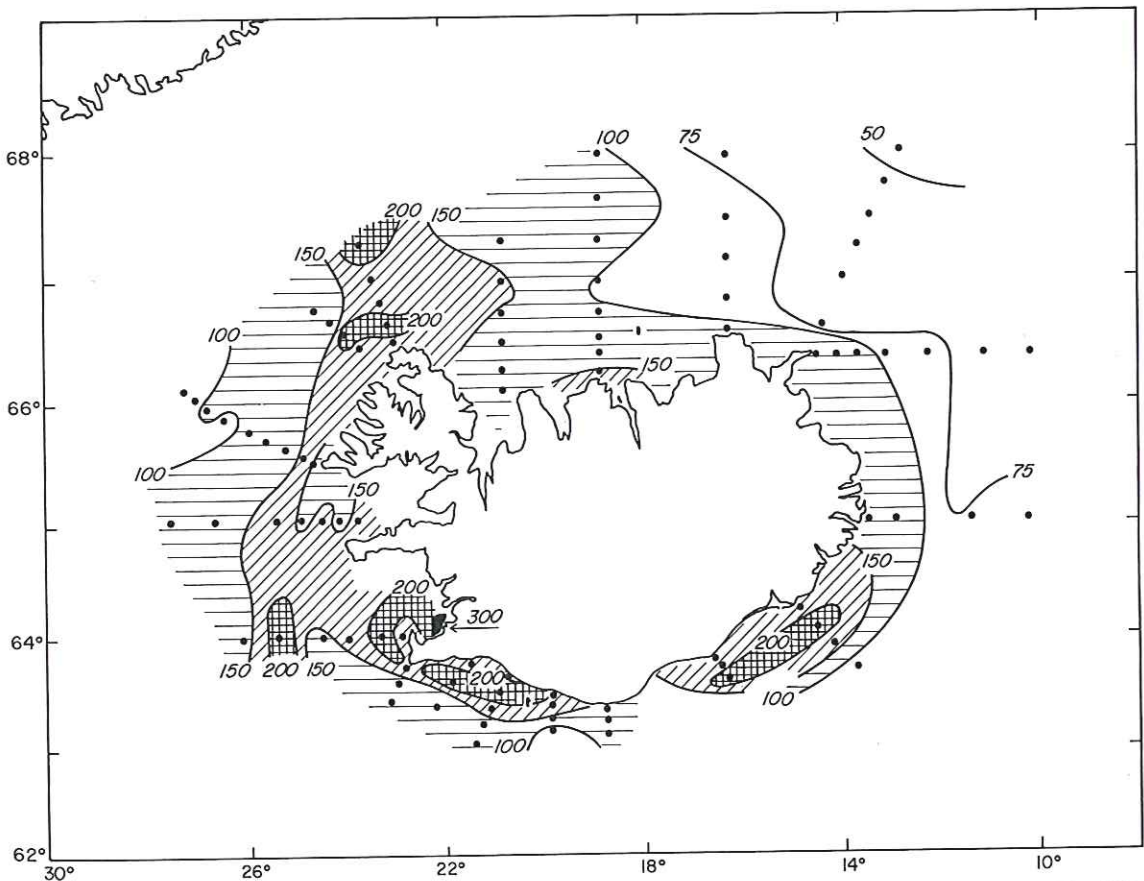
Figure 6.9. The average annual primary production (g C m^{-2} yr^{-1}) in Icelandic waters for the period 1958–1982. (After Thórðardóttir 1993).
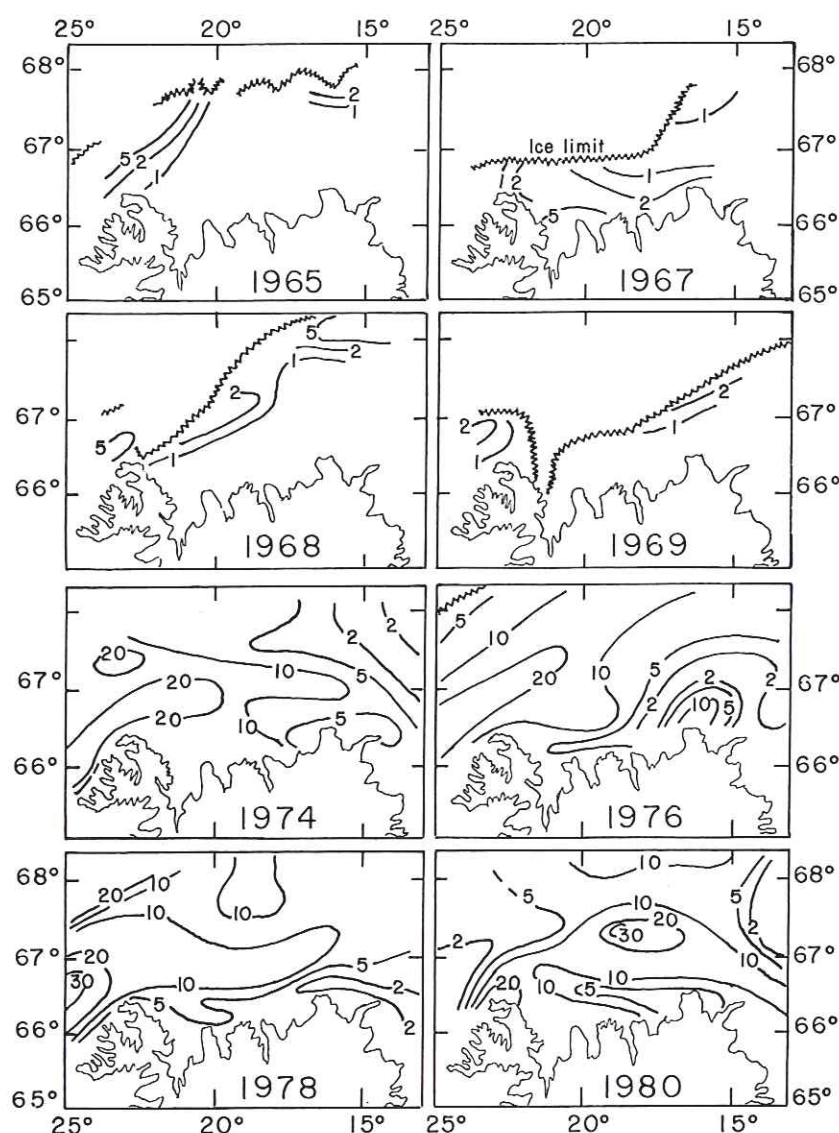
Figure 6.10. Primary production (mg C m^{-3} · h^{-1}) at 10 m in late May/early June in different years. (Redrawn from Thórdardóttir 1975, 1977a, 1977b, 1979 and 1981, in Stefánsson and Jakobsson 1985).

mentioned in section 6.5. Furthermore, wind action in the vicinity of the coast frequently leads to turbulent mixing and as a result, renewal of nutrients in the euphotic zone, thus prolonging the growth period.

The winds are also important for the offshore movement and distribution of fresh water, which also may affect the time at which the blooming starts. Thus, Stefánsson and Guðmundsson (1978) found that accumulation of fresh water in Faxaflói and advection into the bay of low salinity coastal water from the areas south of Reykjanes, following a spell of southerly winds, led to increased stratification, in particular in the near shore region. They concluded that the onset of stratification would be favoured at an earlier time under such conditions. Conversely, northerly winds inside the Faxaflói would be expected to retard stratification and consequently the onset of plant production in the spring, but once the plant production has started they would tend to transport coastal species to offshore areas.

Finally, the inter-annual variation in runoff has an important effect on both the timing and the magnitude of the spring bloom, since spring floods are smaller and occur at a considerably

later date in cold years than in warm years. As an example, the time difference in spring floods and phytoplankton blooming in the area south of Iceland between the cold years of 1977 and 1979 on one hand and that of the warm year of 1981 on the other, was about six weeks. In the first case primary production began in coastal areas around the middle of May but in early April in the latter (Thórðardóttir 1986).

Data on the yearly growth development in the area north and east of Iceland are scanty. Although these waters have been surveyed routinely in spring for more than 3 decades, most of the observations derive from the month of June and, therefore, yield only limited information on what may have happened earlier. However, in the years of 1965, 1966 and 1967, the June surveys were preceded by observations in May. These studies indicated that in the North Icelandic winter water the phytoplankton blooming begins not later than in early May, reaching a maximum in the middle or the latter half of the month. In the very cold years of 1965 and 1967 the primary production measurements indicated an even earlier onset of algal growth in the polar water which then occupied the north Icelandic shelf area (Thórdardóttir 1977a).

As stated earlier, the phytoplankton growth in the Atlantic water farther west over the outer part of the Icelandic shelf does not start until after mid-May. The reason is the earlier formation of a pycnocline in the northern and eastern areas, mainly due to lowered salinity in the surface layer as previously described. The subsequent flow of Atlantic water into the north Icelandic area, therefore, promotes a continued algal growth in the waters north (and later east) of Iceland (Thórdardóttir 1977a).

6.7. Zooplankton

For more than 30 years annual studies of zooplankton abundance have been carried out on standard sections in north Icelandic waters in the late May and early June period. Continuous records for the area south and west of Iceland are also available for that time of the year since 1971. Average zooplankton densities during each year of the observation period 1961–1982 were calculated for the various sections by Ástthórsson *et al.* (1983) using available volume measurements, and similar calculations are also available for the

period 1983–1992 (Anon. 1993a; Ástthórsson and Gíslason 1993). The following is a summary of the main features of zooplankton distribution in Icelandic waters in May/June 1961–1992 using the Siglunes and Selvogsbanki sections as representing the situation in the mixed arctic and polar waters north (and east) of Iceland and that in the Atlantic water south and west of Iceland.

Off the central north coast (Siglunes) the main feature was a large drop in the volume of zooplankton associated with the drastically reduced flow of Atlantic water and increased polar water in the north Icelandic area with resulting changes in food supply during the ice years 1965–1969. This was followed by a recovery which, however, has only been partial. Thus, with the exception of 1971 and 1977, zooplankton volumes of pre-1965 magnitude (7–24 ml/21 m^3) have not been registered during the period 1965–1992 off the central north coast but have remained at a low to moderate level (1–9 ml/21 m^3). Variations in zooplankton volume in May/June on the Siglunes section in the 1961–1992 period are shown in Figure 6.11. Zooplankton development in the western and the eastern north coast areas has followed much the same pattern as that of the central area. Off Northeast and East Iceland the time series does not go back to the early 1960s. The variation in zooplankton densities of those areas is somewhat different from that off the north coast, but there is, nevertheless, little reason to believe that the general picture described above does not apply to the eastern area as well as the waters north of Iceland.

As pointed out in sections 6.4–6.6 the influx of Atlantic water to the area north and northeast of Iceland is important for mixing and nutrient renewal in the near surface layers, thus creating conditions for rich primary production. As stated above this mechanism was severely disrupted in the latter half of the 1960s resulting in much reduced primary production as well as reduced zooplankton stocks in these waters. Although the influx of Atlantic water to the areas north of Iceland has in some years since 1971 resembled that of the period prior to 1964, the zooplankton abundance of these waters has only twice (1971 and 1977) reached its former high level. It has been suggested that the reason for this could be that the short term variability in primary production has caused a reduction in the availability of food for the zooplankton and that longer periods

Figure 6.11. Variations in the average volume of zooplankton (ml/21 m³) on the Siglunes section (for location see Fig. 6.6) in the years 1961–1992. (After Ástthórsson and Gíslason 1993).

of high primary production are necessary for the zooplankton stocks to regain their former levels (Ástthórsson *et al*. 1983).

At the stations farthest offshore in the north Icelandic area the zooplankton densities remained almost the same throughout the 1961–1982 period. At these stations arctic species usually make up a larger part of the zooplankton catch than found for more coastal areas. It seems, therefore, that adverse hydrographic conditions have had less effect on arctic species than on the more temperate ones, and as a result their density is more consistent through the years (Ástthórsson *et al*. 1983). It is, however, clear that variations in temperature and salinity of the waters over the continental shelf north of Iceland have been greater than those in the area farther north.

Data on zooplankton distribution and abundance in the areas south and west of Iceland are not available for May/June in the 1960s. However, due to the lesser variability within the Atlantic water, which dominates in these areas at all times of the year, it is unlikely that the zooplankton community south and west of Iceland

suffered a decline similar to that of the northern and eastern areas in the middle and latter half of the decade. In the 1970s and the first half of the 1980s moderate to high zooplankton volumes were recorded on the Selvogsbanki section off the western south coast. However, in the period 1986–1992 zooplankton abundance has been decidedly lower (Ástthórsson *et al*. 1983; Ástthórsson and Gíslason 1993). Zooplankton volumes, measured on the Selvogsbanki section in May/June 1971–1992 are shown in Figure 6.12.

Ástthórsson *et al*. (1983) also investigated the species composition of the zooplankton. In short, their analysis revealed that *Calanus finmarchicus* of different development stages usually dominated in the samples (Fig. 6.13). Thus the frequency of *C. finmarchicus* was found to be 60–90% in most of the area south of Iceland, with the highest abundance recorded at stations far offshore. Elsewhere off the south coast as well as west of Iceland this species constituted about 60–80% by number. In the immediate coastal area Cirripedia larvae are, however, the most common component, while in the cold arctic or polar waters far off the north and northeast coasts the

dominance of *C. finmarchicus* decreases, and this species tends to become replaced by cold water types such as *C. hyperboreus* and *Metridia longa*.

As pointed out by Ástthórsson *et al.* (1983), their data were limited to a period of about 3–4 weeks in late May and June and, therefore, it was not clear to what extent the changes in the various water masses during the remaining part of the growth season affected the species distribution and volume of the zooplankton in the period 1961–1982. However, the authors concluded that marked changes have occurred in the period 1961–1982, in particular in the shelf area north and east of Iceland. Thus, during the ice years 1965–1971 the warm water species *C. finmarchicus* was in spring largely replaced by arctic species such as *C. hyperboreus* and *M. longa* as well as by Euphauciacea nauplii. This is indeed supported by Jakobsson (1978, 1980) who found through repeated surveying in summer that the once abundant stock of *Calanus finmarchicus* was literally decimated in the mid-1960s and did in fact almost completely disappear from the waters north of Iceland in this period. And as stated above, zooplankton abundance in the north

Icelandic area has not regained its pre-1965 level. Presumably, this is mainly because *C. finmarchicus* has yet to regain its former abundance.

Some changes also appeared in the distribution and percentage frequency of Euphausiacea nauplii north of Iceland (Ástthórsson *et al.* 1983). The young stages of the 4 species of Euphausiacea occurring in Icelandic waters are usually found in considerable numbers in plankton samples north of Iceland in spring. It seems that they have been observed in greater numbers after 1970 than in the preceding decade. Adult stages of Euphausiacea are very common in Icelandic waters and in fact often dominate by volume in the zooplankton community in large areas in summer, autumn and winter. During those seasons they often are the main food item of the capelin, especially among the older age groups of the stock (Sigurðsson and Ástthórsson 1991). Due to their swimming ability and violent escape reaction, adult euphsausiids are seldom caught in the Hensen net that until recently has most frequently been used for the sampling of zooplankton in the Icelandic area. For this reason there are no reliable data available for evaluating
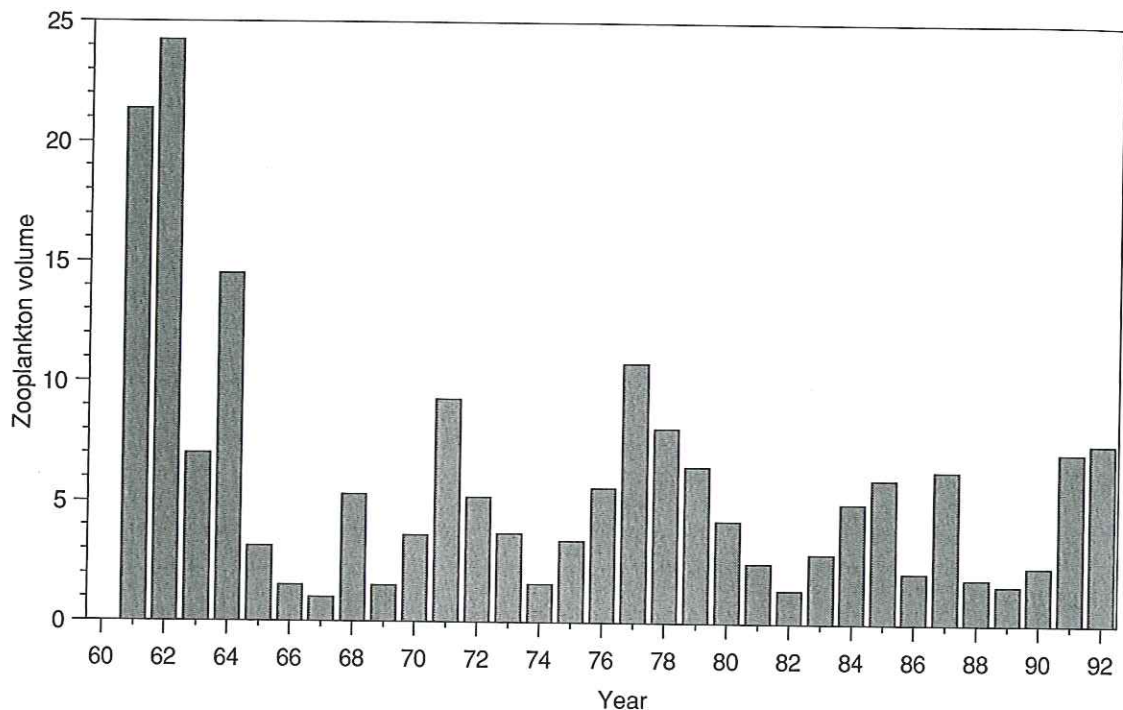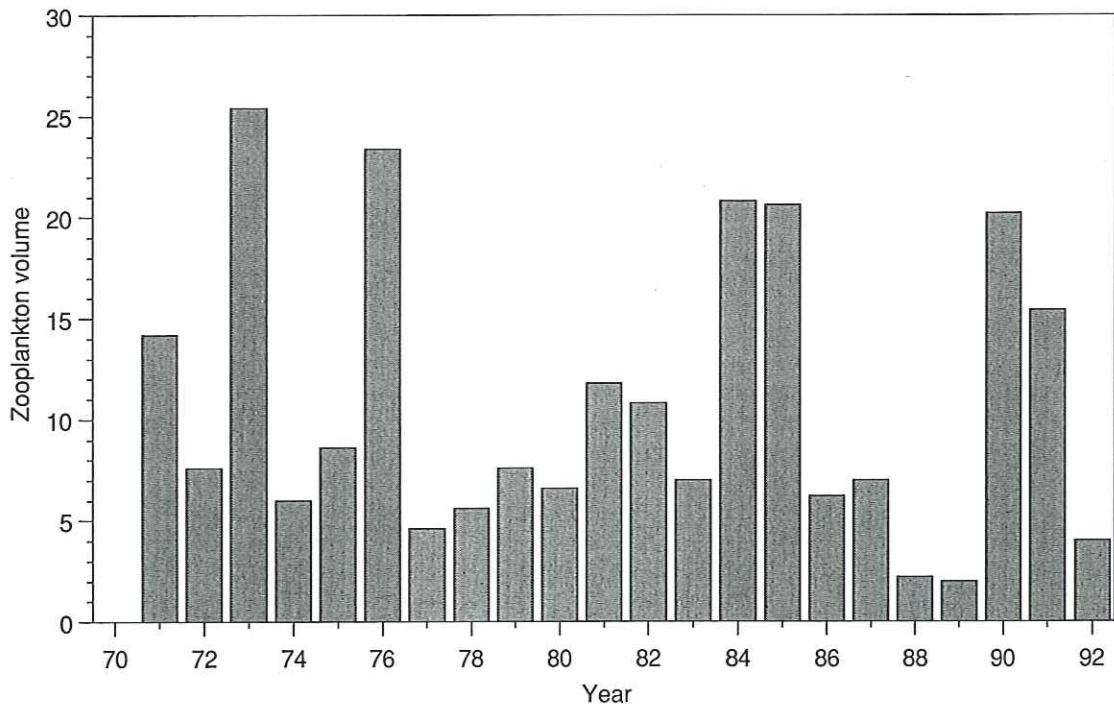

Figure 6.12. Variations in the average volume of zooplankton (ml/21 m^3) on the Selvogsbanki section (for location see Fig. 6.6) in the years 1971–1992. (After Ástthórsson and Gíslason 1993).
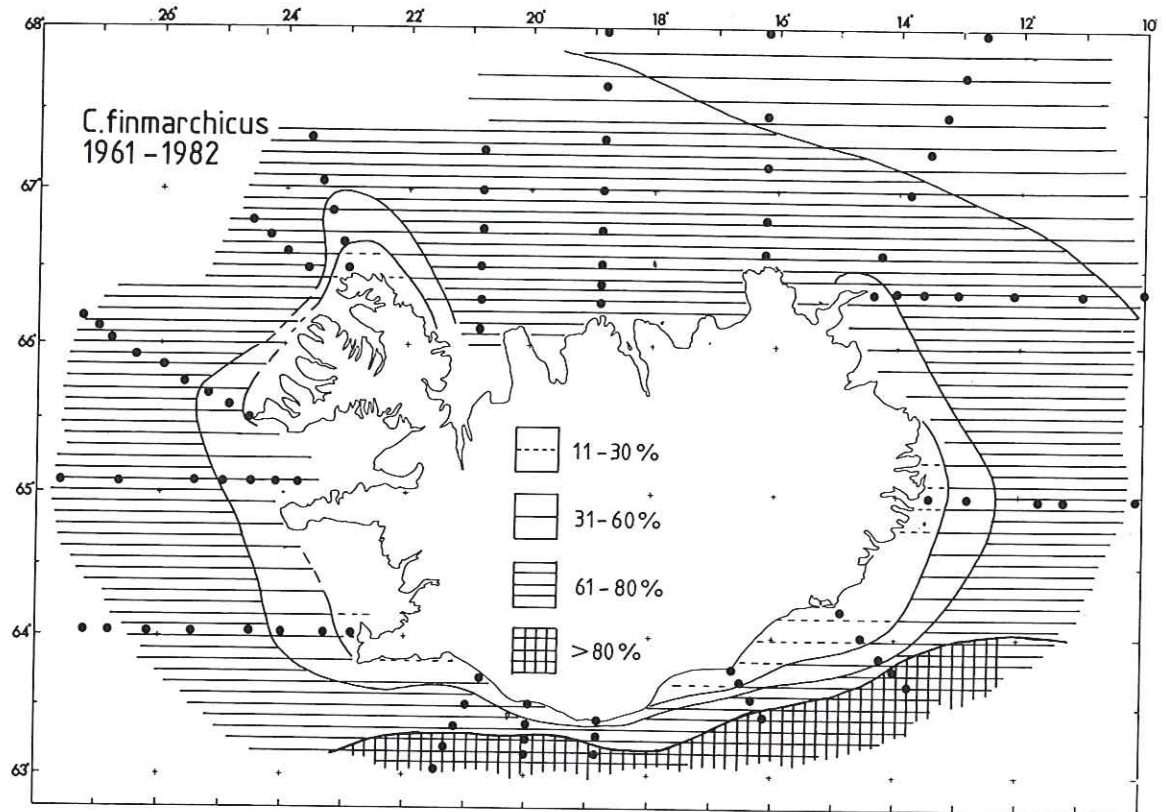
Figure 6.13. The average percentage frequency of *Calalanus finmarchicus* at stations around Iceland in May–June 1961–1982. (From Ástthórsson *et al.* 1983).

the relative abundance of this important food item or possible changes therein as a function of time. Furthermore, in spite of regular monitoring of the physical marine environment four times annually in recent years, very little information is available on seasonal changes in zooplankton abundance in the waters around Iceland.

Although the copepod communities of the Atlantic and mixed waters north of Iceland have only partly recovered their former abundance, it is clear from Jakobsson's (1978, 1980) research, as well as the annual environmental surveys since then, that zooplankton production begins in the shelf area north of Iceland around mid-May and peaks in June. Due to the continued flow of nutrient-rich Atlantic water into the area north and northeast of Iceland, fairly high levels of phytoplankton and consequently of copepod abundance can be maintained almost throughout the summer period. However, as indicated by Jakobsson (1980) and generally is the rule in the North Atlantic (Nemoto and Harrison 1981), there is a secondary production cycle resulting in an additional but smaller late summer peak of copepod production in August in these waters.

7. SPAWNING MIGRATIONS

By the 1920s it had been established that the southern part of the Iceland Sea constituted the main feeding grounds of the capelin and that from there they must migrate to spawn off the south and southwest coasts of Iceland in late winter (Sæmundsson 1926). However, the migrational routes of the stock from the northern feeding grounds to the warm coastal waters off the south and southwest coast were not known.

The 1960s saw the dwindling and finally the collapse of the Icelandic and Norwegian herring stocks upon which a large fleet of Icelandic purse seiners had traditionally operated. Although much of this fleet could for a while occupy itself fishing for herring in the North Sea and adjacent waters, it was obvious that a suitable substitute target species had to be found if this fleet was to be kept operative in the long run.

By the late 1960s a considerable and increasing capelin fishery had developed off Southwest Iceland during the short spawning season in late February and March. Scouting effort in connection with that fishery and comparison with experience gained on the herring grounds in the years before, suggested that the capelin stock was grossly under-exploited (Jakobsson 1969). Therefore, it seemed sensible to design and carry out investigations for determining to what extent the capelin fishery could be expanded in space and time and the catch increased.

For almost a decade, approximately three months of research vessel time were set aside annually for this research. It should be borne in mind that the prime purpose was to assist the fishing fleet. This, together with interruptions due to winter storms, resulted in irregular survey design, data acquisition and processing. The following is a description of the results of some of this extensive work and how it unraveled the migration routes and patterns of the various spawning stock components as well as the large changes these migrations have been subjected to. However, the above limitations, imposed by the specific purpose of the surveys as well as the frequently adverse working conditions, often make it more difficult than it otherwise might have been to relate observed changes in fish behaviour to external factors.

For geographical orientation of place names and positions, referred to in later sections, see Figure 7.1.

7.1. The eastern route of spawning migrations

The location of the main feeding areas of the Icelandic capelin in deep waters to the north of Iceland was well established in the first decades of this century (see *e.g.* Sæmundsson 1926). The same is true for the first arrivals of the spawners in coastal waters off the southeast shores of Iceland in February and the subsequent westward progress of the spawning migrations from there. It therefore comes as something of a surprise that in the older literature there is no reference to the movement of the spawners in the wintertime while migrating from the northern feeding grounds to the easternmost part of the main spawning area in the south.

7.1.1. The location of the eastern spawning route

The first attempt to locate the capelin spawning migration off East Iceland was made in January 1968 (Jakobsson and Vilhjálmsson 1969). In the latter half of the month some capelin were recorded in Lónsvík on the southeast coast as well as some 20–30 naut. miles offshore farther to the southeast. Otherwise, the attempt failed, in retrospect most likely because bad weather prevented search in other than the more inshore areas.

In the last week of January 1969 a short survey was carried out near the edge of the continental shelf east of Iceland (Jakobsson and Vilhjálmsson 1970). The survey revealed abundant concentrations of mature capelin in a large area

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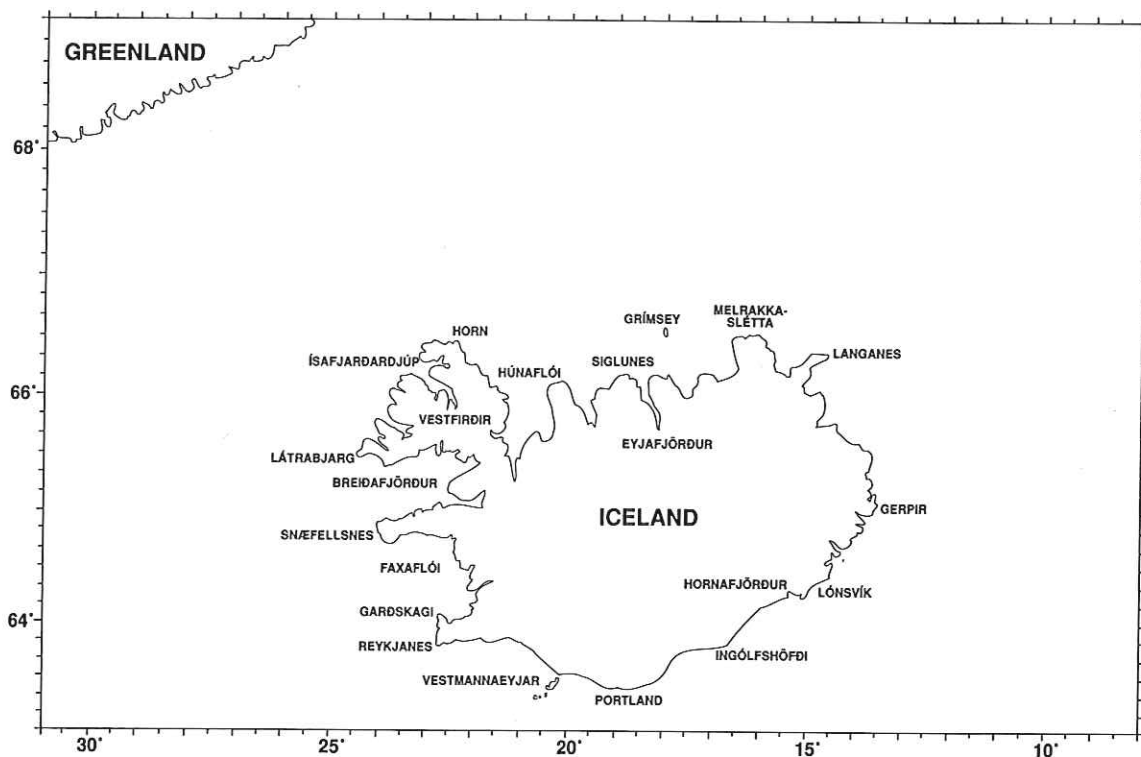
Figure 7.1. A map of Iceland giving the names of the various localities referred to in the following sections and chapters.

at the edge of the shelf about 70 naut. miles off the central and northern east coast of Iceland. Because of severe gales it was not possible to follow the progress of this migration until it arrived in shallow waters off Hornafjörður around mid-February.

In the years that followed, research was begun early in January, usually continued through February and March and sometimes stretching into the first half of April. It was soon established that as a rule the capelin approach the south and west coast spawning areas from the east, more often than not in a number of runs at short intervals each year. The migrations initially follow the outer shelf edge off North and East Iceland in a clockwise fashion. This sea area is characterized by the presence of the boundary zone between the north Icelandic winter water with temperatures of 1.5–2.5°C covering the shelf area and the arctic surface waters of the East Icelandic Current with temperatures of 0–2°C, usually encountered at a short distance outside the edge of the Icelandic shelf.

When arriving in the area about 50–80 naut.

miles off the southern east coast of Iceland, the spawning migrations encounter sharp current boundaries and temperature gradients where the warm Atlantic water (about 7°C) of the North Atlantic Drift meets the East Icelandic Current. The capelin will normally stay on the colder side of the boundary until they have reached that stage of maturity when the weight of the female ovaries is about 8–10% of their total body weight. At this point the migrations will head for the south and west coast spawning grounds, usually following the boundary zone between the cold and warm water masses, to approach the coast in the region of Hornafjörður at Southeast Iceland. Sometimes, however, the capelin may make a detour to the south or southeast and do not approach the coastal area until at or even west of cape Ingólfshöfði some 60–80 naut. miles farther west.

When the capelin with a roe content of 8–10% enter the warmer Atlantic water a rapid increase in the rate of maturation is observed. From then on, maturation proceeds at a rate described by the weight of the female ovaries, increasing by
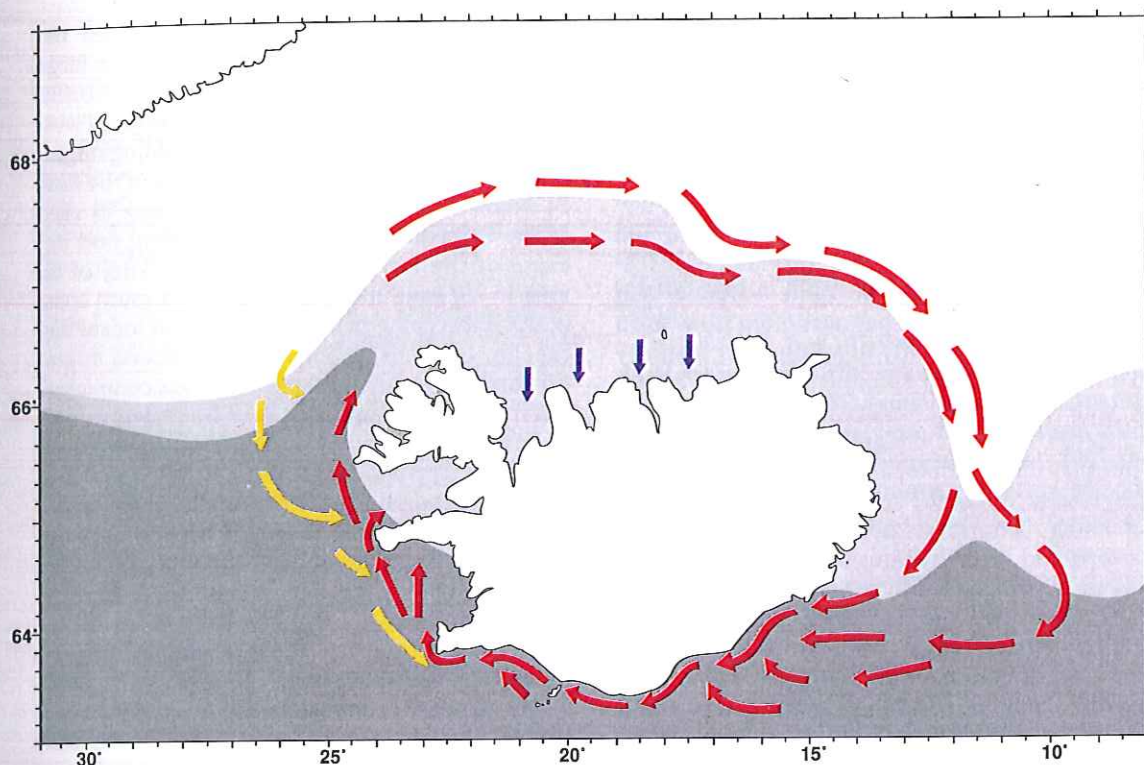
Figure 7.2. The location of the spawning routes of the Icelandic capelin. a) The main, eastern spawning route (red arrows). b) The occasional western approach of part of the spawning stock (yellow arrows). c) North coast spawning approaches (blue arrows). Shaded areas denote different water masses. Darkest shade: Atlantic water, lighter shade: North Icelandic winter water, lightest shade: polar water.

approximately 1% of their body weight per day, until spawning commences about 3 weeks after the capelin encounter the warmer waters at the eastern south coast. In the first and usually largest runs, spawning will normally take place in the western part of the south coast spawning grounds and/or off the west coast. Later migrations may, however, consist of individuals that are more mature when entering the warm coastal waters. In consequence, these fish will spend much less time in the coastal area before becoming ready to spawn, and under normal circumstances they are responsible for much of the spawning products deposited in the easternmost part of the south coast spawning grounds.

The general position of these migration routes in relation to environmental variables (as judged by temperature) in the area is shown in Figure 7.2.

7.1.2. Spatial and temporal deviations of spawning migrations in early January

Over the years, deviations from the average geographical position of the eastern migration route have usually been remarkably small except in the area off Southeast Iceland.

In the areas east and north of Iceland the most obvious exception was the 1977 migration which followed a route approximately 20–40 naut. miles farther off the north and northeast coasts than in any of the previous years. This was evidently due to the relatively wide distribution of north Icelandic winter water in that part of the area as compared to other years. Off the east coast the fish again approached the shelf edge, and from there took the more normal and shorter route along the northern limit of the warm Atlantic water towards the coast (Vilhjálmsson 1977b).

From the areas north and east of Iceland there are also some examples of deviations in the

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shoreward direction, almost all of which are of minor dimensions. In 1980, however, the spawning migration was delayed and finally rounded the northeastern promontories of Melrakkaslétta and Langanes at a distance of about 10–20 naut. miles instead of the usual 50–60 naut. miles (Vilhjálmsson 1981a).

As mentioned above, the behaviour of the capelin at the boundary zone off Southeast Iceland may nevertheless be quite variable. On reaching this area, the spawners often slow down or even stop, apparently to adjust their maturity to a stage suitable for entering the warmer Atlantic waters. The rule seems to be to follow the warm/cold water boundary up to the coast and after that the coastline, as shown in Figure 7.2. If this course is taken, the prominent migratory schooling behaviour, usually exhibited in the eastern and northern areas, may persist all the way up to the the southeast coast.

Alternatively, the spawning migration may scatter in deep waters after crossing the cold/warm water boundary off Southeast Iceland and remain scattered, sometimes to the extent that it becomes difficult to determine the subsequent progress of the migration. The possibility of this state of affairs was first suspected in 1969 and verified in 1971, when the capelin entered the warmer waters while still quite far east, and thereafter for a time followed the edge of the Icelandic shelf on their westward journey. The 1971 winter fishery began some 15–20 naut. miles south of Hornafjörður but was not pursued in the immediate vicinity of the coast until at and west of cape Ingólfshöfði (Jakobsson and Vilhjálmsson 1970; Vilhjálmsson 1972).

A third variant was observed in the area southeast of Iceland in 1972 when the first and second migrations approached the coastal area along two different routes (Vilhjálmsson 1972). Thus, the first migration followed the warm/cold water boundary as described above and arrived in the Hornafjörður region from where it continued as usually westward in shallow waters. A short survey off East Iceland in late January showed that the second migration, located earlier in the month northeast of Iceland, had covered approximately 80–90 naut. miles and arrived in the deep water area just north of the cold/warm water boundary zone off the southern east coast. These capelin were, therefore, expected at the eastern south coast one or two weeks later.

As it turned out, however, this was not the case. In the second week of February a few large schools of capelin were located when approaching land at a position of about 25 naut. miles west of cape Ingólfshöfði, and a huge spawning migration was observed arriving in that area in the next 24 hours. This was somewhat surprising in view of the behaviour of the first migration, and because of the fact that repeated surveying of an area 15–20 naut. miles off the eastern south coast in the intervening period had failed to locate any capelin. It is thus obvious that the second migration arrived at the south coast along a completely different route from that taken by earlier as well as later migrations that winter. Thus, after entering the warm Atlantic water off Southeast Iceland, the second migration must have navigated west along or outside the shelf edge to approximately the longitude of cape Ingólfshöfði before approaching the coast from a southeasterly direction (Vilhjálmsson 1972). In later years, it became obvious that the above examples were no exceptions and that either route might be used. Many skippers even maintain that in some years capelin will keep to the deep waters off the shelf edge, all the way to Vestmannaeyjar before approaching land. This, however, has never been observed from research vessels.

Despite considerable research effort, especially in the 1970s, it has not proven possible to pinpoint exactly what variables, physical or biological, determine which of these routes a migration will take. This is somewhat surprising, particularly since the physical differences between them are considerable. The more oceanic route is much longer, and in effect the capelin have to enter the warmer Atlantic water while still outside the shelf edge off the southern east coast and stay within that water from then on. The more coastal approach is shorter. As stated previously, this route follows the warm/cold water boundary and allows the fish to choose a temperature regime and thus to control to some extent the rate of maturation. In general, it seems that the less advanced in maturity the capelin are when arriving at the warm water front, the more likely they are to take the longer and more southerly route.

In spite of the relatively small deviations, observed of the actual spawning migration route along the edge of the continental shelf east and north of Iceland in January, other and more dras-

tic changes have occurred through the years. Thus, in the period 1974–1993, the distance travelled by the capelin from early January until spawning in February–March has varied by as much as 300–400 naut. miles. The approximate locations of the main spawning migration in the first half of January 1974–1993 are given in Table 7.1. A more detailed description of these changes follows.

Table 7.1. The approximate locations of the main spawning migration in the first half of January 1974–1993.

Year	Latitude	Longitude	Location
1974	65°00′N	11°00′W	Central east coast
1975	66°00′N	11°00′W	East of Langanes
1976	67°15′N	16°00′W	North of Melrakkaslétta
1977	67°40′N	14°00′W	Northeast of Langanes
1978	67°20′N	16°00′W	North of Melrakkaslétta
1979	67°35′N	20°30′W	Western north coast
1980	67°30′N	24°30′W	Northwest of Vestfirðir
1981	67°30′N	13°00′W	Northeast of Langanes
1982–	64°20′N–	10°00′W–	East of
1993	66°00′N	12°00′W	Iceland

In the early 1970s, the first spawning migration was invariably located east of Iceland in the first half of January, the northernmost position in these years being northeast of the Langanes promontory. However, this was soon to change. Thus, in January 1976 the first schools were located some 50 naut. miles north of Melrakkaslétta on the eastern north coast, which was at least 120 naut. miles farther north and west than considered usual at the time (Vilhjálmsson 1977b). And in the beginning of January 1977 the first migration was found some 100–120 naut. miles due north of the central north coast, or still another 50–70 naut. miles farther to the north and west. The capelin remained at this position until almost the middle of the month when they started migrating to the east and southeast at full speed (Vilhjálmsson 1977b).

In the beginning of the year 1978 the first spawning migrations were found approximately at the 1976 position, *i.e.* north of Melrakkaslétta. However, the 1979 migration was located in deep waters north of the western north coast in early January, although it soon began to move rapidly eastward (Vilhjálmsson 1980a).

The westernmost January distribution, ever observed for capelin belonging to the east migrating part of the stock, occurred in the year 1980.

The fishing fleet began searching for capelin on the usual grounds east, northeast and north of Iceland in the first days of January 1980, but without success. Thus, the first part of the spawning migration was not located until 10 January near the ice edge at the outer slope of the Hali bank (66°40′N, 25°W) or some 120 naut. miles farther west than ever recorded before. At the end of the month the spawning migration was still off the central north coast (Vilhjálmsson 1980a, 1981a).

In 1981 the first spawning migration had arrived in the area northeast of the Langanes promontory already by 10 January and the situation thus reverted to the pre-1976 pattern (Vilhjálmsson 1982a). In the period 1982–1993 the first migrations had without exception already reached the area east or northeast of Iceland on that date.

In retrospect, the delay of the eastward migration of the spawning stock in the late 1970s as well as in 1980 concurs with the fact that in those years the spawning stock was distributed in or southwest of the Iceland-Greenland Channel in autumn and early winter but not off the central north coast of Iceland as has been the case since then for most of the spawning stock at that time of the year. Regular autumn surveys of the area north and northwest of Iceland first began in 1976. Therefore, no information is available about the situation before then.

7.1.3. Migration speeds

As already mentioned, the speed of the spawning migration in the more oceanic areas off North and East Iceland has always been extremely variable. The capelin may thus migrate in an irregular fashion at speeds of up to 20–30 naut. miles per day for periods of several days, while slowing down to 10–20 naut. miles per day or even stopping completely for periods of time in between.

The centre of the first migration has most frequently been located in the area off Northeast Iceland in early January. The arrival of these migrations in the cold/warm water boundary zone off the southern east coast, no more than 100–150 naut. miles further south, has nevertheless varied quite remarkably over the years. Thus, in the period 1969–1975 the arrival of the spawning migrations in these waters has varied

Table 7.2. Date of arrival of the first spawning migration at the cold/warm water boundary off Southeast Iceland in 1969–1975.

Year	Day	Month
1969	01	February
1970	05	February
1971	05	February
1972	10	January
1973	25	January
1974	15	January
1975	05	February

within a time span of approximately one month as shown in Table 7.2.

In the period 1976–1980 the maturing capelin were distributed much farther to the north and west at the beginning of the year as described in the previous section. In 1976, 1977 and 1979 the fish were able to make up for a spatial difference of some 100–150 naut. miles, arriving in all cases in the boundary zone off the eastern south coast around 1 February. However, this was not the case in 1978 and 1980 when the spawning migra-

tions progressed exceedingly slowly while off the north coast of Iceland. As a result, the 1978 migration did not arrive off the southern east coast until around 20 February and the 1980 migration probably even later. Although the progress of the 1980 migration south of the Langanes promontory was not monitored, these capelin had not arrived at the eastern south coast when that area was closed to all capelin fishing on 10 March 1980 (Vilhjálmsson 1981a).

The progress of some of the spawning migrations in the 1970s was timed quite accurately. An example is illustrated in Figure 7.3. The findings are illuminating with respect to long and short term average speeds which should be taken into account when carrying out *in situ* stock abundance assessments as will be discussed in a later section.

The onset of the westward migration along the south coast, as well as its speed, may vary even more than the time of arrival at the boundary off the southern east coast and migration speeds in the oceanic area. Thus, the spawning migration of 1970 did not arrive at the southeast coast until
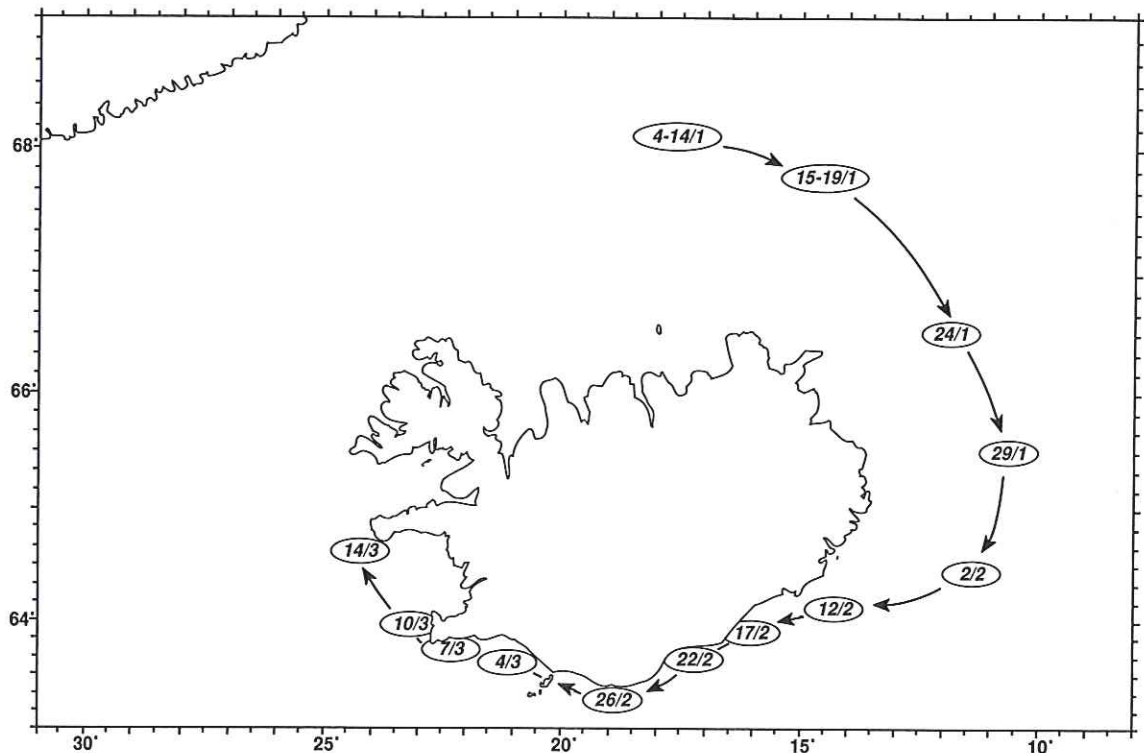

Figure 7.3. The geographical location of the first spawning migration in the period January–March 1973.

25 February, in spite of the fact that these capelin had been observed at a distance of 50–70 naut. miles off the southern east coast about three weeks earlier. That year no spawning at all was detected off the western south coast, not to mention Southwest Iceland (Jakobsson and Vilhjálmsson 1971). In 1972, on the other hand, the first migration arrived off the southeast coast already on 14 January, and that year capelin spawned over the entire area from east of Hornafjörður in the east, to Breiðafjörður on the west coast (Vilhjálmsson 1972).

The reasons for the variations in travel times from the boundary zone to the spawning grounds are far from clear. Varying feeding conditions and temperature in the northern part of the Iceland Sea, as well as elsewhere in the distribution area of the maturing stock during the previous summer, probably constitute part of the explanation by determining the stage of maturity and thus the physiological state of readiness to cross the cold/warm water boundary when the fish arrive there. Thus, the capelin may, in some years, proceed along the outer shelf edge off East Iceland and from there approximately follow the warm water boundary up to the southeast coast at a more or less even speed. At other times the migration may linger in scattered concentrations, particularly in the boundary zone off Southeast Iceland, for a considerable length of time or even make a lengthy detour to the southeast through more offshore and warmer waters as already described.

The speed with which the spawners migrate west along the south coast is also highly variable. Thus, there are instances when the area between cape Ingólfshöfði in the east and the Reykjanes peninsula in the west, a distance of some 180 naut. miles, has been traversed in less than one week, while on other occasions the capelin have taken much longer time to cover this same distance. And in extreme cases, such as in 1970 and 1978, capelin have not even managed to reach the western part of the south coast, let alone the Faxaflói and Breiðafjörður spawning grounds on the west coast (Jakobsson and Vilhjálmsson 1971; Vilhjálmsson 1979a).

The highly variable speed of migration west along the south coast is undoubtedly controlled by a number of variables, both biological and physical, which are difficult to determine. The migration speed may be affected by variable wind direction and velocity which in turn can affect the intensity of the westward flowing coastal current. Thus, Jakobsson and Vilhjálmsson (1971) pointed out the apparent connection between the extremely slow westward progress of the 1970 spawning migration along the south coast and the high frequency of westerly and southwesterly gales in that year, when in fact no capelin spawning was detected west of cape Dyrhólaey on the central south coast. Conversely, in 1971, following a major storm from the east, the first migration rounded the Reykjanes promontory less than 2 weeks after it arrived at the southeast coast in the Hornafjörður region (Vilhjálmsson 1972). In this short period it had thus covered about 240 naut. miles.

However, the reduced spawning area in 1970 may also have been the result of the apparently small spawning stock in that year and an unusually advanced state of maturity on the late arrival at the southeast coast in the last days of February. A similar situation was again encountered in 1978. Admittedly, the size of the spawning migrations was not assessed in absolute terms on either of these occasions. However, there is no doubt that they were comparatively small. In 1978, the roe content of the females was also over 15% just before they arrived at Lónsvík on the southeast coast. Both in 1970 and 1978 negligible spawning activity was registered west of cape Dyrhólaey (Vilhjálmsson 1979a).

The first, main spawning migrations usually spend about 3 weeks in the warm Atlantic waters before spawning, much of that time in rapid migration towards the west coast spawning grounds. Late spawners tend to be more mature when arriving in the coastal area, migrate much more slowly and spend far less time in the warm south coast waters before spawning. As a result, it is the size of the first 1–3 spawning migrations, their speed of progress along the south coast and the time difference between them that determines the duration of the capelin spawning season at South and Southwest Iceland. Usually, these variables also determine the amount of spawn deposition in the main southwestern and western parts of the spawning area. However, deviations arising from the difference in time spent in the warm Atlantic waters in more offshore areas off Southeast Iceland, often complicate the picture and apparently they are sometimes responsible for shortening the time on the
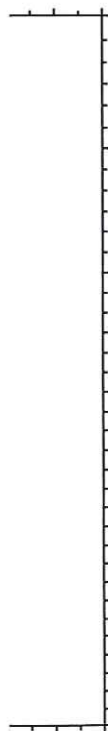
coastal spawning grounds, as compared to the normal situation.

The role of the late arriving and far less numerous south coast spawners in the propagation of the stock has never been determined. In spite of their inferior size and numbers, it could, however, be quite important. This would make for an interesting study and could probably be determined to some extent due to fairly obvious size differences between larval cohorts and different drift patterns. In most instances, spawning on the grounds off the western part of the south coast and the west coast seems to be completed by late March or early April, while off the eastern south coast spawning may be prolonged into May (Magnússon 1966; Friðgeirsson 1980).

7.2. The western spawning route

It was established at the beginning of the southwest coast fishery of the 1960s that migrations of pre-spawning capelin first arrived at the southeast coast of Iceland and proceeded westwards from there. However, the capelin fishery off Southwest Iceland had not been going on for long before a behaviour pattern of capelin schools was observed which did not conform to expectations. This led some of the skippers to theorize that towards the end of the season some of the schools entering the west coast spawning grounds did so from a westerly direction.

7.2.1. Evidence from the fishery

In 1974 the first migration arrived at the southeast coast (Lónsvík) as early as 22 January after having followed the warm/cold water boundary from the east Icelandic area to that position. Later migrations followed the same route and the main spawning activity, which for a time took place over the entire area from Southeast to West Iceland, seemed to be completely over by the relatively early date of mid-March (Vilhjálmsson 1974, 1974a).

However, around the middle of March 1974 large concentrations of mature capelin were located, quite unexpectedly, just off the Snæfellsnes peninsula on the central west coast. No signs of such a migration had been detected farther south and east earlier on, but trawlers operating off the Vestfirðir peninsula in the weeks before had, on the other hand, registered considerable amounts of mature capelin, both by echo sounders as well as in their fishing gear. On arriving at the Snæfellsnes peninsula these capelin were in a less advanced stage of maturity than is usual for capelin, arriving in this area from the east.

After they were discovered, these late arriving capelin could indeed be fished in the Snæfellsnes area for 2–3 weeks before spawning had progressed to the point of making the fishery unprofitable. In other words, the capelin could be fished for almost the length of time which capelin, belonging to the eastern stock component, normally spend migrating west to Snæfellsnes through the warm south and west coast area before spawning commences. Furthermore, it was found that the fish tended to migrate in a southerly direction and for some distance into the Faxaflói bay to the south of the Snæfellsnes peninsula. All the evidence, therefore, indicated that these capelin had indeed remained off Northwest Iceland to migrate to the west coast spawning grounds directly from there, a short distance compared to the usual eastern route (Vilhjálmsson 1974, 1974a).

In late February 1975 a large spawning migration was unexpectedly discovered some 10–15 naut. miles west of Garðskagi (Southwest Iceland). At that time the first known migration, arriving along the eastern route, was still located off the eastern south coast, some 160 naut. miles away. The capelin constituting both of these migrations were found to be at a similar stage of maturity and in the end both spawned on the west coast grounds. Some two weeks later another but smaller aggregation of capelin was located 20–35 naut. miles to the west of the Snæfellsnes peninsula, rapidly heading east towards land. These capelin were followed by fishing and research vessels and found to make their way east along the south side of Snæfellsnes and spawn in northern Faxaflói at the end of the month, an unorthodox route for a migration if it had arrived from the east (Anon. 1976). At the time, these two incidents were again thought to indicate à migration from the northwest. However, it now seems possible that the capelin that were located west of Garðskagi in February may have arrived there from the east along a more offshore route than usual and until then simply gone undetected.

Unfortunately, no vessel time was available for

investigating possible migrations from the north-west area to the west coast spawning grounds in 1976. Nevertheless, it can be stated with certainty that such migrations did indeed take place in that year. On 11 March fishing vessels located large capelin concentrations some 15–20 naut. miles west of the Snæfellsnes peninsula (Vilhjálmsson 1977a). This migration was headed due east, progressing past the tip of the peninsula, and into the northern part of Faxaflói where it turned southward. Having crossed the entire width of Faxaflói bay, a distance of about 60 naut. miles, some of these capelin rounded the Reykjanes promontory to spawn in the coastal area at least 20–30 naut. miles farther east. Although the age composition of these capelin was similar, they were distinctly less mature than the fish belonging to the migrations that had shortly before arrived along the eastern route. Considering all the evidence, it is almost certain that this migration originated from somewhere off the Vestfirðir peninsula and not from east of Iceland.

7.2.2. Research vessel surveying and mapping of the western approach of spawners

In 1977 considerable research effort was, for the first time, devoted to searching for and monitoring migrations of maturing capelin off the northwest peninsula of Iceland (Vestfirðir). However, only small quantities of spawners mixed with immatures were registered at and outside the edge of the shelf between 66°N and 67°30′N. In late February the maturing part of this mixed stock approached the coast by some 10–15 naut. miles but otherwise stayed in the same general area (Fig. 7.4). As it turned out, this capelin spawned in the last days of March and in April on the shelf some 20–40 naut. miles offshore to the west of the southern Vestfirðir peninsula (Vilhjálmsson 1977a; Vilhjálmsson and Malmberg 1977).

Surveying of the area west and northwest of the Vestfirðir peninsula in the winter of 1978 revealed the presence of large amounts of juvenile capelin but no spawners (Vilhjálmsson 1979a). However, in the following year (1979) a survey of this area in early February showed the presence of large amounts of capelin, most of which were maturing spawners. An acoustic abundance estimate indicated that the latter amounted to approximately one half of the 1979 spawning stock
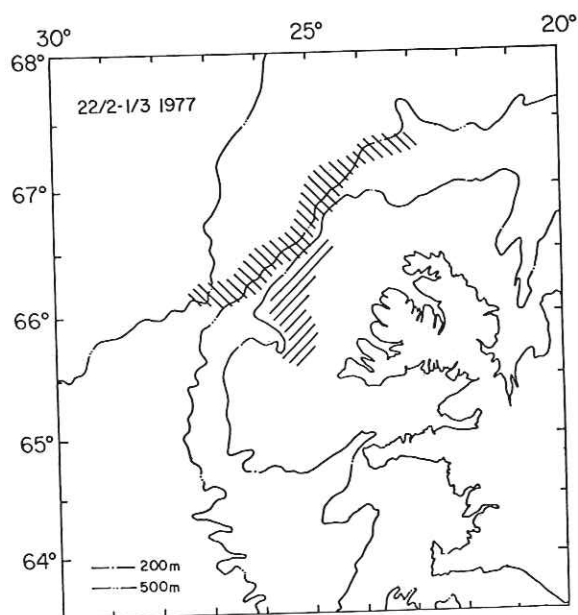
Figure 7.4. The observation of capelin entering the banks off the Vestfirðir peninsula from the west to spawn there in March 1977. Distribution area in February (right slope), spawning area in March–April (left slope).

(Vilhjálmsson 1980a; Vilhjálmsson and Reynisson 1979). Further surveying in the third week of February showed that the spawners had competely separated from the juveniles and were slowly migrating south along the shelf edge. The location of this migration in the first half of February 1979 is shown in Appendix I.1, Figure IIIa and IIIb, and its path of migration in the following 4 weeks south across the outer Látragrunn bank and east along its southern edge to spawn on both sides of the Snæfellsnes peninsula in the latter half of March 1979, is indicated in Figure 7.2 (Vilhjálmsson 1980a).

Around 20 February 1980 a small spawning migration was located at Snæfellsnes and two larger ones a few days earlier on the outer Látragrunn bank as well as west of the Vestfirðir peninsula (Vilhjálmsson 1981a). These capelin gradually migrated to the Faxaflói area and most of them continued south from there to round the Reykjanes promontory. In part, these capelin migrated some 60 naut. miles east along the south coast before they spawned.

In the 1980s it gradually became clear that mature capelin approaching the west coast spawning grounds from the northwest are by no means an annual occurrence. On the contrary, these ap-

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proaches became less frequent and smaller than they had been in the latter part of the previous decade. Although the case is by no means clear-cut, it seems that the presence of appreciable concentrations of mature capelin off the Vestfirðir peninsula in winter, and the subsequent migration directly south and southeast towards the west and/or southwest coast spawning grounds is associated with a western distribution of the spawning stock in late autumn and early winter in the year before. This has not been the case in the 1980s or the early 1990s. In this period the number of spawners, arriving along the western route, have always been of minor importance compared to those from the east. It is also possible that capelin, migrating from the west to spawn, had overwintered in the Dohrn Bank area, *i.e.* in the region of the East-Greenland plateau. However, such cases have never been recorded, neither by research nor fishing vessels.

7.3. North coast spawning migrations

In the 1970s several short surveys were carried out in order to study the abundance and migrations of pre-spawning capelin off the north coast in late March and April. With the exception of 1977, when a small migration of spawners con-sisting of several schools was found in the process of arriving along the western side of the Eyja-fjörður deep from the north, the findings con-sisted of single schools in shallow waters (Vil-hjálmsson 1977).

In the north Icelandic area capelin spawners generally approach the coast from the north (cf. Fig. 7.2) along the troughs in the submarine plateau that often continue from the fjords cut-ting into the coastline. Moving south along these submarine valleys, the capelin tend to follow the western slopes of the valleys and in doing so mi-grate in the direction of the average bottom cur-rent. This behaviour persists after the fish have entered the fjords in which they spawn, from where they will continue outwards on the eastern side if they have not already finished their task (Th. Maríusson, personal communication).

From the evidence that has become available in the last 3–4 decades, it is obvious that, in this period, capelin spawning in other areas than those off South and West Iceland have contri-buted little to the spawning biomass. As men-tioned in an earlier section, mass spawning of capelin at North and East Iceland may, however, have been much more common in the 1920s and 1930s (Sæmundsson 1926, 1934) than has been the case in recent decades.

8. CAPELIN SPAWNING GROUNDS AT ICELAND

8.1. Primary spawning grounds

At least during the last three decades, the main spawning grounds of the Icelandic capelin have been on the sea bed off the south and west coasts as shown in Figure 8.1 (Vilhjálmsson 1983). As pointed out in an earlier section and well documented (see *e.g.* Stefánsson and Jónsdóttir 1974; Malmberg 1978) these areas are hydrographically quite stable and dominated by Atlantic water. At spawning time in March and April and during incubation, the temperature generally ranges from 5–7°C and the salinity equals or slightly exceeds 35.0.

These narrow temperature and salinity limits are, however, not found inside a narrow region, in the immediate vicinity of the coast, where both salinity and temperature may be lowered considerably due to the influence of runoff from land. This influence is mostly limited to the immediate surface layers whereas near bottom temperatures are less affected except in very shallow waters. The results of a study carried out by Malmberg (1974), of the effects of the sudden release of large amounts of fresh water from a sub-surface reservoir in one of Icelands largest glaciers, indicated a drop in near-shore surface temperatures only, while near-bottom temperatures remained
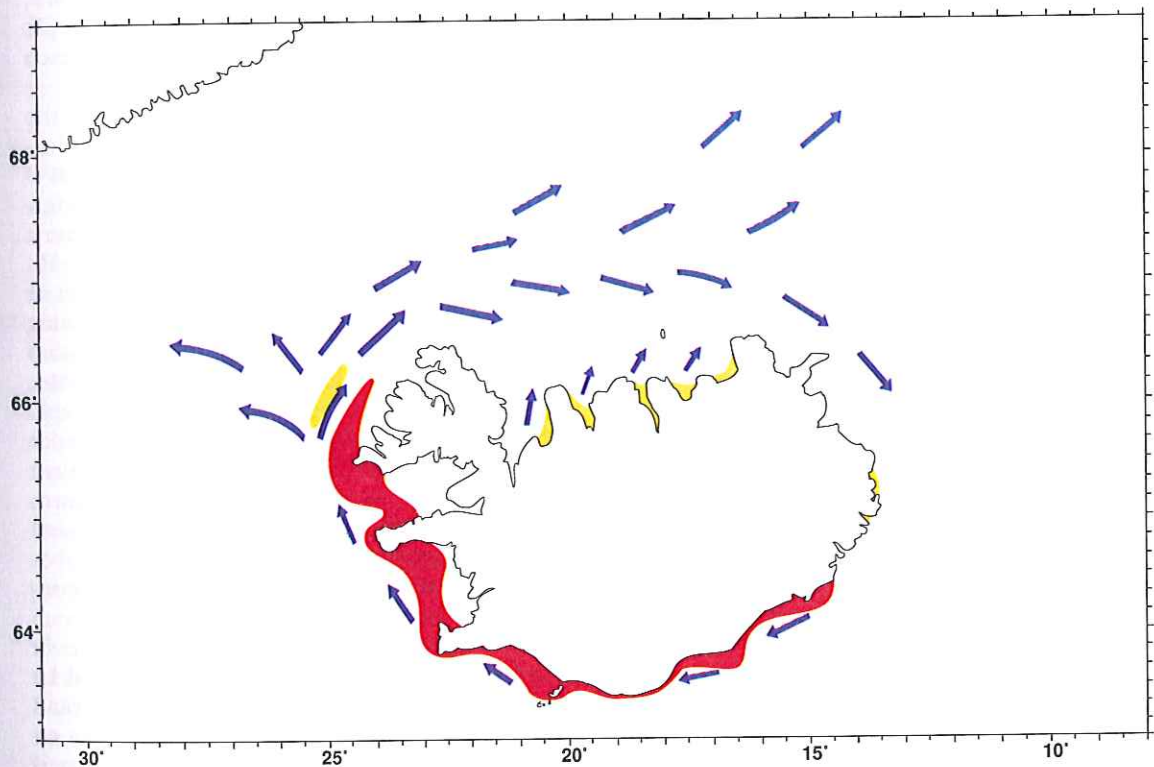

Figure 8.1. The spawning grounds of the Icelandic capelin 1966–1993. Red colour: main spawning areas. Yellow colour: less important spawning areas. The arrows indicate larval drift.

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unaffected except for areas close inshore. As most of the spawning activity and egg deposition takes place outside this area, environmental variables associated with runoff water and cooling caused by the proximity of land in winter, are of minimal importance for the spawning process and during the incubation period.

The spawning temperatures of 5–7°C are higher than those recorded for the two other demersally spawning major capelin stocks of the Barents Sea and the Grand Bank of Newfoundland, both of which are reported to spawn at temperatures of about 2–5°C (Sætre and Gjøsæter 1975; Carscadden et al. 1989, 1989a). Kanneworff (1967) gives temperature ranges of 1.9–3.4°C at the beginning of spawning, increasing to 6.6°C later in the season for the beach spawning West-Greenland stocks. The spawning temperatures at Iceland are, however, lower than recorded for many beach spawning areas, especially in the latter part of the season when solar radiation may sometimes warm the immediate surface layer beyond the temperature tolerance of the spawning capelin (10–11°C) and force them to spawn at depths some distance away from the beach (see e.g. Hart and McHugh 1944; Templeman 1948, 1968; Winters 1966; Velikanov 1984; Pahlke 1985).

Although the Icelandic capelin may sometimes spawn in very shallow waters, the bulk of the stock spawns demersally and well below the low water mark. In his 1979 survey of capelin spawning grounds at Iceland, Thors (1981) found that capelin had deposited their eggs at depths ranging from about 8 to 90 meters with a maximum density between 30 and 50 m. These observations are generally in agreement with indirect evidence from commercial as well as research vessel samples and echo recordings, although from the same evidence it can be inferred that the stock may also spawn outside this range, i.e. from just below the low water mark down to about 150 m depth.

In the literature there are several earlier references to capelin being found stranded on beaches at South and Southwest Iceland in the spawning season, even to the extent of forming a layer of almost 12 inches in thickness (e.g. Eiríksson 1782; Sæmundsson 1926, 1927; Steinsson 1944; Kristjánsson 1985). It is doubtful whether this phenomenon can be taken as a sign of beach spawning acivity as observed for example in

Newfoundland and Labrador. To this author's knowledge that phenomenon has never been reported from the south and west coasts of Iceland. A more likely explanation of stranded capelin on Icelandic beaches seems to be that offered by Sæmundsson (1926, 1927) who states that dead or dying capelin may drift ashore during periods of onshore winds. Thus, it is not difficult to visualize the possibility of the occasional school being caught by the odd outsize breaker in the heavy winter surf and thrown upon the beach. This is supported by the fact that when the present author had the opportunity to observe stranded, spent capelin on a Reykjavík beach in March 1983, there were no obvious signs of spawning products on that beach or in the immediate neighbourhood as is the rule where beach spawning occurs.

Records of stranded capelin on Icelandic beaches have been very few and far between in the latter half of this century. It should be noted, however, that the coastline near the main spawning areas is uninviting and out of the way of every-day human traffic. These locations are, therefore, not frequented nowadays as people fortunately no longer have to forage on the beach for their food.

Thors (1981) determined that the nature of the spawning substrate off South and Southwest Iceland ranges from muddy sand to sandy gravel (grain size 0.125 to 4.0 mm) with a clear preference for gravelly sand (grain size 1 to 4 mm). Muddy sediments seemed to be avoided. He reasoned that otherwise sediment size was not of importance in the selection of capelin spawning grounds at Iceland for the simple reason that there is little other than a fairly fine substrate, consisting largely of volcanic material, available in the area. Thors concluded that water depth and in particular the rate of water circulation are the decisive factors in the main Icelandic spawning areas as active circulation will not only ensure the necessary oxygen supply and remove metabolites, but also prevent siltation which can be considerable in south Icelandic waters.

Thors' observations on sediment size are in good general agreement with those reported by Pitt (1958) for the Southeast Shoal of the Grand Bank (0.5–2.2 mm), as well as for populations on both sides of the Pacific, where the preferred grain size of the spawning substrate is reported to range from 1–5 mm (Hart and McHugh 1944;

Velikanov 1984). However, it must be borne in mind that Pitt's estimates were obtained from samples of capelin eggs adhering to patricles of substrate in haddock stomachs and may not represent a valid sample of the spawning substrate (Sætre and Gjøsæter 1975). Templeman (1948) observed a much coarser substrate in the range of 2.5–15 mm for capelin spawning on Newfoundland beaches, whereas Sætre and Gjøsæter (1975) give 5–15 mm as the preferred range for the deep spawning Barents Sea capelin.

8.2. Secondary spawning grounds

In addition to the south and west coast areas, capelin spawning takes place annually in fjords and bays on the north and northwest coasts of Iceland and sporadically on the banks off the Vestfirðir peninsula (cf. Fig. 8.1). Observations of capelin spawning at the east coast of Iceland have been rare in the last few decades. Water temperatures in the northern and in particular the eastern areas are much lower than in the

Table 8.1. Environmental variables at some major spawning sites of capelin as given in the literature. FS: fine sand, SG: grarelly sand.

Location	Temperature °C	Subtrate grain size in mm	Depth in m	Source
Northern Norway-Murman	1.5–6.5	5–15	10–100	1), 2), 3)
Iceland	5.0–7.0	0.1–4.0	5–90	4), 5), 6)
West-Greenland	1.9–8.5	?	0–5	7)
Newfoundland				
East and south coast	5.5–10.7	≈ 2.0	0–10	8), 9)
Grand Bank	2.0–5.0	0.5–2.2	40–50	10), 11)
Eastern Pacific area	5.0–10.6	FS – SG	0–5	12)
Western Pacific area	2.0–14.0	0.3–10.0	1–2	13)

1) Prokhorov (1967); 2) Bakke and Bjørke (1973); 3) Sætre and Gjøsæter (1975); 4) Sæmundsson (1926); 5) Thors (1981); 6) Vilhjálmsson (1983); 7) Kanneworff (1967), 8) Templeman (1948); 9) Nakashima and Taggart (1990); 10) Pitt (1958a); 11) Carscadden et al. (1989); 12) Pahlke (1985); 13) Velikanov (1984).

Recently, Carscadden et al. (1989, 1989a) have shown that the Southeast Shoal capelin mainly spawn in a specific part of the Grand Bank, an area that once was an exposed beach. They have also shown that for the probable reasons of survival the main spawning activity is delimited broadly by bottom temperatures in excess of 2°C and suggest that specific locations of high spawn deposition are further determined by types of substrate. Recent investigations by Nakashima and Taggart (1990) of grain size and capelin egg deposition on exposed Newfoundland beaches indicate a preferred size of about 2 mm and consequently a much narrower range of substrate particle sizes than previously thought. It seems, therefore, that most capelin stocks prefer a much finer grained spawning substrate than that observed *in situ* by divers for the Barents Sea stock.

A comparison of environmental variables at the spawning grounds of various capelin stocks or population complexes is given in Table 8.1.

south (1–3°C in March and April) which makes for a later spawning that may sometimes last through May into June. In comparison to the south and west coast spawners, the north and east coast capelin are usually smaller in size and the numbers limited. Since they tend to keep fairly close to the shore and the surface, they are often conspicuous, attracting much attention locally. Although the spawning of the north coast capelin has been observed from the shore (G. Jörundsson, personal communication) it seems doubtful from the description whether this spawning activity can be classified as belonging to the spectacular beach spawning category. What has been observed on such occasions is simply capelin spawning on the bottom in shallow waters.

In the 1970s several surveys were carried out in the north Icelandic area in order to determine the abundance and feasibility of a large scale fishery. The results were disappointing and, as stated in a previous section, it is quite clear that at least in the last 2–3 decades only minor proportions of

the stock have spawned outside the south and west coast grounds. But this need not necessarily always have been so. In connection with the large scale warming that occurred in Icelandic waters in the 1920s and 1930s, Sæmundsson (1934) reported a scarcity of capelin at Southwest Iceland, as well as in the westernmost part of the south coast area as of 1928, concurrent with an increase in capelin abundance in the north and east during the spawning season. While there is no reason to doubt the general validity of Sæmundsson's observation that capelin did not migrate as far west as usual along the southwest coast, it should be borne in mind that he had no means to judge the situation quantitatively in other areas which the capelin continued to visit. At any rate, the extremely cold period in the late 1960s and the comparatively warmer conditions of most years since the early 1970s did not result in any obvious or drastic long-time changes in the location of the main spawning grounds of the Icelandic capelin.

The Icelandic stock of capelin does not seem to have any important spawning grounds outside Icelandic waters in spite of the fact that this capelin stock may undertake extensive migrations in the Iceland Sea in summer. Although the presence of spawners in the vicinity of Jan Mayen has been established, their abundance was found to be very low (Anon. 1986). As far as is known the same holds true for capelin spawning in the fjords on the east coast of Greenland, but these capelin need not be part of the capelin of the Iceland Sea and Icelandic waters, *i.e.* the Icelandic capelin stock as here defined.

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9. SPAWNING BEHAVIOUR

The spawning act as exhibited by beach spawning capelin has been described by many authors (cf. Jeffers 1931; Sleggs 1933; Templeman 1948). The description given by Winters (1969) for capelin spawning on Newfoundland beaches is as follows:

"Generally one female is confined between two males in the groove formed by the ventral and dorsal spawning ridges and the enlarged projecting fins of the males. Occasionally, for the lack of a suitable partner, only one male will participate . . . . Masses of capelin are deposited on the beach by the onrush of a wave, and the recession of the wave causes the capelin to change direction and now face the beach swimming against the receding water. The spawning contact is then made as the female is positioned in the hollow formed between the two males. The triplet or pair then carry out violent wriggling motions which scoop out a hollow into the sand into which are deposited the eggs of the female (up to 60,000) mantled by the milt of the male(s). After separating there is a few seconds' respite before the next wave comes in, and if they are fortunate they will be carried back into the sea again. Many fail to regain the water and become stranded on the beach and die. Owing to their constant attendance on the beach most of the stranded capelin are males which by the end of the spawning season are so exhausted and emaciated that many die anyway."

Due to the demersal spawning habit the spawning behaviour of the Icelandic capelin has not been studied directly *in situ* in any detail. In the mid 1970s, however, a study of spawning behaviour of some 300 capelin (about equal number of males and females) was carried out in an aquarium at Vestmannaeyjar off the central south coast (Friðgeirsson 1974, 1976).

In the beginning of the experiment the capelin schooled and exhibited random distribution of sexes as well as strong responses to light and other unexpected stimuli, a behaviour which is typical for the migration phase. An example of such a school is shown in Figure 9.1. About three days before the first spawning occurred the males began leaving the schools to swim in a searching fashion near the bottom, this behaviour becoming more frequent as the time of spawning approached.

As spawning began individual females entered the group of males where one and occasionally two males attached themselves to the females by means of the spawning ridges and upturned pelvic and pectoral fins. The pair or threesome would then move rapidly for 1–2 seconds along the substrate, oblivious of any hindrance that might be in their way, leaving a depression of 0.5 to 1 cm in the sand and spreading eggs and milt over a 10–15 cm wide stretch on the bottom (cf. Fig. 2.5 a and b).

After the intense process of copulation the sexes separated, the female swam away while the male rejoined his fellows and resumed spawning behaviour after a while. On almost all occasions the male would mate more than once while the female appeared to spend all her roe in one copulation. After becoming spent the females swam randomly around in the aquarium tanks, apparently out of phase with the other capelin. In the aquarium, the spawning activity seemed to occur in periods of about 10–15 minutes duration, with considerable time elapsing between them. The onset and cessation of spawning activity seemed to be determined by the presence or absence of ripe females.

Many capelin of both sexes were wounded during the spawning process, this being much more extensive and frequent in the case of the males. These wounds did not heal and invariably led to death. In this particular aquarium experiment all males died while about 10% of the females were still alive about one month after spawning when the experiment was discontinued.

Figure 9.1. A pre-spawning school of capelin in an aquarium tank. The special "spawning dress" of the male, *i.e.* the longitudinal hairy ridges, the concave shape of the pectoral and pelvic fins and the swollen base of the anal fin, can be clearly distinguished in comparison with the single female, visible in the upper centre of the picture.

(Photo: Sigurgeir Jónasson).

That Friðgeirsson's aquarium observations represent a fair simulation of the natural situation is supported by many sources. Thus, all *in situ* observations on the actual spawning act closely resemble those of Friðgeirsson's, but for obvious reasons these are mostly limited to beach spawning stocks (cf. Jeffers 1931; Sleggs 1933; Templeman 1948). Practically all reports on the spawning behaviour of beach spawning capelin note the pre-spawning separation of the sexes, the females entering the dense aggregations of waiting males as the females become ready, and the apparently higher spawning mortality of the males. Off northern Norway, Sætre and Gjøsæter (1975) reported a drastic change in schooling and behaviour patterns when on or near the spawning grounds. This included a dissolution of the large migratory schools and the formation of local, dense near-bottom schools and less dense concentrations in the upper layers nearby. They were, however, not able to observe the actual sex segregation or the actual spawning process.

However, Carscadden (personal communication) has observed that prominent pre-spawning segregation of sexes takes place among capelin of the Southeast Shoal of the Grand Bank. This appeared as echosounding records on the bottom and in midwater where sampling with bottom and midwater trawls respectively revealed that the near-bottom schools consisted almost exclusively of males, while the pelagic catch consisted of 45–96% females.

Vilhjálmsson (1974a) reported an approximately even sex distribution in commercial catches taken off East Iceland in the beginning of the year. For the first two weeks in the warm south coast waters he found that females persistently represented more than one half of the catch by number, the ratio increasing to about 75% in the third week. Shortly thereafter further fishing tended to return catches with complete predominance of males. These results may be explained as follows:

While capelin are still in the cold waters east of Iceland as well as during the first stages of the migration along the south coast, schooling is usu-

ally of the migratory type with the sex distribution approximately equal. As spawning approaches, the sexes apparently begin to segregate with the formation of dense near-bottom schools containing predominently males and somewhat looser aggregations higher in the water column where females predominate. This phenomenon is frequently seen on echo recordings and with experience it has proven possible to a certain extent to catch the sexes selectively from then on. After having taken part in the spawning act the females tend to disperse while the males stay on at the same place. Therefore, if the fishery on a spawning ground persists throughout the spawning period, it becomes progressively more difficult to find and fish females. In the end, the catch will consist exclusively of males which remain available to the fishery practically until death.

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10. HATCHING AND LARVAL DRIFT

The average egg size among Icelandic capelin is 1.12 ± 0.12 mm (Friðriksson and Timmermann 1951). It has been shown that at the temperatures prevalent on the spawning grounds off South and Southwest Iceland (5–7°C) hatching takes place in 20–25 days (Friðgeirsson 1976). In the immediate vicinity of the coast, temperatures may, however, be somewhat lower and hatching delayed beyond the above time limit. In Friðgeirsson's experiment salinity variations between 25.9 and 35.0 did not seem to affect hatching or larval development. Later laboratory experiments on Balsfjord capelin (Davenport and Stene 1986) and capelin spawning at Iceland (Davenport 1989) have shown that capelin embryos are extremely resilient with regard to salinity variations, developing normally within a range of 1.7 and 78.0 salinity units.

With the bulk of the spawning normally taking place in March, the hatching of capelin larvae usually starts in late March and peaks in April. However, as stated in the previous section, spawning may in exceptional cases begin already in mid-February or its onset may be delayed until mid-March and the first larval emergence be advanced or delayed accordingly. Due to the fact that the small, late arriving migrations tend to be in a more advanced state of maturity on arrival than those arriving first, they almost always spawn off the eastern south coast and may extend the spawning season to last nominally throughout April and even into May. Similarly, small migrations from the northwestern overwintering area may arrive as late as April or even early May on the west coast grounds. Capelin larvae may, therefore, continue to appear in the main spawning areas off South and West Iceland until late May or even early June, a fact which was confirmed during a study programme of these most important spawning grounds in the years 1976–1979 (Friðgeirsson 1980). In this context it is of interest to note the recent record (10 June 1992) of spawning capelin and capelin roe in haddock

stomach samples some 20–25 naut. miles off Látrabjarg, the southernmost promontory of the Vestfirðir peninsula.

In the subsidiary spawning areas off northern and eastern Iceland, the main spawning activity usually takes place one to two months later than in the south and west and at temperatures that are about 2–3°C lower. At the north and east coasts spawning is, therefore, usually observed in April and May, the larvae emerging in May and June or even as late as July (Jespersen 1920). There is, however, much less documentation available on capelin spawning activity in the north and east Icelandic area than off the south and southwest coasts.

In an aquarium experiment it was found that on hatching, the larvae measured 7.2 mm in length (Friðgeirsson 1976). However, during a study of the early stages in the life history of several fish species spawning off South and Southwest Iceland, which was conducted in the period 1976–1979, the smallest larvae caught were about 5 mm in length (Friðgeirsson 1979). The size at hatching may, therefore, apparently vary between about 5 and 7.2 mm.

It has been shown that among beach spawning stocks, capelin larvae tend to stay within the spawning ground substrate to emerge during periods of onshore winds, and that frequent onshore winds will enhance the physical condition of the larvae at emergence. This mechanism also seems to influence survival due to increased availability of food and reduced predator abundance (Frank and Leggett 1981; Leggett et al. 1984). Frank and Carscadden (1989) have shown how in 1986 the formation of the dominant larval cohort among the bottom spawning stock on the Southeast Shoal of the Grand Bank coincided with a storm event which resulted in sharp increases in bottom currents and temperatures. Similarly, in 1987 when there were no significant storm events, they recorded no dominant larval cohorts and larval abundances in that year were

indeed 1–2 orders of magnitude smaller than in 1986. Thus, it appears that, as in the case of beach spawners, hatching of the larvae of the demersally spawning capelin of the Southeast Shoal may indeed be triggered by such external events which in turn may also enhance their chances of survival.

On the other hand, Friðgeirsson (1976) stated categorically that the larvae of the Icelandic capelin ascend to the surface immediately on hatching. He did not, however, qualify his statement except by saying that on hatching the larvae have reached that stage in morphological development which enables them to take external food. There have been no studies, similar to those of Frank and Carscadden (1989), carried out in the Icelandic area. Although the capelin spawning grounds off South and West Iceland are probably in many ways more environmentally stable than those on the Southeast Shoal of the Grand Bank, it is clear that seasonal but irregular natural events do occur there and may have decisive influence on developments in the food chain, especially in the shallower part of the area. Obvious examples are storm events, varying wind directions as well as the onset and intensity of the spring floods which enhance stability and biological production (Ólafsson 1985; Thórdardóttir 1986; Stefánsson and Ólafsson 1991).

On ascending to the surface waters the capelin larvae start drifting with the surface ocean currents to the areas west and north of Iceland, to some extent spreading out into more offshore waters as they do so (cf. Fig. 8.4). No comprehensive research has been carried out specifically in order to map the temporal/spatial progress of the capelin larvae during the first months of their life. Nevertheless, it is clear that this may be quite variable. Thus, Friðgeirsson (1980) found that in the 1975–1979 period practically no capelin larvae had progressed farther north and west than Látrabjarg on the Vestfirðir peninsula by mid-June, while Magnússon (1966, 1968) reported capelin larvae in abundance off the central north coast at the same time of year in 1962 and 1964. It is fairly obvious that the rate of progress of capelin larvae to the western and northern areas is linked to fluctuations in the intensity of the coastal current as well as variations in the rate of advance of Atlantic water to the north Icelandic area in spring and early summer.

11. DISTRIBUTION OF 0-GROUP CAPELIN IN AUGUST

The distribution of 0-group capelin in the Iceland-Greenland area has been recorded annually since 1970 (Vilhjálmsson and Friðgeirsson 1976; Anon. 1978–1981; Vilhjálmsson and Magnússon 1981–1986; Magnússon et al. 1987–1989; Magnússon and Sveinbjörnsson 1990–1993). These surveys have generally covered the Icelandic shelf area together with deeper waters to 68°N off the north and northwest coasts and the northern Irminger Sea from approximately 63°N to 66°N. Survey methods and data handling were described by Vilhjálmsson and Friðgeirsson (1976).

Table 11.1. The percentage division of the 0-group capelin index by number in the various parts of the distribution area.

Year class	Northwestern Irminger Sea	West	Iceland North	East
1970	9	73	18	0
1971	+	37	63	+
1972	+	42	58	+
1973	12	34	40	14
1974	19	33	43	5
1975	3	42	53	5
1976	6	16	31	47
1977	5	44	44	7
1978	+	7	93	+
1979	8	39	51	2
1980	7	44	46	3
1981	35	45	20	0
1982	+	62	38	+
1983	+	14	82	4
1984	+	7	61	32
1985	3	26	61	10
1986	+	43	46	11
1987	7	43	43	7
1988	6	42	50	2
1989	0	70	30	0
1990	+	33	57	10
1991	15	4	79	2
1992	9	32	59	+
1993	4	41	26	29
Average	7.9	34,8	49.4	7.9

In general, 0-group capelin may in August be found over the submarine terrace to the west, north, east and southeast of Iceland, from the coast to the outer edge of the shelf. In the area east of Iceland the distribution does, however, as a rule not reach so far out from the coast. In addition, 0-group capelin are in most years observed to drift west along the northern edge of the Irminger Sea basin to Greenland. When 0-group capelin are plentiful they may indeed be recorded almost continuously, although in varying quantities, in all of these areas and even off the south coast (Fig. 11.1a and 11.1b) while at other times the distribution may be more limited and patchy (Fig 11.1c). High densities of 0-group capelin off East Iceland generally coincide with indices of high coastal current intensity. Thus, in 1984, when a large proportion of the 0-group capelin had drifted to the area east of Iceland, the coastal current index was about twice that of 1980 when the 0-group capelin distribution was much more westerly.

The percentage distribution of the 0-group capelin by number in the various parts of the total distribution area is given in Table 11.1. In the period 1970–1993 considerable changes have been observed in the size of the distribution area as well as in the densities of 0-group capelin within subdivisions of this area. The west and north Icelandic areas have, however, always been the richest in 0-group capelin, and with few exceptions (1976, 1981 and 1984) generally contained between 75 and 100 percent of the 0-group capelin by number with an average of about 85 percent for the 24 year period.

The remainder of the 0-group capelin are found in the East Icelandic area or in the northwestern Irminger Sea, over the outer part of the Greenland shelf, westwards from the Dohrn Bank to the area south and southeast of Ammassalik. As seen in Table 11.1 the drift to these outlying parts of the distribution area is extremely variable. On the average, each of these areas

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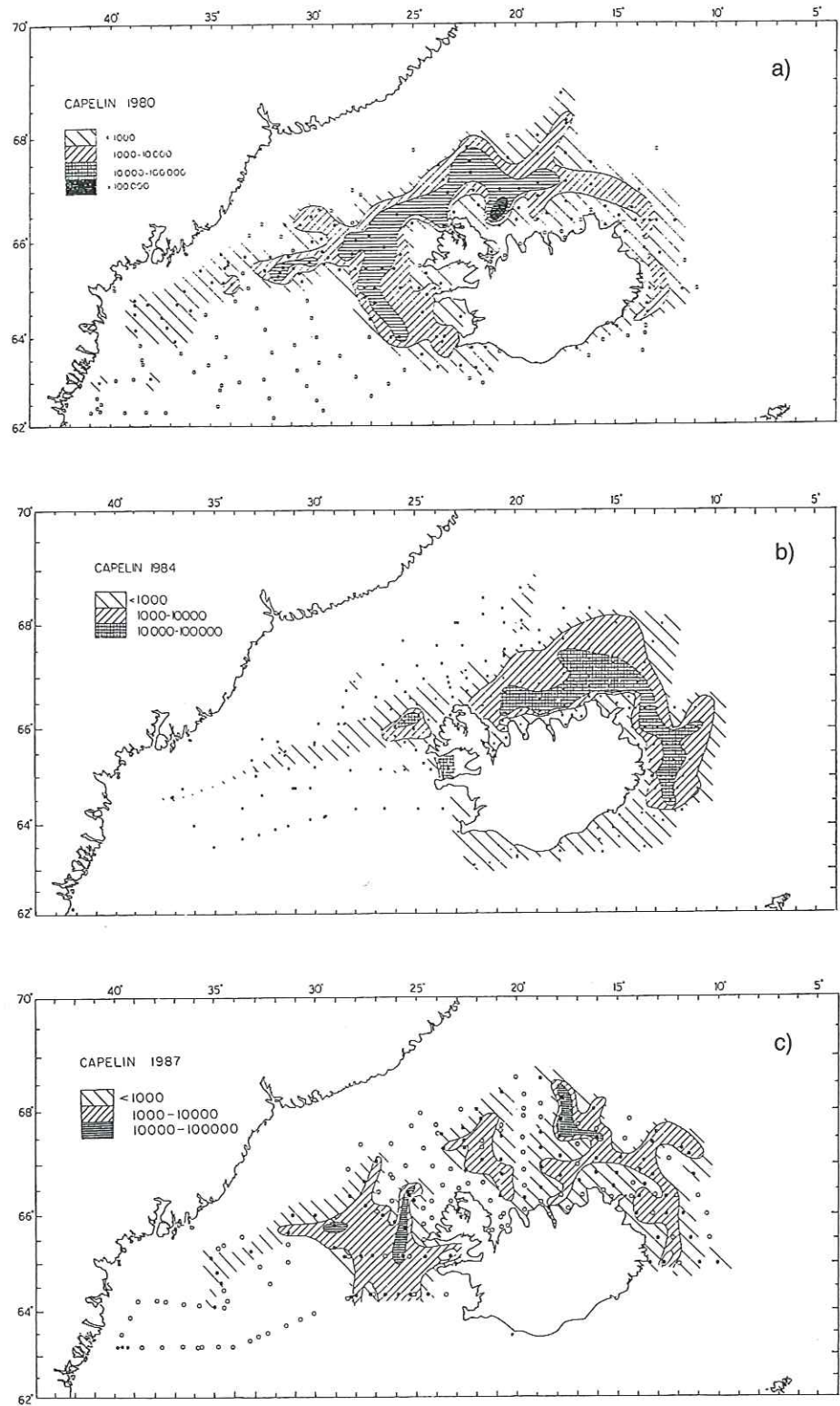Dohrn
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Figure 11.1. Examples of the distribution of 0-group capelin recorded a) in August 1980 (high abundance, westerly distribution), b) in 1984 (high abundance, easterly distribution) and c) in 1987 (low abundance).

contains about 8% of the number of capelin larvae in August, but the share of the total annual larval production has varied from practically zero to a maximum of 35% and 47% respectively for the Greenland and East Iceland parts of the distribution area. The extent to which the 0-group capelin have drifted towards Greenland, and probably also into the north Icelandic area, is most likely connected with changes due to meteorological variables affecting the flow of Atlantic water in spring and early summer past the Vestfirðir peninsula into the north Icelandic area from the west.

During acoustic surveys of the maturing part of the stock, that have been carried out in the Iceland Sea in October/November in the last 15 years, very high concentrations of 0-group cape- lin have sometimes been recorded on both sides of the equidistance line between Iceland and Greenland, in the region of the Iceland-Greenland Ridge and the southern Iceland-Greenland Channel. At the same time, 0-group capelin are often also recorded in the oceanic area to the north of the edge of the submarine terrace off North and Northeast Iceland, as well as in much higher quantities than observed in August off the east coast of Iceland. It seems, therefore, that the 0-group capelin, recorded west of Iceland in August, often end up in the area over the Iceland-Greenland Ridge later in the autumn. Similarly, the eastward drift to the east Icelandic area as well as the outward drift off the north coast often continues well into the autumn.

12. DIET AND FEEDING

Very limited information on the food and feeding habits of the Icelandic capelin can be gleaned from the older literature. Thus, Sæmundsson (1926) only mentions important prey species for capelin but does not provide quantitative data.

In May 1983, Jónsson and Friðgeirsson (1986) studied the diet and feeding of recently hatched capelin larvae (9.5–13.5 mm) in their first stages of feeding at the end of and in the first weeks after the yolk-sac stage at 4 stations off the southwest coast of Iceland. They found a fairly low feeding intensity of capelin larvae (19–31% with food in the stomach) as compared to that of other species (45–84%). However, they point out that because of the simple and straight formation of the alimentary tract of capelin larvae, this may be an artifact due to regurgitation. The most frequent food items were found to be copepod nauplii, eggs and copepodites, taken in that order. In relation to depth, the maximum density of capelin larvae was found to vary from 10 to 25 m and generally to follow maxima in zooplankton abundance in the area.

The food and feeding of 0-group capelin (39.6– 65.4 mm) in the area south, west and north of Iceland in August was studied in detail by Pálsson (1973, 1974, 1977). He found that on the whole *Calanus finmarchicus* was by far the most important single food item, both by weight and number. In the area south of Iceland *C. finmarchicus* was, however, outnumbered greatly by the much smaller *Oithona*, while north of Iceland other important contributors were *Acartia* spp. and juvenile euphausiids. The contribution of the various species by volume to the diet of 0-group capelin as measured by Pálsson (1974) for the various areas is shown in Figure 12.1.

In view of the high numbers of capelin in comparison to the available food supply, Pálsson suggested that the ingestion by the 0-group capelin of secondary food items was due to intraspecific competition and would in some cases eventually lead to food shortage and starvation. While this is a reasonable conclusion, it should be noted that there is a much closer relationship between parent stock size and the total 0-group abundance in August than there is between the abundance of 0-group capelin and zooplankton
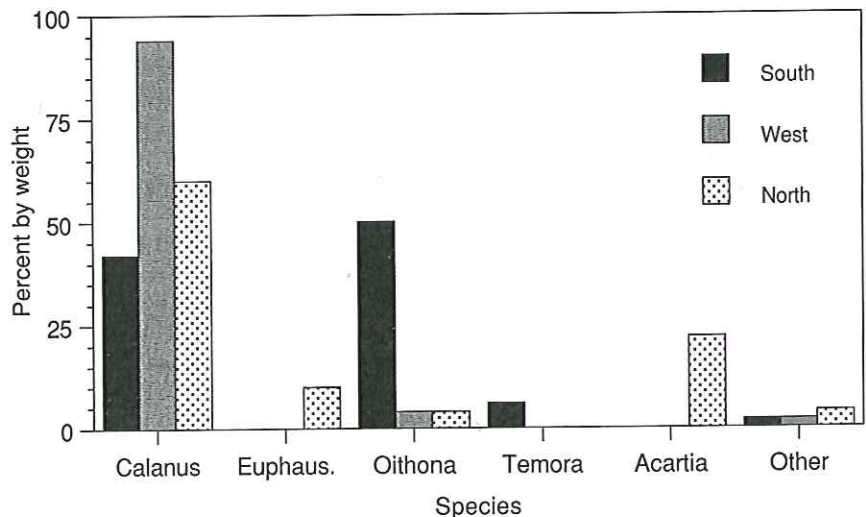

Figure 12.1. The species composition of the diet of 0-group capelin to the south, west and north of Iceland. (Modified after Pálsson 1974).
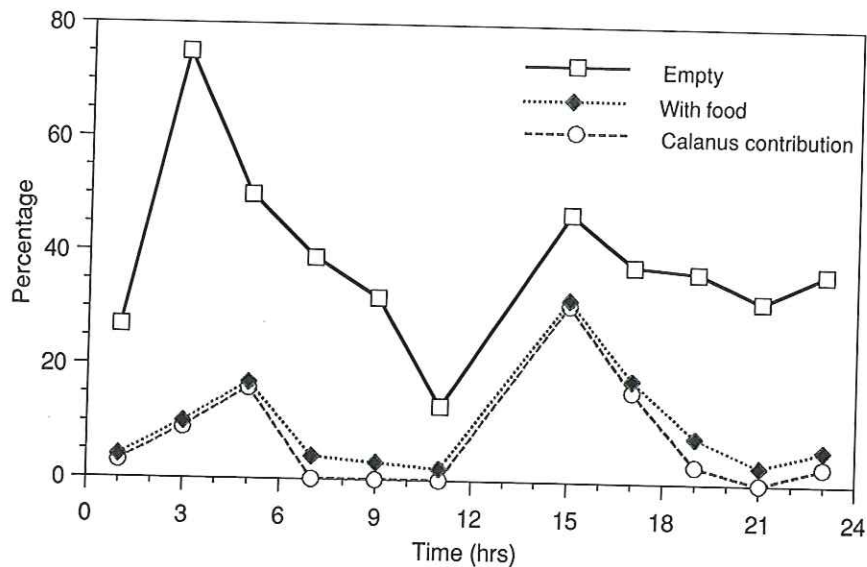
Figure 12.2. The variations in the degree of fullness of 0-group capelin stomachs containing food, with time (hours) and the percentage of empty stomachs at the same points in time. (Modified after Pálsson 1974).

(see section 15.1). Although 0-group abundance thus seems to be largely determined by parent stock size, a comparison with zooplankton abundance indicates that the availability of suitable food is a limiting factor in some years (cf. Figs. 6.11 and 6.12).

Pálsson (1977) also investigated diurnal changes in the quantity of food in the stomachs of the 0-group capelin. He found that there were two maxima: One in the early morning at about 04–06 hours and another in the afternoon between 14 and 16 hours (local time) with considerable periods of low feeding intensity following each maximum. As mentioned earlier, the diet, in volume, was dominated by C. finmarchicus. Pálsson noted the high frequency of empty stomachs and the strange observation that the occurrence of empty stomachs was most frequent during periods of intense feeding (Fig. 12.2).

An investigation of the food and feeding of 3–19 cm capelin (0-, 1- and 2-(3-) group) was carried out in conjunction with acoustic assessment surveys in August, November and December 1989 (Sigurðsson 1990; Sigurðsson and Ástthórsson 1991). The length distribution of the capelin from which stomachs (1240) were sampled as well as the proportion of empty stomachs are shown in Figure 12.3. The proportion of empty stomachs was particularly high among the smallest size groups and only in August did these contain significant amounts of food. Feeding intensity decreased from August to December

which is demonstrated by the increased proportions of empty stomachs and decreased degree of fullness.

As noted by Sigurðsson and Ástthórsson (1991) their material was mostly collected at a time when the adult, and in part the juvenile capelin also, return to the southern Iceland Sea from their summer feeding migrations in higher latitudes. By October, the summer feeding period is largely over and many of the zooplankton stocks depleted. The low food consumption in late autumn may also be related to gonadal development and other structural changes connected with the preparation for spawning. Vesin et al. (1981) reported similar reduced feeding intensity in autumn for capelin in the Gulf of St. Lawrence, and Prokhorov (1967) categorically stated that after the intensive summer feeding season the Barents Sea capelin practically starve for the duration of the fall/winter period. This was, however, contradicted by Panasenko (1984) who reported considerable feeding activity in February and March.

Sigurðsson and Ástthórsson (1991) found that in August the stomach contents of the smallest capelin was by number dominated by the small copepod Oithona spp., while other small copepods and unidentified calanoid copepods were also found (Fig. 12.4). However, Pálsson (1974) found Acartia spp. to be the most numerous food item among 0-group capelin north of Iceland. As pointed out by Sigurðsson and Ást-

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thórsson (1991) this is probably due to the fact that *Acartia* is a neritic species and Pálsson's material was sampled in comparatively shallow waters compared to the material collected by themselves. In the 9–11 and 11–13 cm length groups *C. finmarchicus* was, on the other hand,

the most numerous food item along with *Metridia* spp. and unidentified calanoid copepods, probably *C. finmarchicus*. Among the largest fish (length groups 13–15 and 15–17 cm) larger zooplankton species, such as *Thysanoessa inermis* and unidentified euphausiids, gained increasing
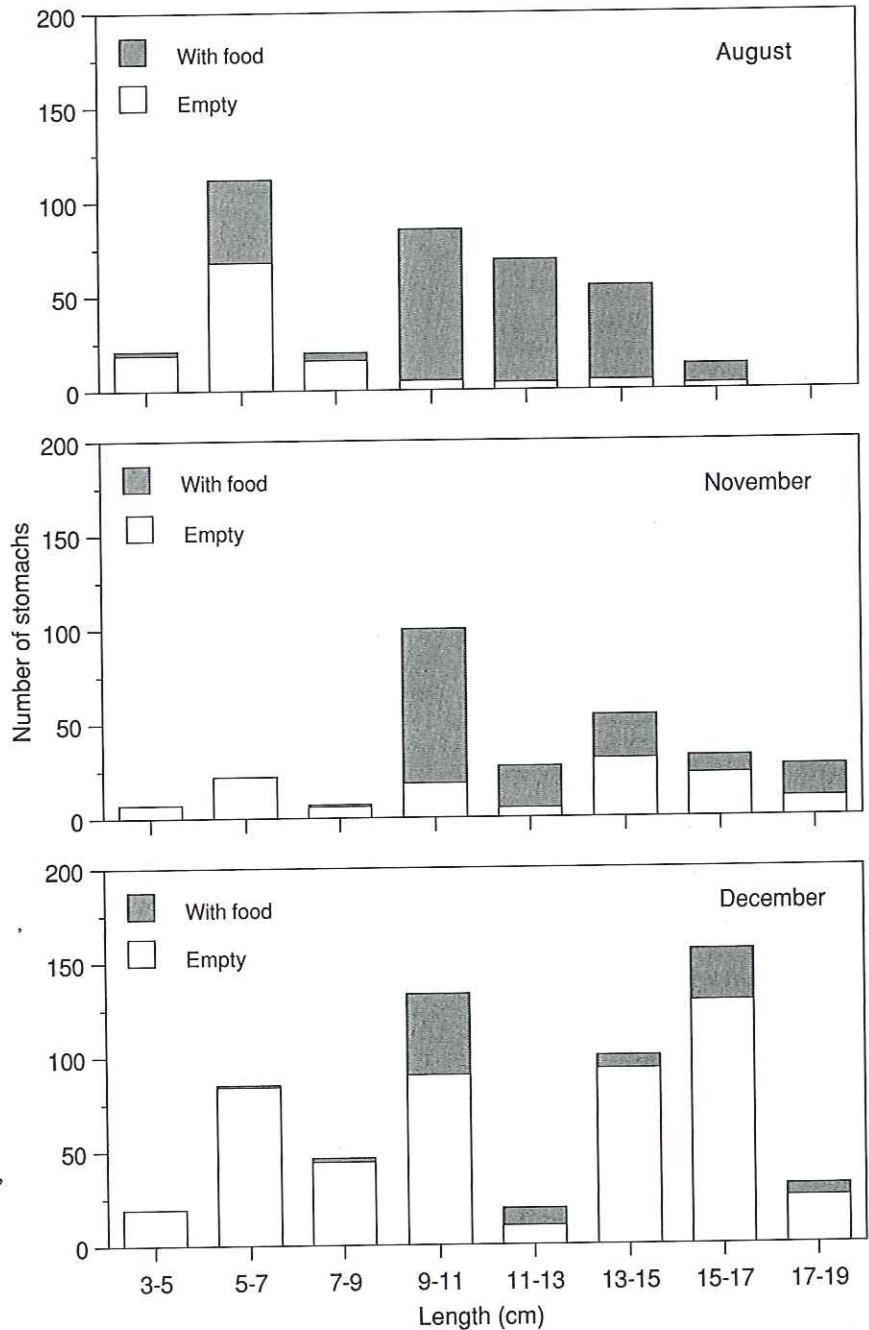
Figure 12.3. Length frequency histograms of capelin sampled for stomach analysis in August, November and December 1989. The shaded parts of the bars denote capelin which had food in their stomachs. (After Sigurðs-son and Ástthórsson 1991).
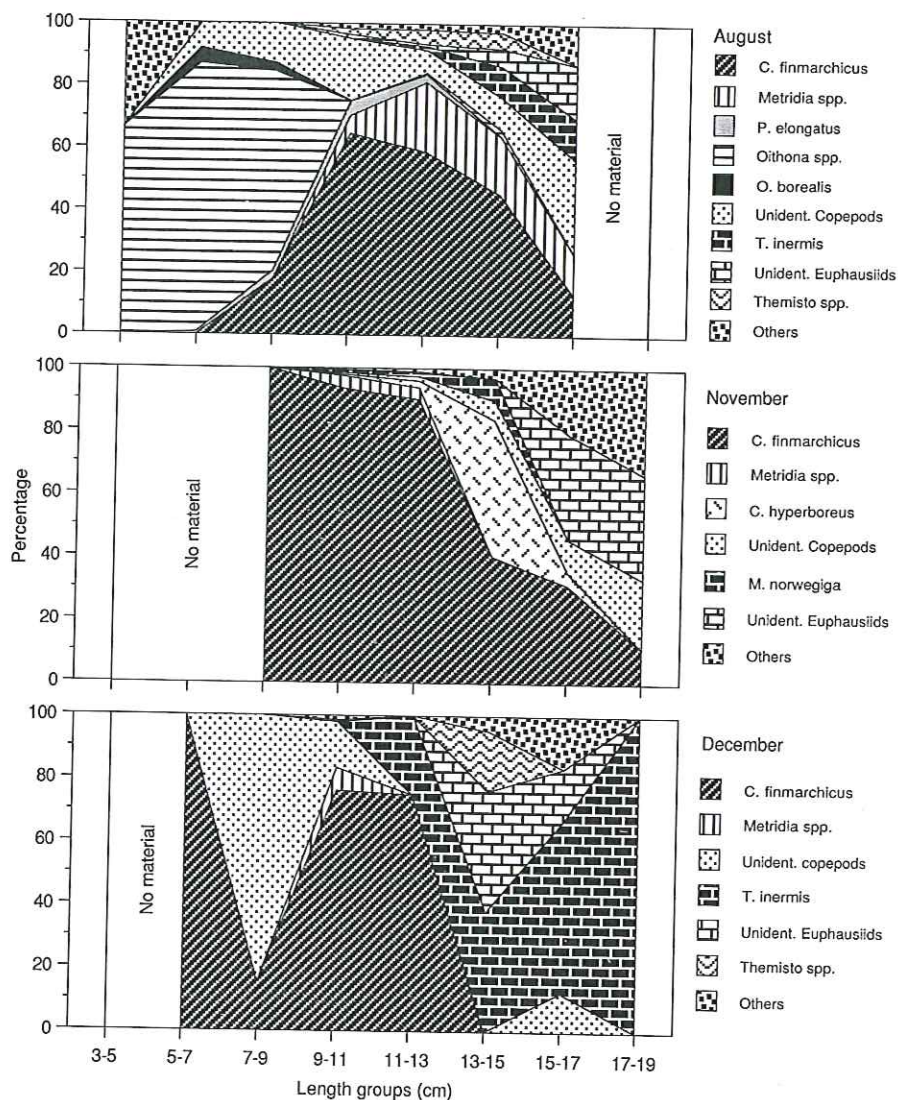
Figure 12.4. The food composition (percentage by number) of capelin north of Iceland in August, November and December 1989. (After Sigurðsson and Ástthórsson 1991).

importance at the expense of *C. finmarchicus* and other calanoid copepods.

In November (Fig. 12.4) the food composition in the stomachs from the different length classes was in general similar to that observed in August. Thus, *C. finmarchicus* dominated the diet of all fish up to 13 cm, but was in part replaced by *Calanus hyperboreus* in the 13–15 cm group. As in August, the food of the very largest capelin consisted of relatively many food groups with *C. finmarchicus*, unidentified calanoid copepods and euphausiids (*T. inermis*, *Meganyctiphanes norvegica* and unidentified) being the most numerous food items.

In December (Fig. 12.4) the composition of the food was again largely similar to that observed in August and November with the exception that euphausiids were even more numerous than previously among the largest fish. Thus *C. finmarchicus* dominated among fish smaller than 13 cm except for unidentified calanoid copepods which were most numerous in the 7–9 cm length group. Euphausiids, mostly *T. inermis*, dominated the diet of the largest capelin.

Due to the different sizes of the various prey groups, counting may give a misleading picture of their relative importance in the diet of the capelin. In order to get a better idea of the relative

importance of the different zooplankton groups, Sigurðsson and Ástthórsson (1991) converted numbers to weights using information from the literature and their own measurements of weight. The results are shown in Figure 12.5 and clearly demonstrate the transition from the smaller copepods to the larger euphausiids and amphipods as the capelin grow beyond the 11–13 cm size group. The same general pattern of changes in prey size and species with increasing predator size is reported by Vesin *et al.* (1981) and Panasenko (1984) from the Gulf of St. Lawrence and the Barents Sea respectively.

On the whole, euphausiids constituted 74% by weight of the food taken by capelin in the area north of Iceland, while copepods and amphipods (*Parathemisto* spp.) made up 15 and 11% respectively (Sigurðsson and Ástthórsson 1991). While the same food groups are reported to be the main constituents of the diet of Barents Sea capelin, their relative importance may be somewhat different. Thus Ellertsen *et al.* (1982) found the percentage occurrence by weight of copepods, euphausiids and amphipods to be 47, 33 and 6 respectively for 14–16 cm fish in the main feeding season. For capelin larger than 13 cm Panasenko

(1984) found percentages of 41, 43 and 12 respectively for these food groups in summer and autumn while stating that practically only euphausiids (90%) are taken in winter and early spring. On the other hand, Prokhorov (1967) gave the percentages of 26, 48 and 16 by weight for copepods, euphausiids and amphipods respectively on an annual basis.

Sigurðsson and Ástthórsson (1991) also studied diurnal changes in the feeding activity of capelin (Fig. 12.6). This was done from calculations of 4 hour means of stomach fullness and the state of digestion of stomach contents. They found clear evidence for two periods of main feeding activity, the first one in the morning (08–12 hrs) and a second one in the afternoon (16–20 hrs, local time) which coincided with sunrise and sunset in late autumn at 66°N. Thus, stomach fullness was at a maximum but digestion at a minimum at 08–12 hrs and at 16–20 hrs. A secondary low in digestion was also indicated during 00–04 hours when similarly a small increase in stomach content occurred. Likewise, Vesin *et al.* (1981) found morning and evening peaks in feeding activity among capelin in the Gulf of St. Lawrence in spring and summer but
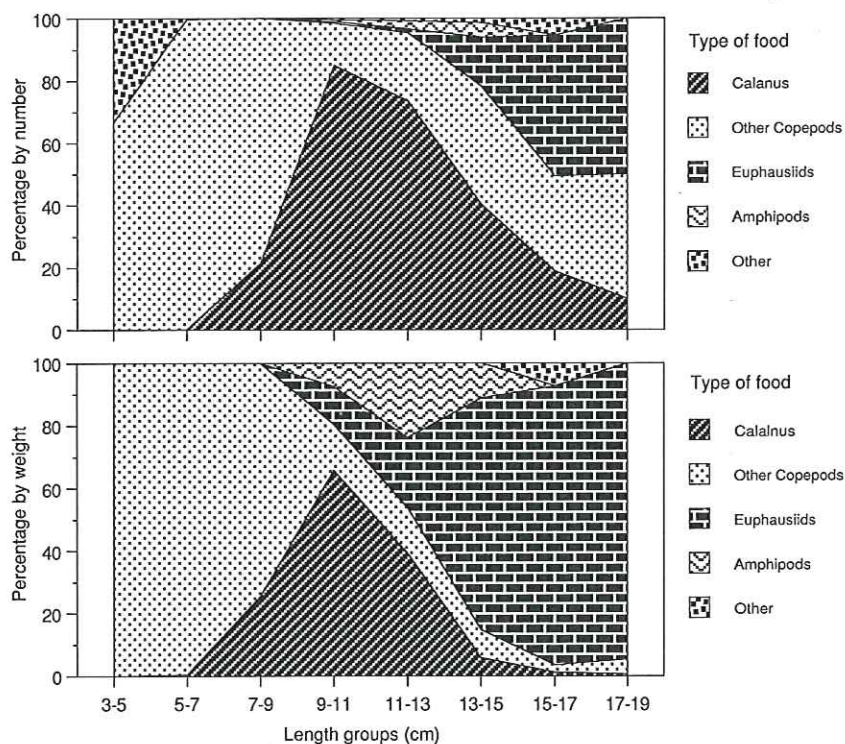

Figure 12.5. A summary of the food composition of capelin north of Iceland, in all samples from autumn and early winter 1989 combined, in terms of numbers and weight. (After Sigurðsson and Ástthórsson 1991).
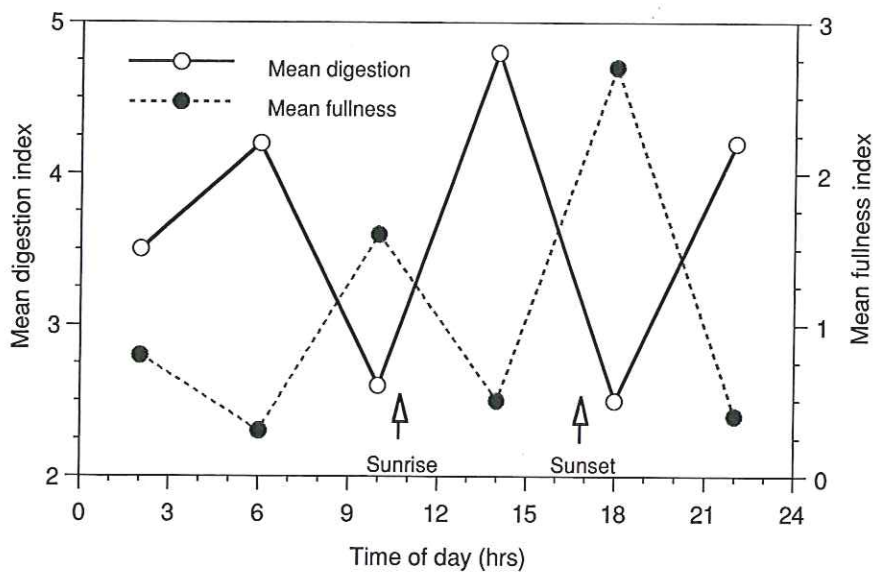
Figure 12.6. Digestion and fullness indices at different times of the day for capelin north of Iceland (all samples combined) in autumn and early winter 1989. (After Sigurðsson and Ástthórsson 1991).

only a single peak at midday in the autumn material. On the other hand, Panasenko's (1984) studies of the Barents Sea capelin showed considerable variation in feeding intensity between size groups but in general a single feeding maximum in the daytime with lower consumption rates at night.

Winter feeding among the Icelandic capelin has never been studied systematically. Nevertheless, it has been noted that the larger fish, especially the maturing part of the population, may continue to feed quite intensely in the area north and east of Iceland in winter, *i.e.* until the spawning migration enters the warm Atlantic waters off the southeast coast (Sveinbjörnsson 1991, 1992). A further indication of winter feeding is the observation of a considerable growth, both in length and weight, in the period November – January (see section 14.1 and 14.2). It seems that the available winter food consists almost exclusively of euphausiids and that the inci-

dence and intensity of winter feeding may be greater when feeding conditions during the preceding summer were poor. Thus, winter feeding was particularly prominent in the seasons 1989/90, 1990/91 and 1991/92 when summer migrations to the feeding grounds in the northern Iceland Sea were at a minimum (Sveinbjörnsson 1990, 1991 and 1992).

In many if not most years the Icelandic capelin migrate largely out of the mixed water shelf areas north and east of Iceland to feed in the arctic waters in the deeper part of the Iceland Sea. As yet, information on their food and feeding in these waters is mainly based on a single study (Sigurðsson and Ástthórsson 1991) from the more southern part of the feeding area. Obviously, there is a need for much more extensive and detailed research before the feeding dynamics of the capelin can be fully understood and explained.

13. FEEDING AND EARLY WINTER MIGRATIONS

13.1. 0-group capelin

In chapter 11 it was explained how the 0-group capelin were in August mainly distributed over the submarine terrace off Northwest and North Iceland and to a lesser and more irregular extent off East Iceland as well as over the outer parts of the East-Greenland shelf in the northern and northwestern Irminger Sea (cf. chapter 11 and Fig. 11.1). It was also stated that in some years at least, part of this stock component had continued to drift to the central Iceland Sea. By late August 0-group capelin are less than 1 g in weight and generally range in length from 30–65 mm, the largest individuals usually distributed in the more offshore areas and farthest to the west and north.

Specific studies of distribution, drift patterns or possible active migrations of 0-group capelin in autumn and early winter have never been undertaken. On the basis of observations made during surveys of older stock components, it seems, however, that the 0-group capelin overwinter mainly in the shelf areas off North and East Iceland, from the coast to the outer edge of the shelf. In addition, 0-group capelin belonging to this stock are often numerous over the western part of the Iceland-Greenland Ridge, particularly north of the Dohrn Bank and in neighbouring areas in late autumn and early winter. That the waters north and northeast of Iceland constitute the main overwintering areas of the 0-group capelin, is supported by the distribution of 1-group capelin in August, when most of them are usually recorded in or near the same general area, as explained in the next section.

Because of its small size and apparently poor swimming ability, it seems likely that the location of the main winter distribution area of 0-group capelin is mostly the result of its drift-pattern and only in part due to active migration, if at all. As stated previously, 0-group capelin are sometimes recorded in quantity in the central Iceland Sea in autumn and early winter. The subsequent fate of these fish is, however, uncertain. Nevertheless, if they had migrated to more southerly latitudes, 0-group capelin should in these years have been recorded in unusually high numbers in the outer part of the shelf area north of Iceland during surveys in January – February, which was not the case. Furthermore, 1-group capelin were recorded during some of the July–August Norwegian capelin surveys in the area between Jan Mayen and Greenland. This was for example the case in 1985–1987. Thus, it seems most likely that 0-group capelin which drift into the central Iceland Sea area must overwinter there. That the survival rate of these fish may sometimes be quite high is supported by the comparatively rich Norwegian 1-group recordings between 69°30′N and 70°30′N in early August 1985.

13.2. Juvenile 1-group and immature 2-group capelin

For clarification it must be pointed out that the age prefix of a year class is changed on 1 January and not at its actual time of birth, which in this case would be nearer to 1 April. From this follows that as of 1 January age group 1 suddenly becomes age group 2 and so on.

Since 1982 the annual 0-group surveys carried out in August have included acoustic measurements of the abundance of 1-group capelin in the southern Iceland Sea and adjacent waters. These surveys have provided a fairly detailed picture of the distribution of 1-group capelin at that time of the year and, together with surveys in late autumn and winter, have revealed the general migration pattern of this stock component in the summer, autumn and winter periods.

In August the distribution pattern of most of the 1-group capelin has been remarkably similar in the 11 year period 1982–1992 of which an example is given in Figure 13.1. Thus, this stock component has generally been found over the Icelandic continental shelf, from 20–50 naut.
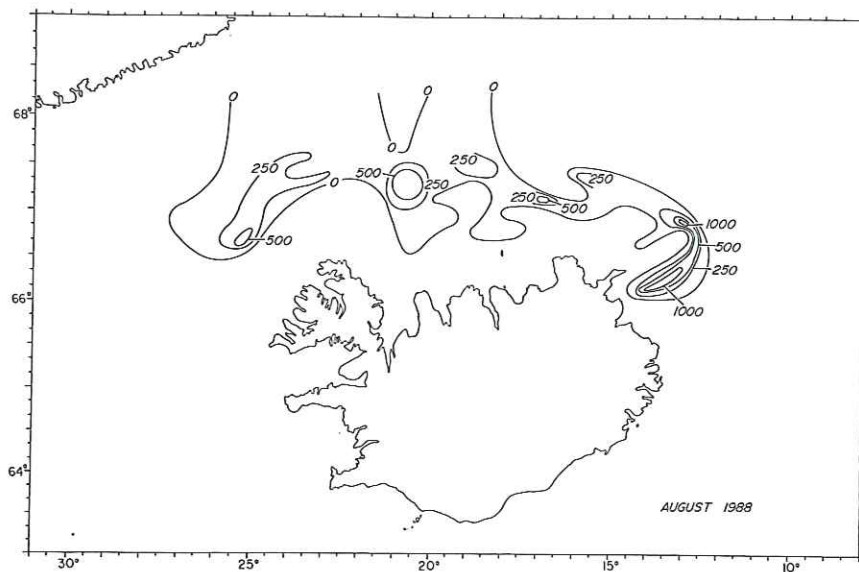
Figure 13.1. An example of a typical distribution pattern of 1-group capelin in August.

miles offshore to the shelf edge in the area from east of Iceland, north- and westward to about 30°W. However, the main distribution area has usually been off the central and western north coast of Iceland, where the distribution of 1-group capelin may at times be still farther offshore.

Although the extreme northern limit of the 1-group distribution in August has most frequently been about 68°N – 68°30′N, 1-group capelin have occasionally also been recorded in the central Iceland Sea. This was especially noticeable during a Norwegian acoustic survey of the area north of 68°30′N in early August 1985, when this age group was widely recorded as far north as Jan Mayen (71°N). Similarly, in the central Iceland Sea 1-group capelin were recorded this far north by Norwegian surveys in 1986 and 1987, but in lesser quantities and generally distributed farther to the west in the vicinity of the East-Greenland shelf. The Norwegian records of 1-group capelin at such high latitudes do not necessarily indicate migrations from more southern areas. As pointed out above, these capelin might also represent individuals that as 0-group had drifted towards the central and northern part of the Iceland Sea in the previous summer and subsequently overwintered within the cyclonic eddy over the central Iceland Sea basin (cf. Figs. 6.2 and 8.1).

As a rule, a considerable part of each year class will not mature and spawn as three year olds. The proportion of a year class not maturing to spawn until at age 4 seems to depend on year class size and be higher the larger the year class. Since the year class size is highly variable, the total numbers of these capelin may vary greatly and sometimes amount to more than one half of very large year classes. Thus, by number only 40% of the capelin belonging to the very large 1983 year class spawned at age 3, leaving 60% remaining immature for one more year to spawn at age 4. On the other hand, the corresponding maturing ratio for the small 1987 year class was 80% spawning at age 3, while over 90% of the very small 1980 year class spawned at that age. Maturing ratios are further discussed in section 14.5.

Immature 2-group capelin will remain in that state of maturity until in their third year, when the maturing process sets in for spawning at age 4. The above surveys have shown that the feeding migrations of immature 2-group fish are similar to those of the 1-group juveniles, with the exception that they generally have a more northerly as well as westerly distribution. In summer, therefore, these capelin have a wider distribution and are found over and outside the slopes of the submarine terrace off the western north coast of Iceland and in the deep waters of the Iceland-Greenland Channel. At times, immature 2-group capelin may also be found still farther west and north, *i.e.* near and over the East-Greenland shelf from north of Scoresby Sound to the Dohrn Bank region as well as in the southern Iceland
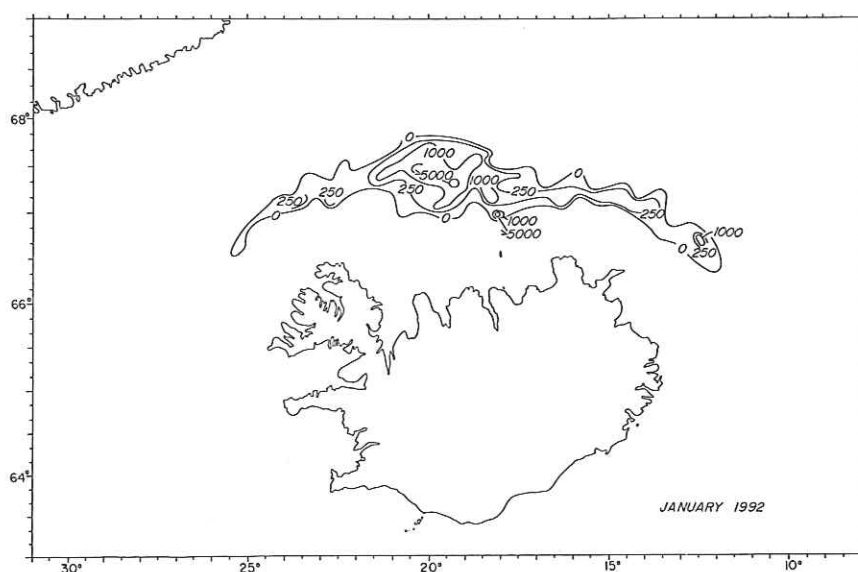
Figure 13.2. A typical mid-winter distribution pattern of juvenile 2-group capelin in the 1980s and early 1990s.

Sea. Information from 0-group surveys indicates that, at least in some years, immature 2-group capelin, probably originating from Iceland, may also be found over the Greenland shelf from the Dohrn Bank to the the area southeast and south of Ammasalik, *e.g.* in 1991.

Icelandic and Norwegian surveys, conducted in October – December, show that some of the 1-group stock component may remain off East and Northeast Iceland during this period. However, in the last months of the year much of the 1-group capelin population usually migrates slowly westwards to overwinter off the western north coast of Iceland and/or in the Iceland-Greenland Channel as well as farther south over the Iceland-Greenland Ridge, some 50–90 naut. miles off the Icelandic coast. At the same time, the 1-group juveniles and the 2-group immatures that in summer were distributed at higher latitudes in the area between Greenland and Jan Mayen and over the East Greenland shelf in the region off Scoresby Sound, retreat towards south along the Polar Front as the flow of cold arctic waters from the north increases and cools down the surface layers in autumn. It seems that this part of the capelin stock generally arrives in October and November in the area near the outer slope of the shelf over the Iceland-Greenland Ridge and/or on either side of the Iceland-Greenland Channel to the west of the Vestfirðir peninsula.

In the 1980s and the early 1990s, the centre of the mid-winter (January – February) distribution of most of the juvenile 2-group capelin and the immature part of the 3-group has been off the western north coast and the Vestfirðir peninsula (Fig. 13.2). However, this is probably not always so. During surveys of the migrations and behaviour of the spawning stock in the late 1960s and early 1970s, it was discovered that immature 2- and 3-group capelin (1- and 2-group before the turn of the year) sometimes followed the spawning migrations to the east Icelandic area in large numbers (Fig. 13.3). These capelin would then spend the last months of winter there before migrating to the more northern and western feeding grounds in the spring. This was the case in 1969 and 1970 but apparently not in 1971 (Vilhjálmsson 1972a). In the next four years (1972–1975), however, annual surveys in March and April revealed the presence of large amounts of immature 3-group capelin off East and Northeast Iceland (Vilhjálmsson 1973b, 1974b, and 1976). The same seems to have been the case in 1976, but the northward feeding migration had begun and the immatures had in part dispersed when this stock component was surveyed in the first half of March 1976 (Vilhjálmsson 1977b). This, together with negative results when scouting for capelin off the north and northwest coast, was at the time thought to indicate that as a rule practically all of the immature 3-group part of the stock overwintered in the area off East and Northeast Iceland.
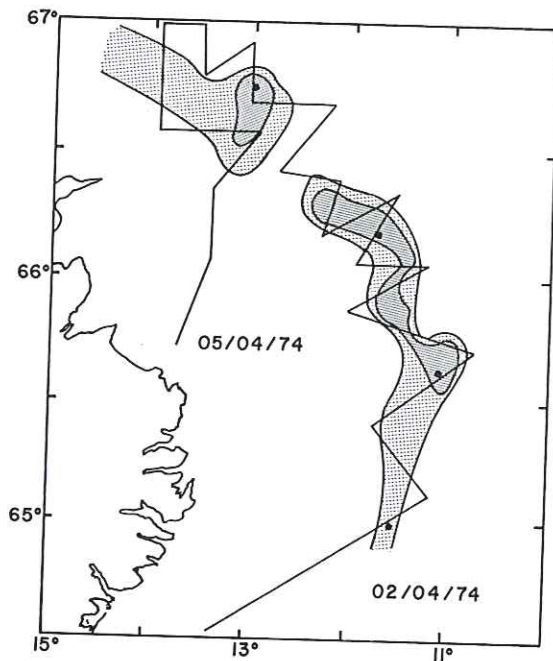
Figure 13.3. A common late-winter distribution of juvenile 2- and 3-group capelin in the 1970s.

In the first half of April 1977, a survey of this area largely failed to locate immature 3-group capelin. At the time, this was attributed to the northward feeding migration having already begun, with the usual dispersal of the overwintering schools (Vilhjálmsson 1977b). However, in the following year it was found that only insignificant numbers of immatures had followed the spawning migrations to the east Icelandic area. Instead, fairly large concentrations of immature capelin were located to the west and northwest of the Vestfirðir peninsula in January–March 1978 (Vilhjálmsson 1979a).

Although little survey effort could be allocated in the next two years, specifically for the purpose of locating and assessing the overwintering areas of the juvenile stock component, it is quite clear that its geographical distribution followed that of the adult stock which had a westerly winter distribution in these years. Thus, very few juveniles were located off East Iceland as well as off the eastern north coast in the winters of 1979 and 1980. However, the early January distribution of the spawning stock reverted from the extreme western location to the more usual area off East and Northeast Iceland in 1981, where it has been found in January in the years since then. In spite

of this, the immature component did not follow suit to the same extent. As a rule, only relatively small concentrations of immatures, both of age groups 2 and 3, have thus been recorded off East and Northeast Iceland in winter in the period 1981–1992 as compared to the mid-1970s. Instead, the bulk of this stock component has, during this period, been distributed off the central and western north coast and/or off the Vestfirðir peninsula at this time of the year. An exception, however, was the year 1986 when large amounts of immature capelin were recorded in January/February east of Iceland as well as off the north coast. A possible explanation of this finding will be discussed in section 13.5.

13.3. The adult stock

In the 1960s extensive scouting for herring was conducted in the central and eastern Iceland Sea. Occasionally, these cruises would also locate schools of capelin in this area in the months of June, July, August and September (Jakobsson 1978, 1980). Thus, large capelin schools were found in deep waters off the western north coast of Iceland in June/July and July/August and also at the shelf edge off the eastern north coast in September 1963. In the following year, large capelin schools were again located both off the western and eastern north coast in August as well as off the central north coast of Iceland in September. In all of these cases the distance from the nearest Icelandic coastline was some 60–80 naut. miles, and the schools proved to consist of maturing capelin. In June/July 1966, however, large amounts of mature capelin were located about 120–150 naut. miles off the central north coast of Iceland, i.e. near the present division between the exclusive economic zones of Iceland and Greenland. And in July/August 1967 much capelin were again registered in a large area some 50–60 naut. miles west-southwest of Jan Mayen at 70°30′N (Jakobsson 1978, 1980). The approximate positions of these oceanic summer records of capelin in the 1960s are shown in Figure 13.4.

Although these findings could certainly be interpreted as indicating far-reaching feeding migrations, they were too few and distant in space and time for establishing migration routes or patterns. In the period June – September 1969 considerable scouting activity took place in the area

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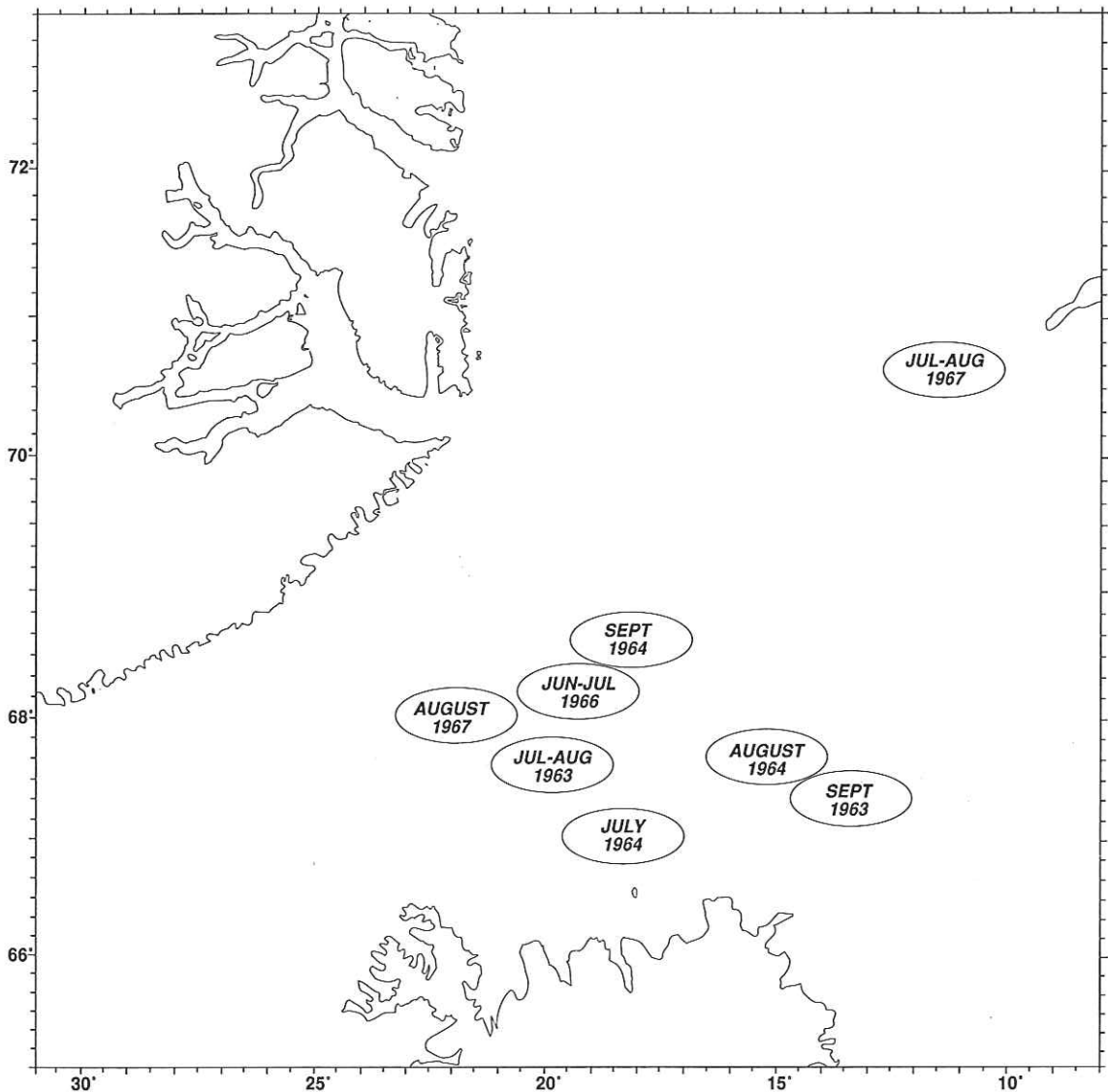
Figure 13.4.   Positions of summer records of capelin off the north coast of Iceland and in the Iceland Sea in the 1960s.

over the outer part of the shelf off North and Northwest Iceland as well as in deeper waters north and northwest from there. The objective of this work was to investigate the possibility of a summer capelin fishery. Concentrations of adult as well as juvenile capelin were frequently located, both off the central and western north coast and in the area of the Iceland-Greenland Channel. These investigations were, however, much restricted due to their experimental fishing aspect, limited to the area south of 68°30′N and

consequently did not yield much new information on capelin distribution or migrations (Jakobsson 1976).

Another attempt to locate and fish capelin north of Iceland and study their migrations in summer was made in 1975. The experiment was unsuccessful, for the most part due to especially unfavourable ice conditions (Jakobsson 1976). However, similar studies were resumed in the following year during the period June – September. The Iceland Sea area was then relatively

Figure 13.5. The weekly movements in latitude of the Icelandic capelin fishing fleet in summer and autumn 1978. The broken lines indicate northern and southern limits of fishing areas.

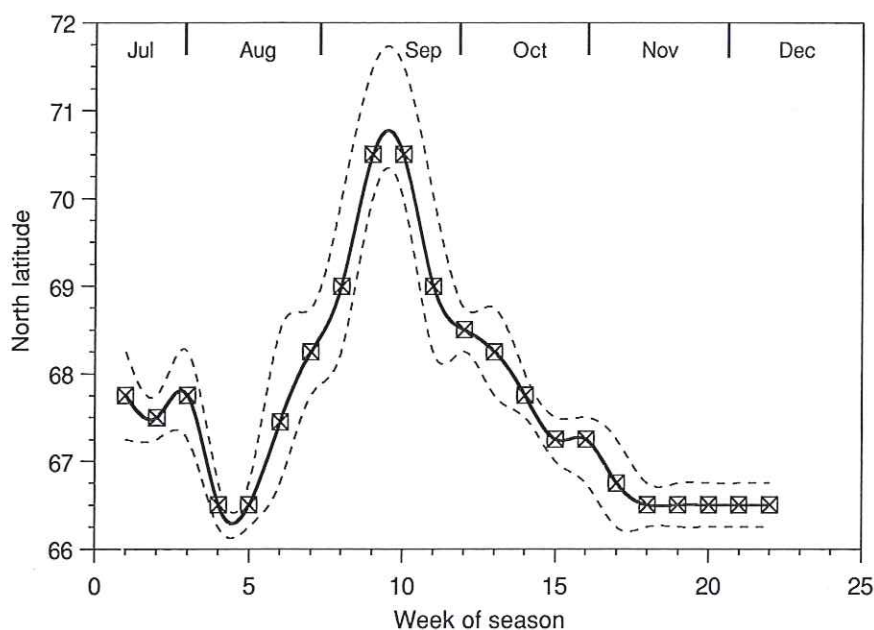ice-free, and large concentrations of adult and juvenile capelin were located in the area between Northwest Iceland and Greenland as well as north of Iceland. Most of the capelin were recorded south of 68°30′N with only scattered concentrations extending to 69°30′N in the month of September (Vilhjálmsson 1976, 1977).

In the 1970s Norway became interested in the possible occurrence of capelin in summer in the northern Iceland Sea, between Jan Mayen and Greenland. Therefore, the area south of 71°N was searched in 1970 and 1971 but with negative results (Blindheim *et al.* 1971; Revheim 1971). Surveying of this area was then discontinued but was resumed in 1977 following the beginning of the Icelandic summer capelin fishing season off North and Northwest Iceland in 1976. However, two extensive scouting cruises to the area between Jan Mayen and Greenland in July and September 1977, as well as search by several fishing vessels in July, were unsuccessful (Sangolt 1977). Indeed, it was not until in the summer of 1978, 11 years after the first observation of capelin in the Jan Mayen – Greenland area, that their presence in these waters was observed again. Thus, in 1978 a Norwegian scouting vessel located and fished capelin west of Jan Mayen around mid-August. Shortly thereafter a Norwegian capelin fishery started in the Jan Mayen area and continued until the latter half of September 1978 (Nilsen 1978).

In July 1978 the Icelandic capelin fleet began fishing in an area approximately 100 nautical miles to the north of the Vestfirðir peninsula. These capelin gradually scattered and in early August new grounds were located over the Iceland-Greenland Ridge, about 100 naut. miles farther to the south and west. This fishing area gradually shifted to the northeast during August and finally the capelin dispersed, the last catches being taken to the southeast of Scoresby Sound at the end of the month. The Icelandic vessels then joined the Norwegian ones in the Jan Mayen area. There the capelin also dispersed in the latter half of September and apparently began a southward migration at about the same time. The southward migration was then followed by the Icelandic fishing fleet to the wintering area off the Vestfirðir peninsula where the maturing fishable stock arrived in October – November. The weekly movements in latitude of the Icelandic capelin fleet in the period July – November 1978 are shown in Figure 13.5 and clearly demonstrate the feeding migration of that part of the capelin stock which was being fished during that period.

The virtual absence of adult capelin south of 70°N in September 1978, as well as the onset of the southward migration from the area west and north of Jan Mayen in the last week of the month, was also documented during an Icelandic

research cruise at the time (Vilhjálmsson 1979). During the first half of October large concentrations of capelin were again located 70–90 naut. miles north of the Vestfirðir peninsula as well as more scattered registrations farther to the northeast. The capelin remained in this area until late in the month when the southward migration was resumed (Vilhjálmsson 1979). An extensive Norwegian scouting survey, carried out in Oc-

tober from 72°N to 69°N, did not locate any capelin except near the edge of the Greenland shelf to the east and southeast of Scoresby Sound (Sangolt 1979).

Thus, in 1978 the combined information from scouting operations and the fishery clearly demonstrated a feeding migration of adult capelin from the north Icelandic area along the Polar Front to the area west and northwest of Jan
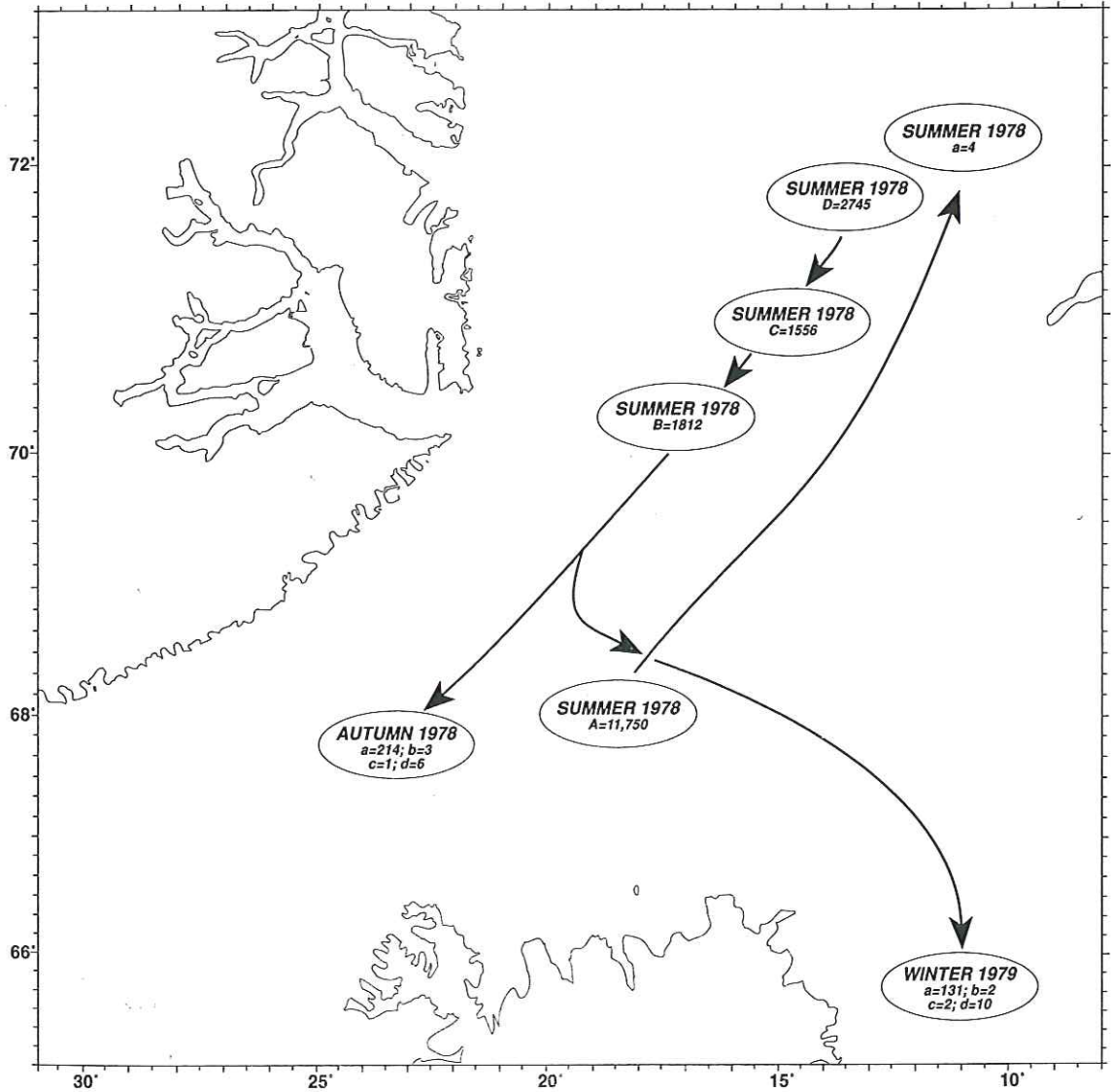
Figure 13.6. The movements of the fishable stock in 1978–1979 as illustrated by the tagging of capelin and returns of capelin tags from Norwegian and Icelandic meal and oil factories. Capital letters denote taggings and low case letters denote recaptures.
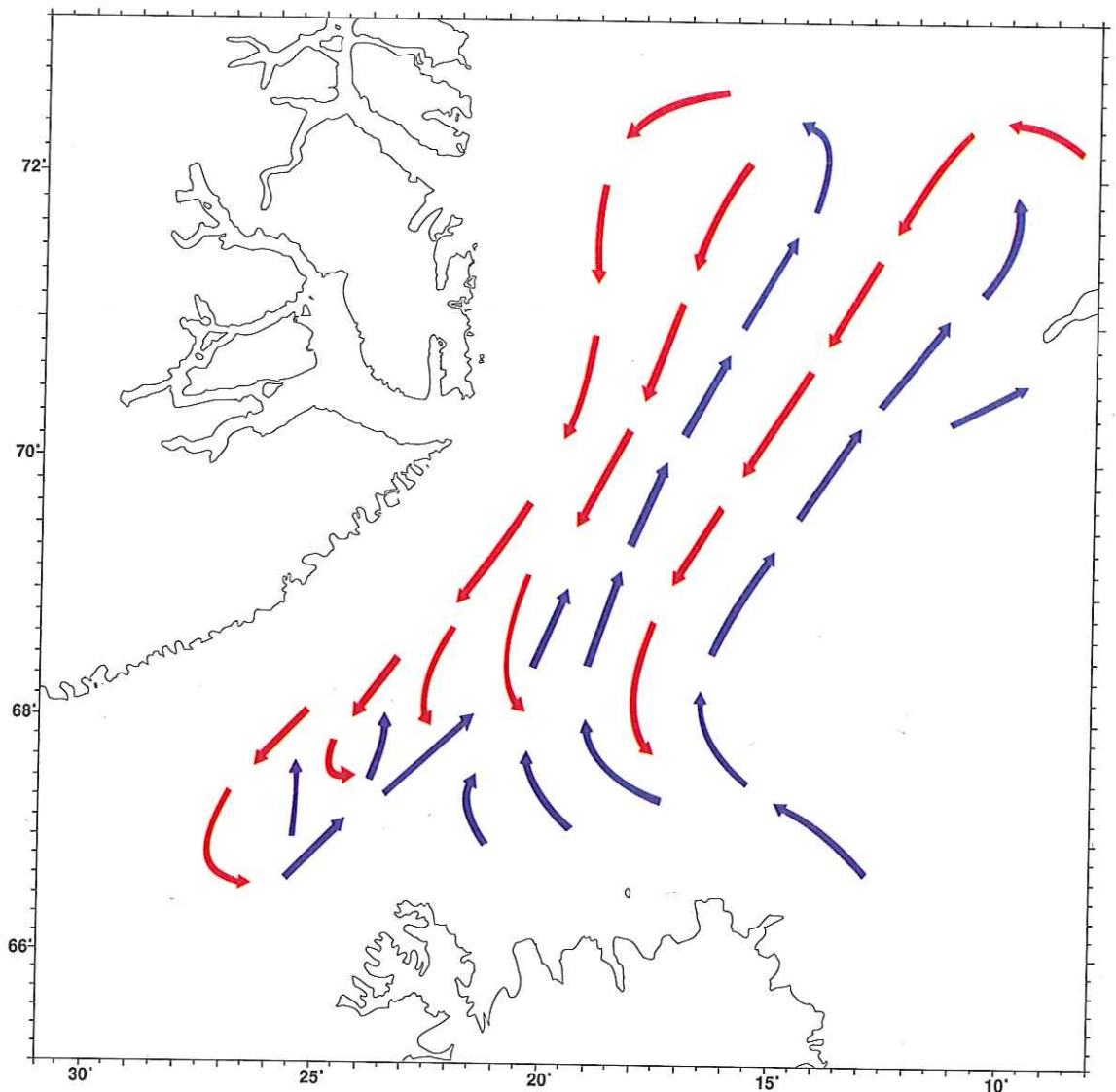
Figure 13.7. A common migration pattern of the maturing part of the capelin stock in the feeding season. Blue arrows: spring and summer. Red arrows: autumn.

Mayen in July and August 1978 and a return migration south along the front in September and October.

These migrations were also documented by the results of tagging experiments carried out in July and early August 1978. A total of 11,750 capelin were marked with internal steel tags off the western north coast of Iceland and the Vestfirðir peninsula (Vilhjálmsson and Reynisson 1979). Four of these tags subsequently turned up in re-

duction plants in Norway from catches taken in the Jan Mayen area, mostly in September.

In late September 1978, further 5,113 capelin were tagged by the same method to the west and northwest of Jan Mayen. From this experiment 10 tags were recovered in October – December 1978 from catches taken to the north and northwest of the Vestfirðir peninsula. Additional 14 tags from the Jan Mayen experiment were recovered from the fishery off Northeast, East and

Southeast Iceland in January – March 1979. Thus, the tagging experiments also verified the return migration.

On 17 and 18 October 1978 some 1,441 capelin were tagged in rough sea conditions on the fishing grounds north of the Vestfirðir peninsula. The survival rates among these capelin were obviously low and the experiment was discontinued after a few liberations. Nevertheless, some 44 recoveries were obtained in the 1978 autumn fishery and 7 of the capelin, tagged in October 1978 off the Vestfirðir peninsula, were recovered from the 1979 winter fishery off eastern Iceland (Vilhjálmsson and Reynisson 1979).

The migrations of capelin to the region between Jan Mayen and Greenland in the summer of 1978 as well as their return to the area off North and Northwest Iceland in autumn is, therefore, clearly demonstrated by tag returns. The recoveries also illustrate the subsequent migration to the east and south to reach the spawning grounds at the south coast of Iceland. Thus, 131 tags from the summer 1978 tagging experiment off the north coast of Iceland were recovered from the 1979 winter fishery east of Iceland together with the 14 tags from the experiment in the area between Jan Mayen and Greenland previously described. The movements of the fishable stock as described by these tagging experiments are illustrated in Figure 13.6.

Through research as well as information from the fishery, a more detailed picture was established in the following years of the summer/autumn feeding migrations of the adult Icelandic capelin stock in the Iceland Sea. In this period the adult or maturing stock was often divided between two areas during the feeding season, which have often been referred to as northern and southern components (Vilhjálmsson 1983).

The southern component feeds in the waters over the Iceland-Greenland Ridge and off North Iceland where it is often mixed with juveniles. This part of the stock generally does not migrate much beyond 68°–69°N, i.e. the area where the East-Icelandic Current branches off from the East-Greenland Current. The northern component, consisting of the oldest and largest fish, on the other hand, undertakes a long northward migration to the area between Greenland and Jan Mayen and to the north of Jan Mayen to 72°–74°N. As a rule, these capelin are not mixed with juveniles in summer and autumn and in late September they start migrating back south again. In October – November both components begin to assemble and mix in the wintering area near the outer edge of the submarine terrace off North or Northwest Iceland. From there the spawning migration usually starts in December and as a rule follows the shelf edge off North and East Iceland in a clockwise direction as described in section 7.1.

The general movements of the maturing stock in summer and autumn are illustrated in Figure 13.7. It is assumed that they describe the most common migration pattern of the adult stock during the feeding season. However, in spite of the relatively short period of observation (15 years), it has become equally clear that these migrations are subject to changes, which sometimes may indeed be quite dramatic as will be described in the following section.

13.4. Variations in feeding migrations of the adult stock

In order to obtain information on the summer distribution and abundance of the maturing fishable stock, Norwegian research vessels carried out extensive acoustic surveys of the northern part of the Iceland Sea in July/August 1979–1992 with the exception of 1981 and 1984 when this area was not surveyed. At about the same time, Icelandic research vessels surveyed the area south of 68°–68°30′N between about 12°W and 30°W, and together these data sets provide a fairly good picture of capelin distribution in this area in summer. Furthermore, Iceland and Norway carried out joint annual acoustic surveys to assess capelin distribution and abundance in the Iceland Sea and adjacent waters in October/November 1979–1983. Since then the autumn surveys have been conducted with two Icelandic research vessels. Lists of reports on all of these surveys are given in Appendix I.3.1 (autumn and winter surveys) and Appendix I.3.2 (summer surveys).

Although the summer surveys as well as some of the autumn surveys have fallen somewhat short of attaining their goal of stock abundance estimation and do not give details of stock migrations, they provide reliable annual pictures of the general stock distribution in two seasons, i.e. summer and autumn. As the timing of these surveys has remained approximately the same
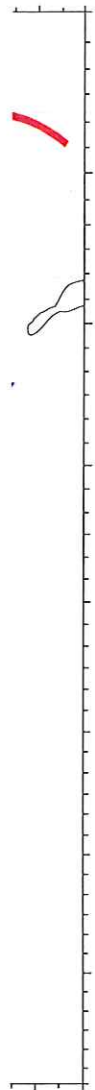
Figure 13.8. Capelin distribution and temperature at 50 m depth in August 1979. The position of the ice edge is also indicated.

throughout the years 1979–1992, the recorded distributions provide good descriptions of the variations that have occurred in the feeding migrations of the adult part of the stock in that period.

In the summer of 1978 no surveys, comparable to those of later years, were carried out in August. Judging by the findings of some general scouting surveys as well as fisheries statistics, it seems safe to assume that in the beginning of summer 1978 the northward migration followed a relatively westerly course. On reaching higher latitudes (>71°N), however, the 1978 feeding migration headed to the northeast. Thus, Norwegian catches in late August were taken some 40 to 70 naut. miles northwest of Jan Mayen, while the September fishery took place 60–140 naut. miles northwest and north of the island. An Icelandic scouting survey in September as well as a stock assessment survey in October, indicated that the stock more or less retraced the course of the summer feeding migration (Vilhjálmsson 1979).

In August 1979 Iceland and Norway conducted the first of a series of cooperative 2–3 vessel surveys of the summer distribution and abundance of the stock. The August survey showed the presence of capelin over the Iceland-Greenland Ridge as well as farther north off the Vestfirðir peninsula. In addition, part of the stock had migrated northeastwards along the eastern border of the East Greenland Current in an area 90–150 naut. miles off the coast of Greenland. Some of these capelin had already reached latitude 72°N by the middle of August (Fig. 13.8). This distribution pattern appeared similar to that of the year before with the exception that the eastward migration in the northernmost part of the distribution area was not observed in 1979, most of the stock instead feeding about midway between Greenland and Jan Mayen. The return migration in September and October took place somewhat farther to the west, *i.e.* along and just off the continental shelf of Greenland. For a time, the capelin gathered in deep waters some 120 naut.
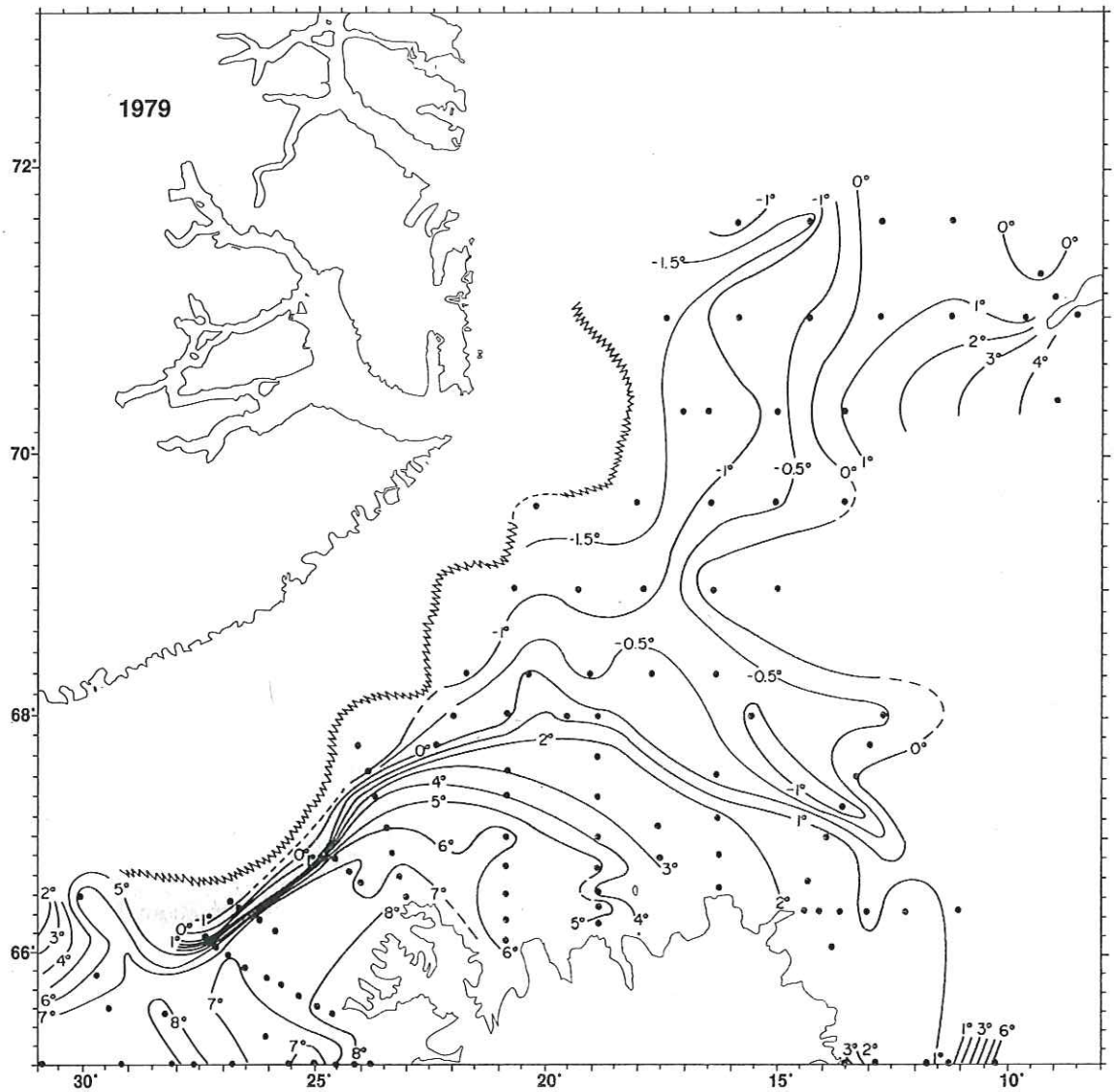

Figure 13.9. Capelin distribution and temperature at 50 m depth in August 1980. The position of the ice edge is also indicated.

Figure 13.10.   Capelin distribution and temperature at 50 m depth in August 1981. The position of the ice edge is also indicated.

miles off the central and western north coast of Iceland, but in November much of the mature, fishable part of the stock continued to the south-west to assemble for a while off the Vestfirðir peninsula (Vilhjálmsson 1980).

In the summer of 1980 the feeding migration of the northern component appeared to follow a much more westerly route than before, apparently as a result of less admixture of polar water from the East Greenland Current and higher temperatures in the central and eastern Iceland

Sea in general (Fig. 13.9). In the area between 67°30′N and 70°30′N the capelin thus migrated along the edge of the Greenland shelf and over the shelf up to 20–30 nautical miles off the coast. However, north of 70°N the migration took a more easterly course, and as in 1978 the northern component then spent about a month feeding in the area to the northwest and north of Jan Mayen (Fig. 13.9). The autumn surveys indicated that although the 1980 return migration took place farther to the east than in the years before, most

of the stock assembled in the area between the Vestfirðir peninsula and Greenland before the onset of the spawning migration in the winter (Vilhjálmsson 1981).

In August 1981 there were no research surveys of the Iceland Sea north of 68°N. However, a Norwegian scouting survey of the area, carried out in the latter half of July, showed adult capelin migrating northward, between 15°W and 18°W in the area from 67°00′N to 70°40′N, in the immediate vicinity of the ice border (Fig. 13.10).

This is 90–150 naut. miles farther to the east than the route of the 1980 migration as observed in August that year. Norwegian and Icelandic catches were taken some 80–120 naut. miles west of Jan Mayen in August and September 1981 (Vilhjálmsson 1982), and the joint autumn survey in October of that year indicated a return migration along a route similar to that of the year before, *i.e.* farther to the east than in 1979.

Norwegian and Icelandic surveys in August 1982 indicated an early northward summer feed-

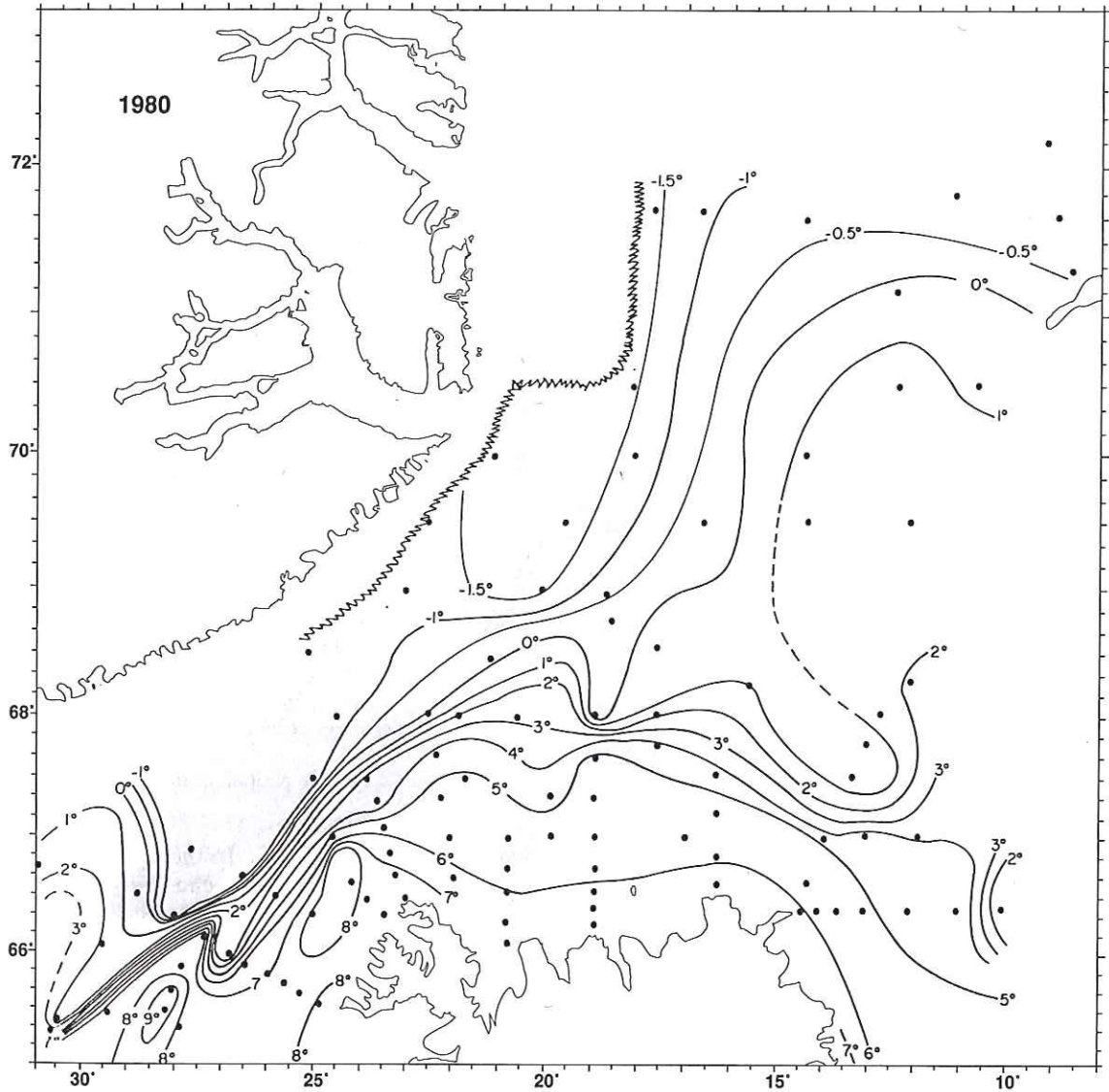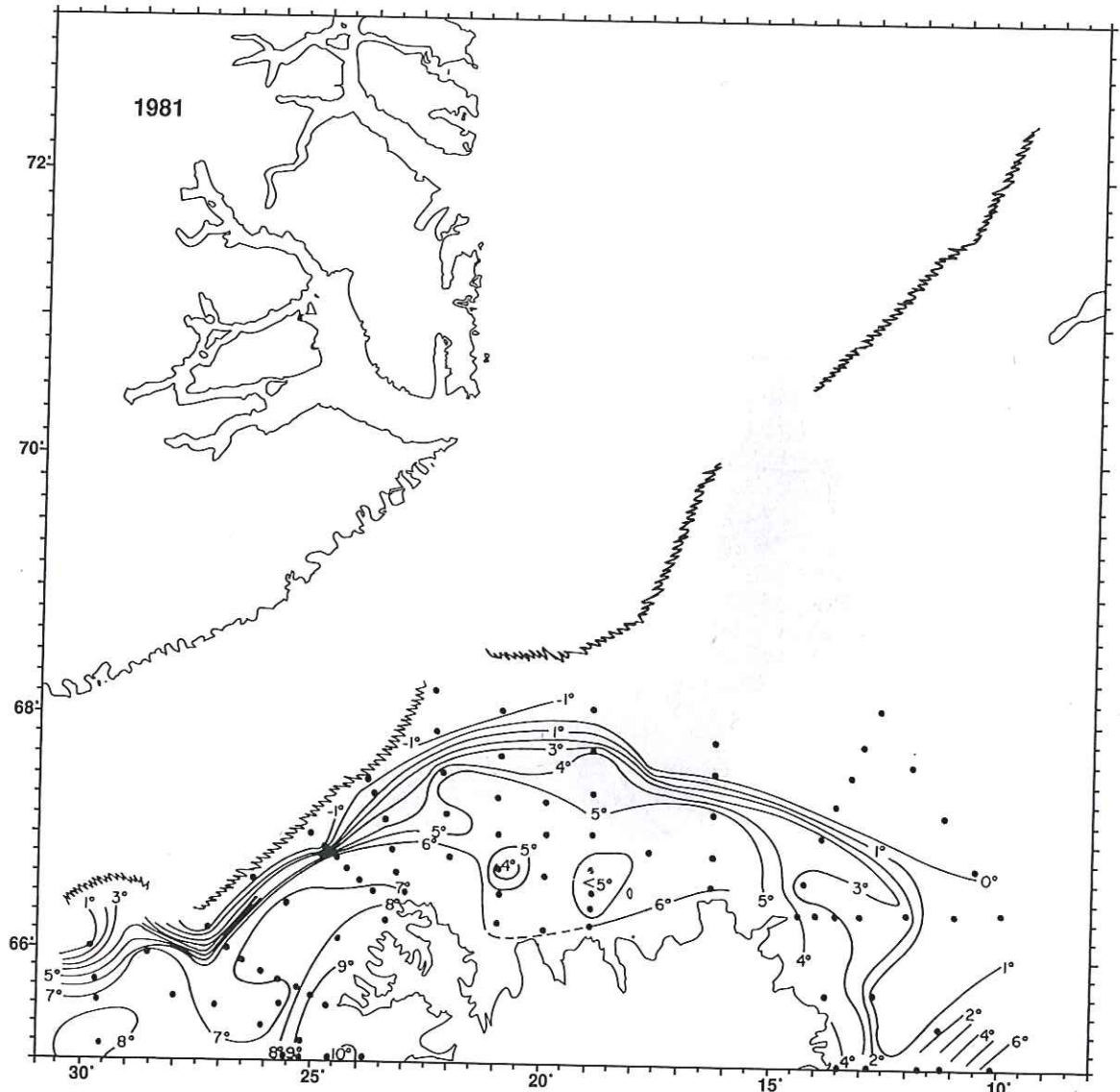Figure 13.11. Capelin distribution and temperature at 50 m depth in August 1982. The position of the ice edge is also indicated.

Figure 13.12. Capelin distribution and temperature at 50 m depth in August 1983. The position of the ice edge is also indicated.

ing migration of the adult stock and a more easterly route than ever observed before, especially in the northern part of the area. Thus, the capelin seem to have migrated from position 68°N, 18°W to 70°N, 12°W and from there northeastwards, close to the west and north coasts of Jan Mayen, to feed in the area west and north of the island east of 13°W–14°W (Fig. 13.11). In this northern part of the area the western boundary of the summer 1982 capelin distribution was about 150 naut. miles from the coast of Greenland. Again the

joint autumn survey showed the capelin more or less retracing their northward migration route on their return journey.

In the northern area, polar water from the East-Greenland Current was much less extensive in Agust 1983 than in the previous summer. In consequence, the capelin were distributed farther to the west in the region between 69°N and 71°30′N, where the main concentrations were found in the vicinity of the ice border west of 15°W (Fig. 13.12). Apparently, there were not

many adult capelin in the area between 68°N and 69°N in August 1983, but part of the adult stock was, on the other hand, located between the Vestfirðir peninsula and Greenland as in previous years. While the autumn survey revealed the presence of small concentrations of capelin in the neighbourhood of Jan Mayen, most of the northern stock component in that general area was migrating southwards much farther west.

The area north of 68°30′N was never surveyed in the summer of 1984 and the autumn survey did not take place until November when the adult stock had already assembled off North Iceland. In consequence, there is no direct research evidence of the summer distribution of the adult fishable stock. However, an August survey of the area south of 68°30′N revealed considerable quantities of adult capelin off the central north coast of Iceland north of 67°30′N as well as over the Iceland-Greenland Ridge and in the Iceland-Greenland Channel. In addition, about 125,000 tonnes of capelin were taken by a multinational

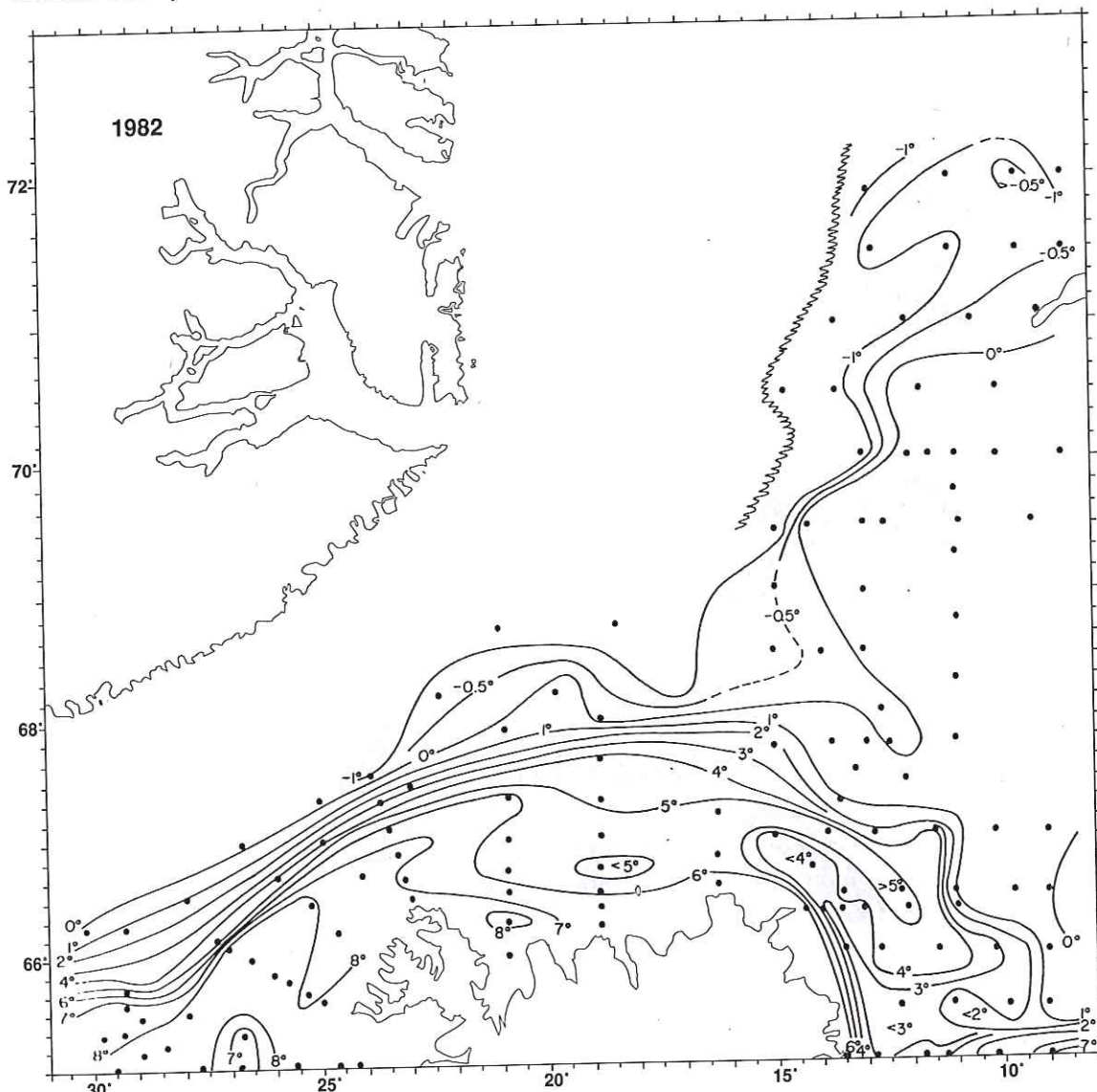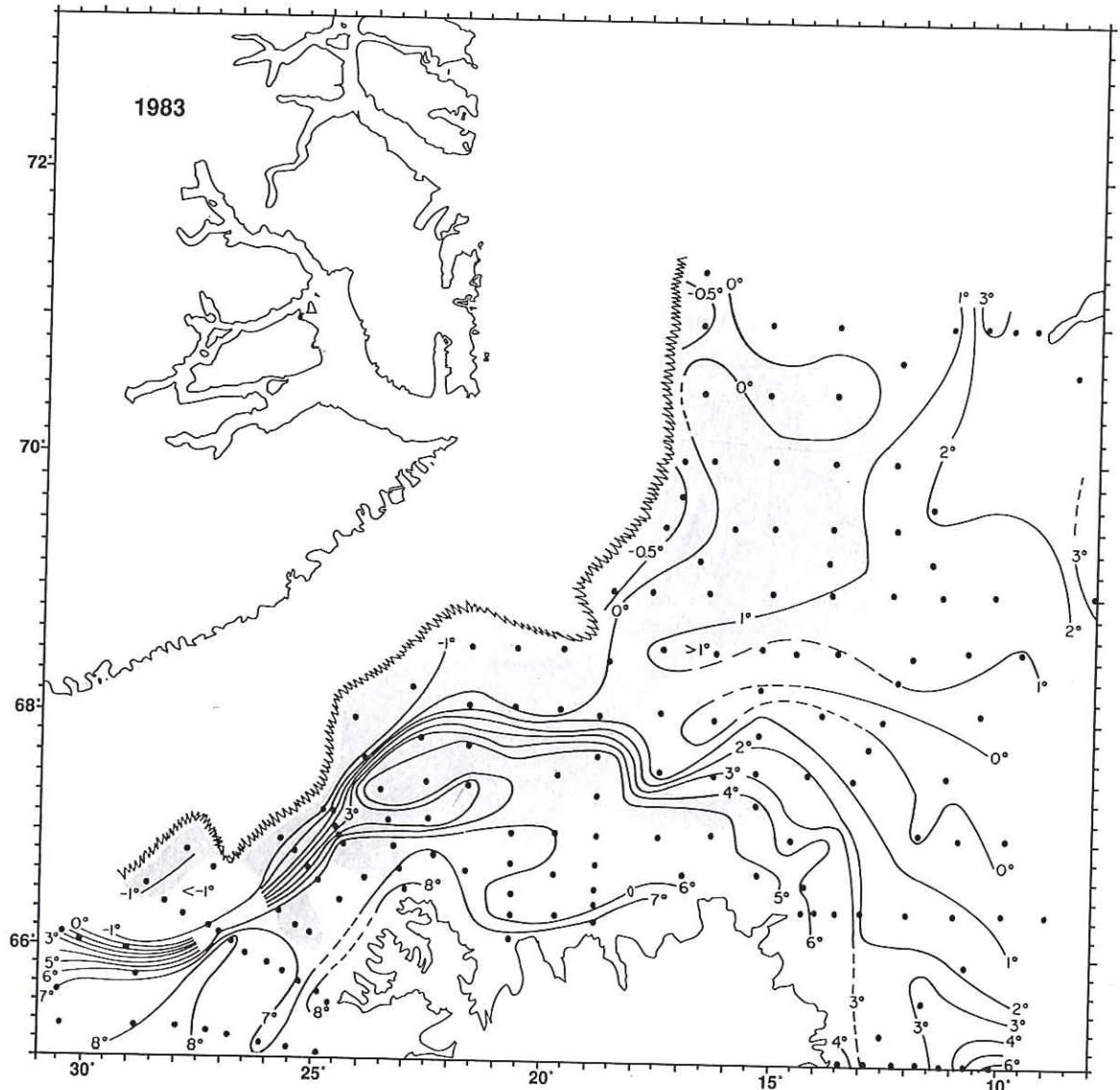Figure 13.13. Capelin distribution and temperature at 50 m depth in August 1985. The position of the ice edge is also indicated.

Figure 13.14. Capelin distribution and temperature at 50 m depth in August 1986. The position of the ice edge is also indicated.

fishery in an area approximately mid-way between Jan Mayen and Greenland in August and September. Since the first part of the Icelandic autumn fishery in October and early November took place off the Vestfirðir peninsula over the Iceland-Greenland Ridge, it seems a reasonable assumption that in the 1984 feeding season the adult capelin stock must have consisted of two components as before. The southern stock component seems to have spent the summer in the area of the Iceland-Greenland Channel while the northern component migrated to feed mainly in the central part of the Iceland Sea. The north-migrating part of the stock appears to have returned south along the Kolbeinsey Ridge and assembled off the eastern part of the north coast and northeast of Iceland in early November where Icelandic vessels began fishing around the middle of the month (Vilhjálmsson 1985).

In the summer of 1985 temperatures in the area north of 68°N were unusually high east of 18°W, especially in the surface layers. During the

Norwegian August survey adult capelin were found to be distributed almost exclusively to the west of 15°W, in places almost up to the edge of the Greenland shelf, some of them having reached latitude 71°30′N (Fig. 13.13). However, in this northernmost part of the area, the capelin seem to have migrated farther to the east later, since considerable fishery took place between 12°W and 15°W to the west of Jan Mayen. South of 68°N, an Icelandic survey recorded large concentrations of adults, mainly 2-group capelin, in the area of the southern Iceland-Greenland Channel and over the Iceland-Greenland Ridge. The autumn survey indicated that the northern stock migrated south again along a route that was much farther to the east than the northward feeding migration (Vilhjálmsson 1986).

In 1986 the summer distribution of the adult capelin stock was similar to that of the previous year. In accordance with somewhat lower temperatures in the Iceland Sea than in 1985, the main part of the northward migrating component

Figure 13.15. Capelin distribution and temperature at 50 m depth in August 1987. The position of the ice edge is also indicated.
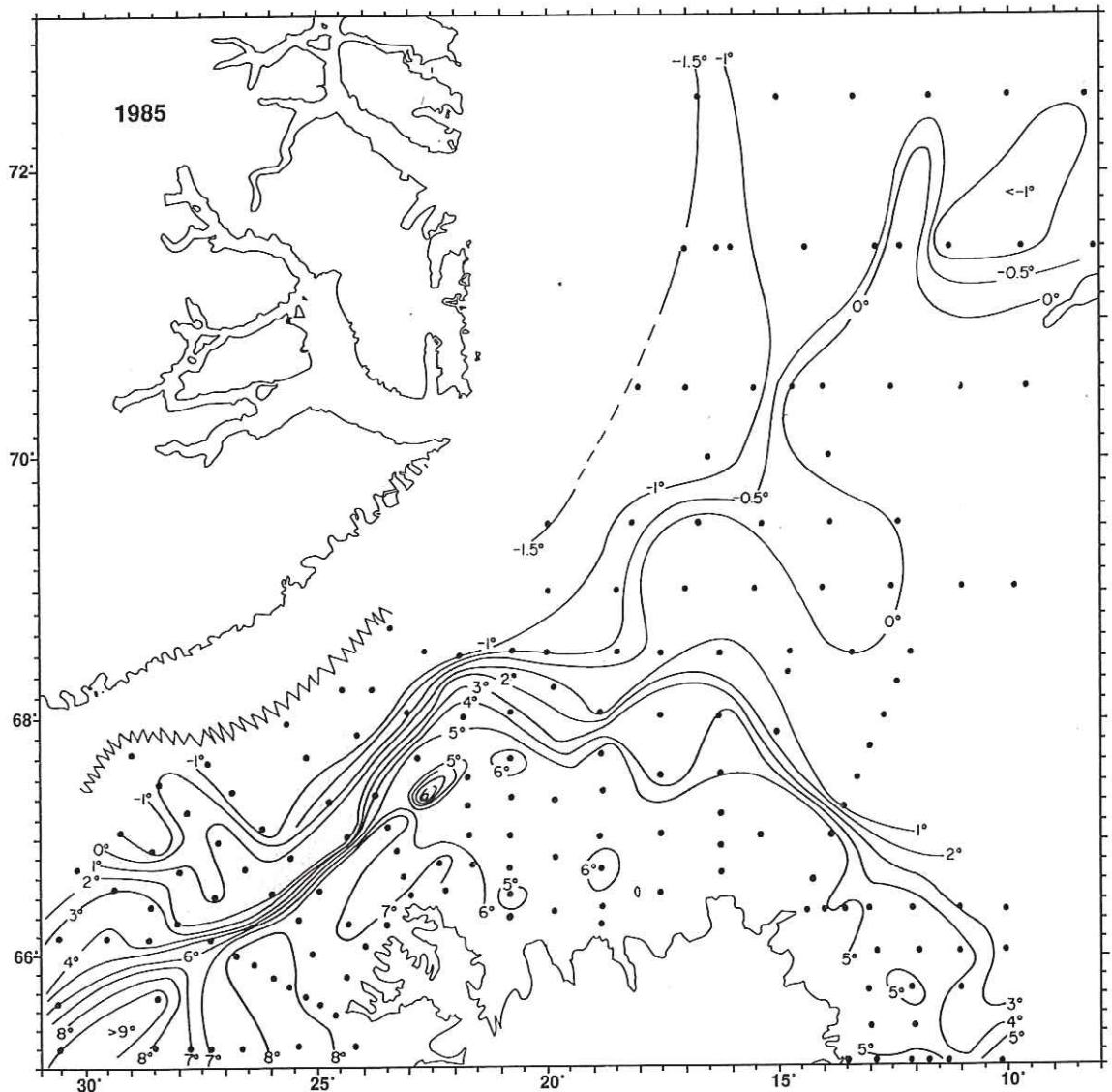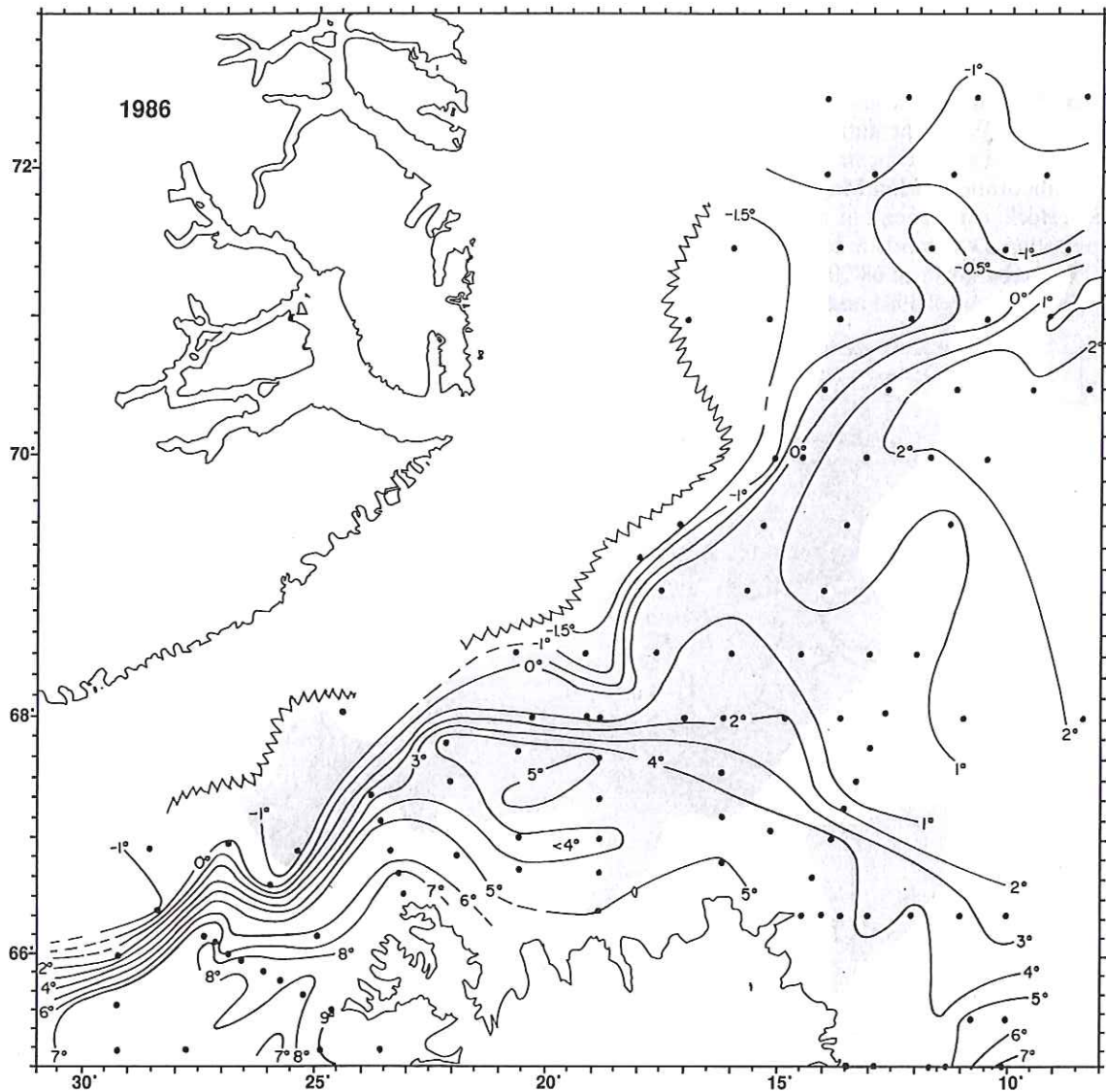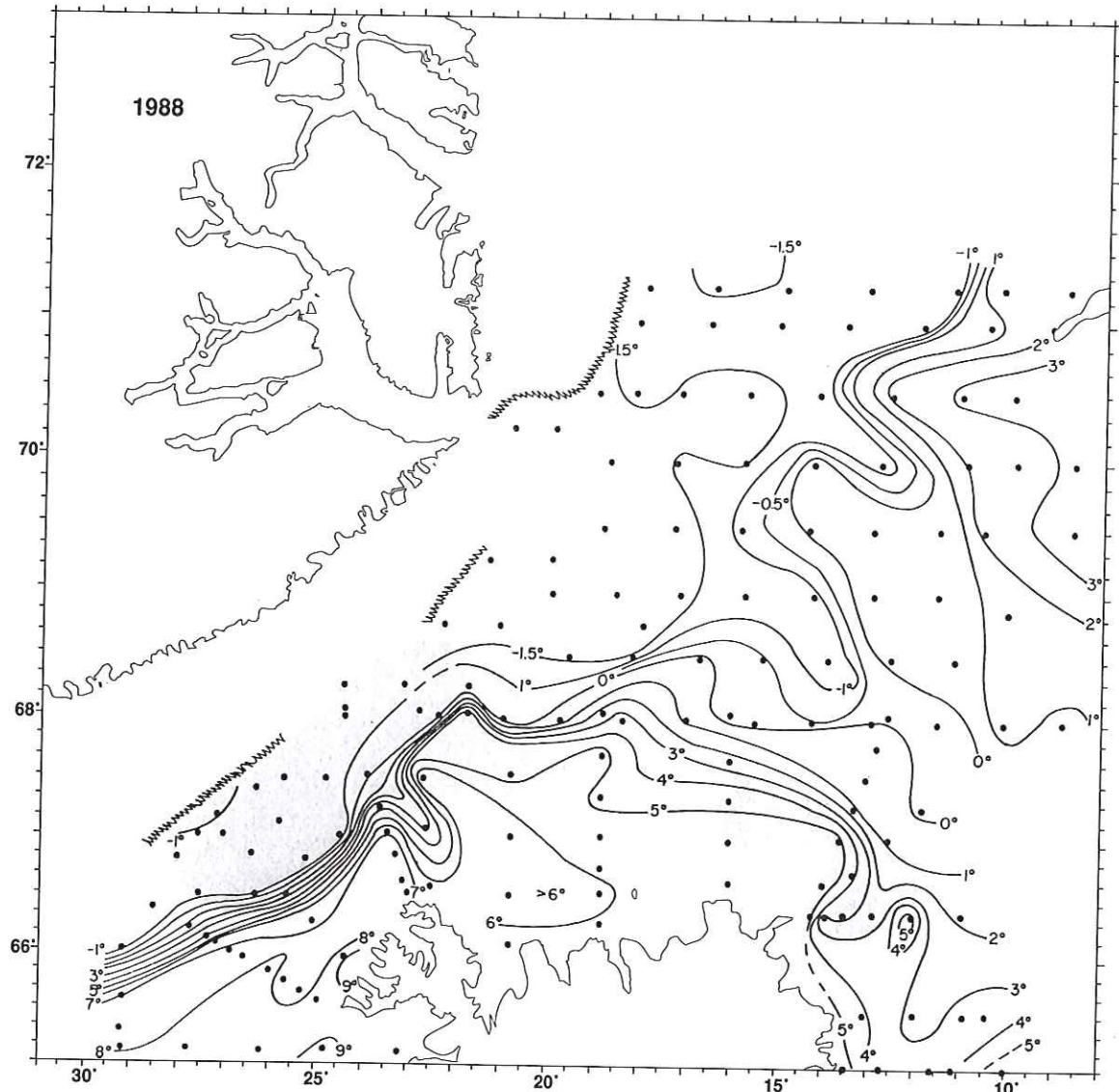
Figure 13.16. Capelin distribution and temperature at 50 m depth in August 1988. The position of the ice edge is also indicated.

took a more easterly route and the stock was distributed farther east in the northernmost part of the area (70°30′N–72°30′N). Again, there was much adult capelin mid-way between Northwest Iceland and Greenland (Fig. 13.14). However, judging from the observed autumn distribution, the southward migration of the northern component took place along or just off the edge of the Greenland shelf, *i.e.* much farther west than the northward feeding migration earlier on (Vilhjálmsson 1987a).

Surface temperatures were relatively high in August 1987 and the distribution of polar water small. Consequently, the main route of the feeding migration to the northern areas was along and in places over the edge of the Greenland shelf north to 71°N (Fig. 13.15). In the first half of August scattered capelin were recorded from this position northeastwards to approximately 72°N, 5°W. A survey in October revealed an extreme western distribution of the northern component and little capelin recordings in the Icelandic area.

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In October the densest recordings were thus obtained on the Greenland shelf at the ice edge east and south of Scoresby Sound, some 40–70 naut. miles from the coast of Greenland. In fact, the October survey had to be abandoned and the fishable stock assessed again in November, when the adult stock had at last migrated out of the ice covered area in the region off Scoresby Sound and assembled off Northwest and North Iceland as usual (Vilhjálmsson 1988).

Norway surveyed the traditional distribution area of the northern component in the summer of 1988, which was relatively a very cold year with a large distribution of polar water in the central and eastern Iceland Sea. In spite of extensive coverage and good surveying conditions, practically no capelin were found north of 68°N and east of 22°W. However, on extending the usual survey area farther to the southwest, the Norwegians located large concentrations of maturing capelin in a restricted area mid-way between the Vestfirðir peninsula and Greenland (Fig. 13.16).

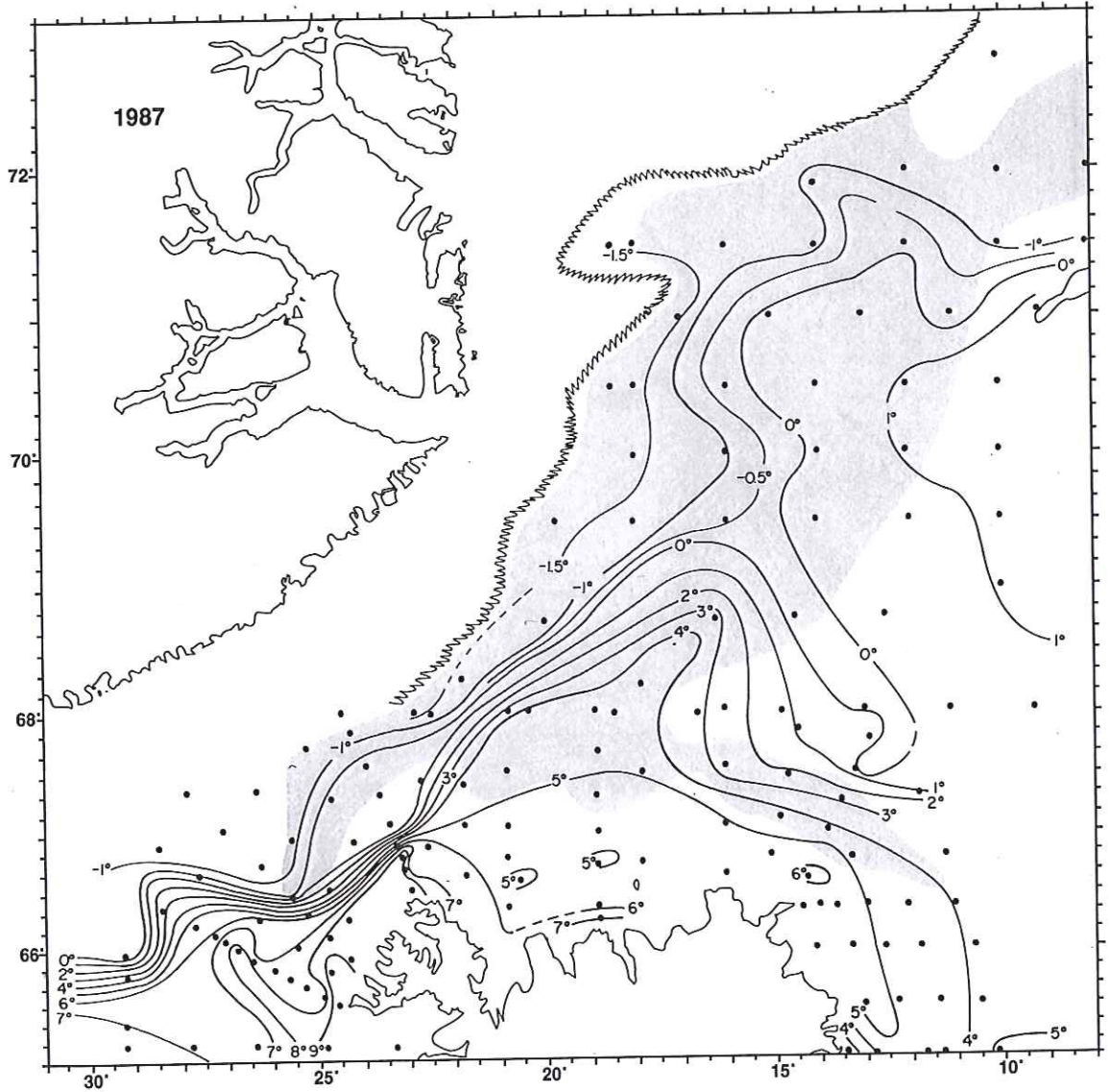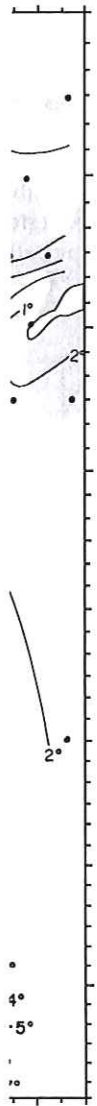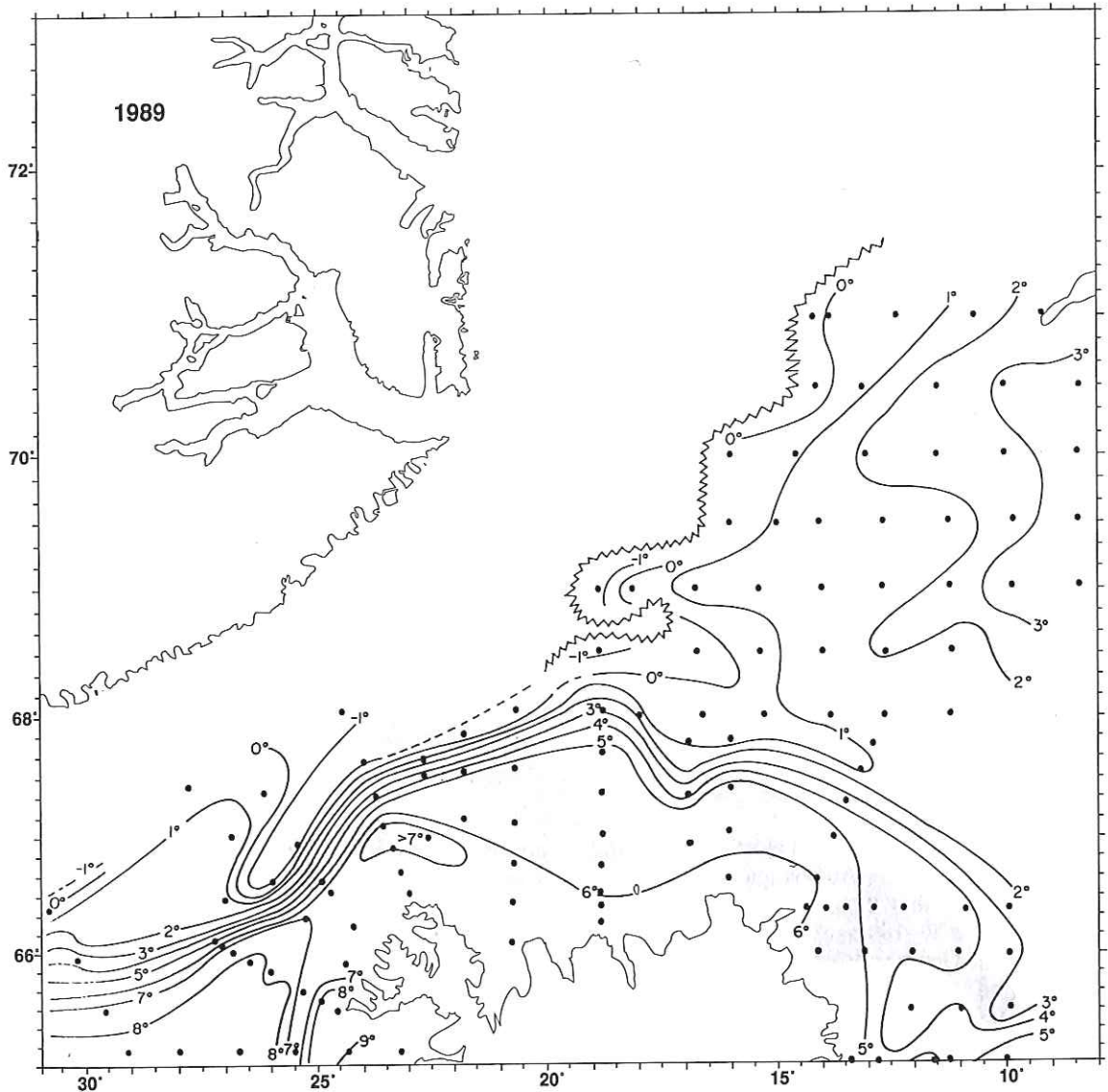Figure 13.17. Capelin distribution and temperature at 50 m depth in August 1989. The position of the ice edge is also indicated.

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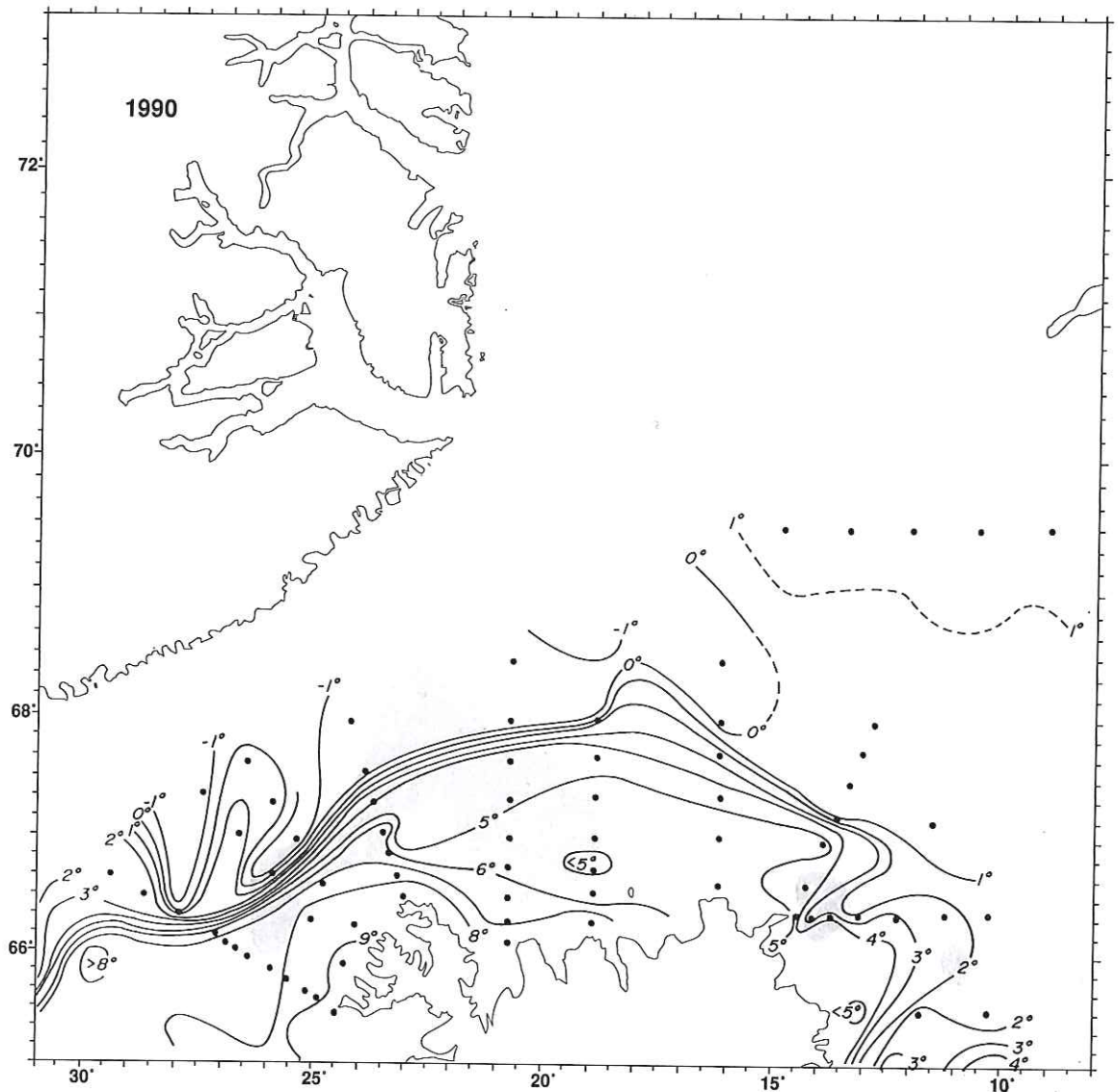
Figure 13.18. Capelin distribution and temperature at 50 m depth in August 1990. No ice was encountered.

Surveying of the area between Northwest Iceland and Greenland later in August and again in September showed that most of these capelin had migrated some 50–100 naut. miles farther to the northeast. In October this stock component was still located to the southeast and south of Scoresby Sound, a short distance off the Greenland continental shelf. However, the remaining, smaller part of the adult stock was distributed over the shelf off the central and western north coast of Iceland. In consequence, the Icelandic and Norwegian 1988 summer capelin fishery was a failure and practically the only catches in the July – October period were taken by Faroese vessels, fishing under Greenlandic licence, in the deep water area southeast of Scoresby Sound. It is, therefore, quite clear that in 1988 the maturing fishable part of the capelin stock did not undertake the usual feeding migrations into the northern part of the Iceland Sea (Vilhjálmsson 1989).

In July – August 1989 the Norwegian survey of

the Iceland Sea between 71°N and 68°N failed to locate any capelin except in a small area from 68°30′N to 69°00′N between 13°W and 14°W, or approximately 150 naut. miles north of the Langanes promontory. Although the area north of Iceland was not as cold as in the previous year, there was extensive drift ice in the northern Iceland Sea at this time, the ice edge lying in a direction from approximately 71°30′N, 12°W in the northeast to about 68°30′N, 17°W in the southwest (Fig. 13.17). In the weeks that followed, repeated multi-national attempts failed to find and

fish capelin in the northern deep water area, and therefore it seems unlikely that adult capelin migrated to feed in the northern Iceland Sea in 1989. However, due to persistent southerly winds there was much drift ice in the area between the Vestfirðir peninsula and Greenland as well as in the southern Iceland Sea in late August and September. These conditions prevailed into autumn and early winter and, in consequence, a valid map of the distribution of adult capelin in the summer, autumn and early winter of 1989 could not be prepared (Sveinbjörnsson 1990).
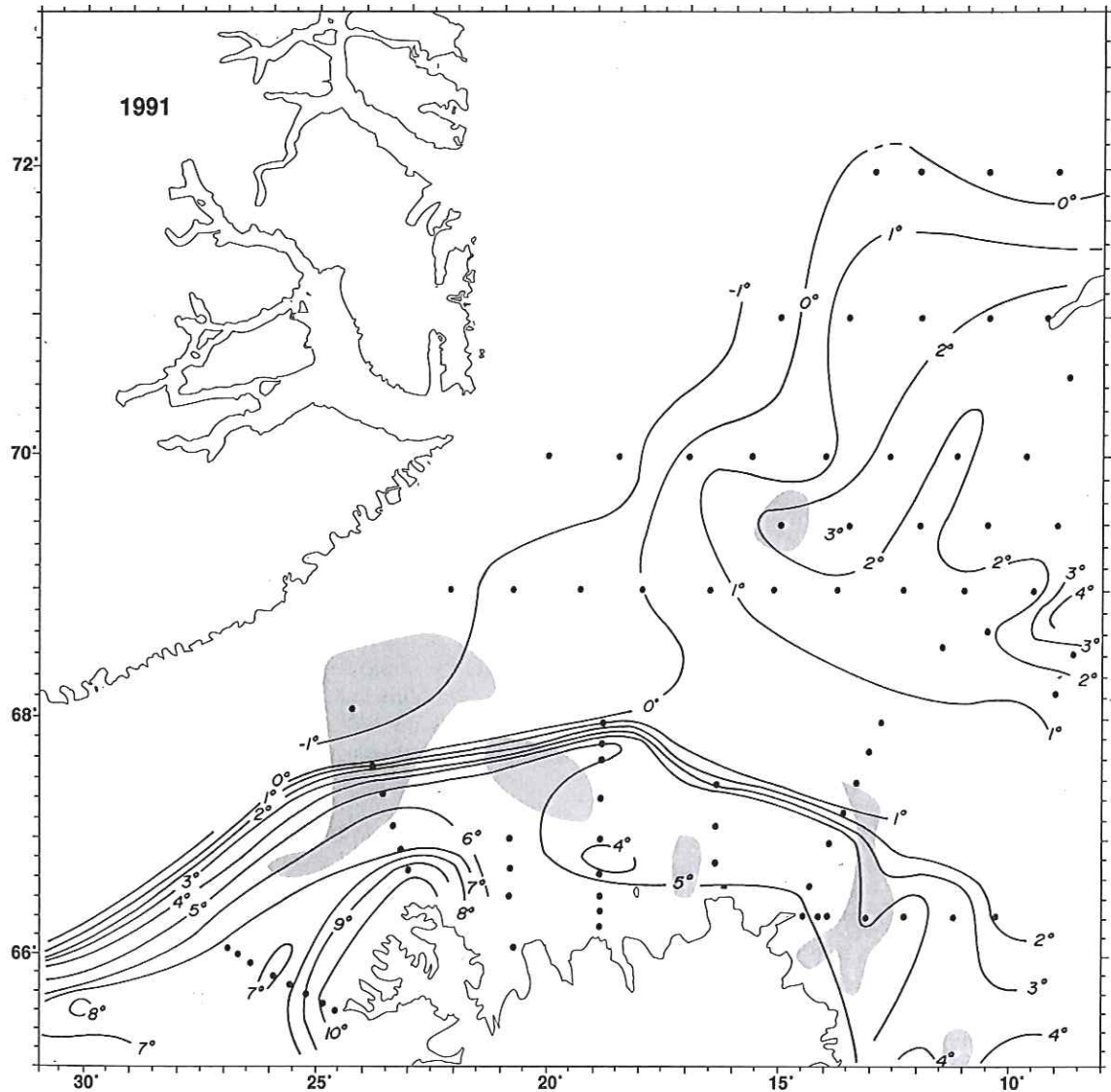
Figure 13.19.   Capelin distribution and temperature at 50 m depth in August 1991. No ice was encountered.

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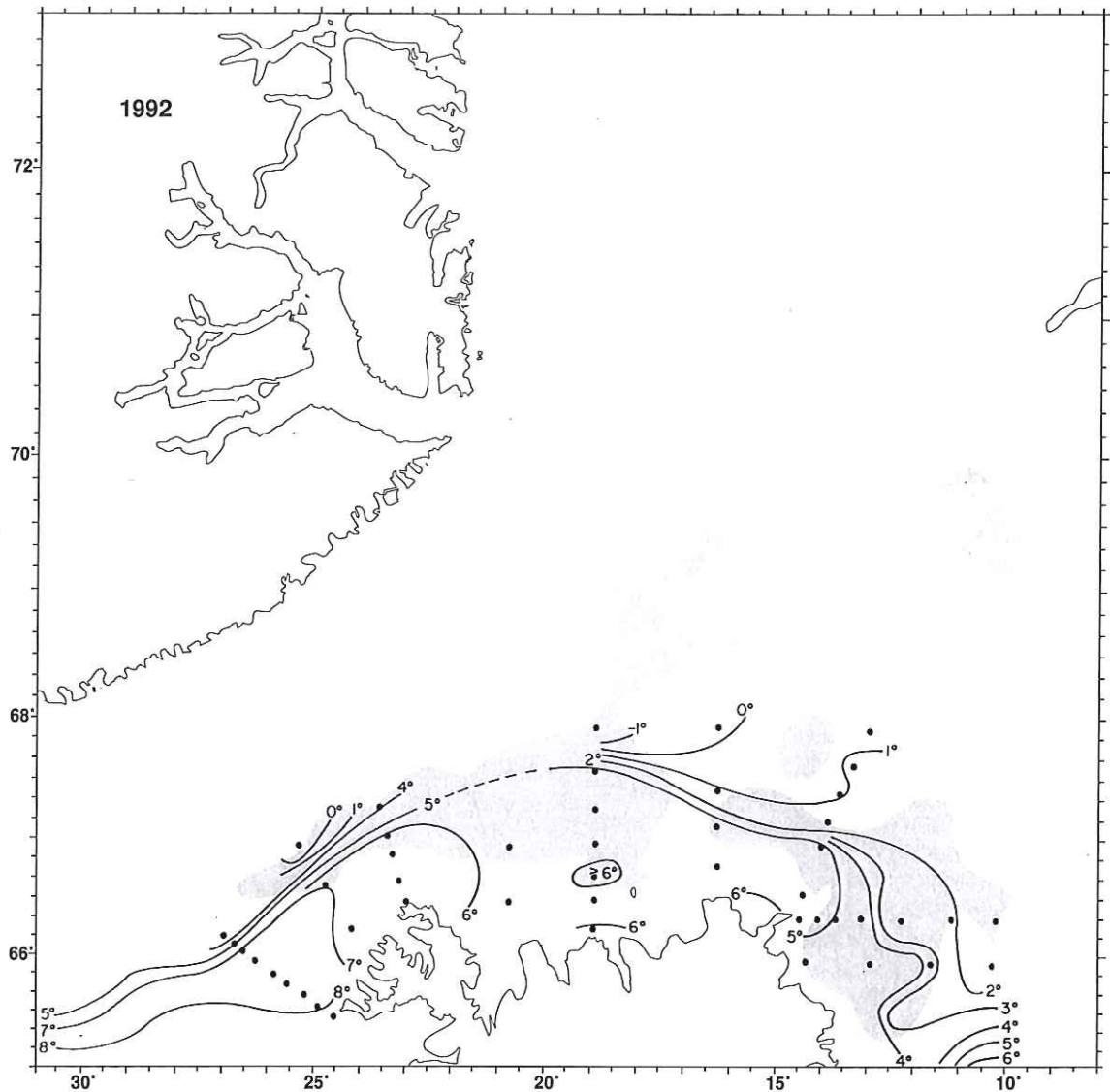
Figure 13.20.   Capelin distribution and temperature at 50 m depth in August 1992. No ice was encountered.

In the period 15 July – 20 August 1990 considerable capelin scouting was carried out by Norwegian vessels in the Iceland Sea. In late July small concentrations of capelin were located about 110 naut. miles north of Melrakkaslétta, resulting in a short lasting Norwegian and Faroese fishery off the eastern part of the north coast of Iceland at position 68°20′N, 16°20′W. A Norwegian vessel searched the area from 72°N, 12°W south and westward to about 66°30′N, 27°30′W for three weeks in August. The results were negative except for a small area at the shelf edge off Northwest Iceland. Unfortunately, there are no hydrographic data available from the Norwegian scouting surveys, but Icelandic August data from the area south of 68°30′N show that the shelf waters north and east of Iceland were comparatively cold (Fig. 13.18). In spite of intense surveying in October and November 1990, absolutely no capelin were observed north of 68°N, and it seems fairly certain that for the third year running no capelin had migrated to the

central and northern Iceland Sea for summer feeding (Sveinbjörnsson 1991).

In July/August 1991 Norwegian investigations in the Iceland Sea covered an area from 68°30′N to 73°00′N from about 6°W to the Greenland shelf. The only capelin record was north of Melrakkaslétta, near 69°40′N, 15°00′W, but temperatures were considerably higher than in many previous years and this was also the case in the shelf area north of Iceland (Fig. 13.19). Because of a total ban on capelin fishing in summer and early autumn of 1991 there were no fishing vessels in the area in the period July – September. However, prior to the Icelandic stock abundance survey in October, 4 fishing vessels carried out a pilot survey of the traditional autumn distribution area (Appendix I.1, Fig. XLII). In the first week of October these vessels reported capelin schools in deep waters, located in a narrow area just outside and in the general direction of the Greenland shelf southeast of Scoresby Sound, between approximately 68°20′N and 69°30′N from about 22°W in the south to 18°W in the north. However, when the Icelandic research vessels arrived in the area, about one week later, practically no capelin were registered north of 68°N. Although it is thus possible that some capelin migrated to feed in the Iceland Sea in 1991 it seems most likely that their numbers were low (Sveinbjörnsson 1992).

Capelin resumed their feeding migrations towards the central and northern Iceland Sea in 1992. This was established during a Norwegian scouting/fishing trip to the Iceland Sea in July (Fig. 13.20). The summer fishery that followed began around mid-July when good catches of large capelin were taken between 68° and 69°N, around 16°W. Catch rates remained reasonably high in and north of this area to approximately 70°N until in the second week of August. Then this part of the stock suddenly turned back and migrated quickly south towards Iceland again. Around 20 August the migration was located about 50 naut. miles north of Melrakkaslétta on the eastern north coast of Iceland, whereupon it turned west to mix with other mature capelin and large concentrations of immatures located off the western north coast. After this, Icelandic fishing vessels did not locate capelin in the Iceland Sea and the October 1992 survey registered practically no capelin north of 68°N (Sveinbjörnsson 1992).

13.5. Discussion of changes in the migrations of age groups 2 and 3

In autumn and early winter the bulk of the 1-group capelin are located in the area north and northeast of Iceland. It seems that in the January – April period most of these capelin will, as 2-group, migrate slowly westward to the area off the western north coast and to the northwest and west of the Vestfirðir peninsula. From there these capelin subsequently start their feeding migrations in spring. The remainder overwinters off East and Northeast Iceland.

The 2-group immatures, on the other hand, often show a tendency to follow the spawning migration eastward off the north coast to the area off Northeast and East Iceland in variable quantities and stay there, until beginning their feeding migration to the north as 3-group in the spring of the following year. What determines the magnitude of these eastward migrations of the immature 2-group capelin is not clear. To some extent they might be the result of variable hydrographic conditions in the north Icelandic area, but might simply be a part of the natural built-in behaviour pattern of this stock. It is of interest to note that in the 1981–1992 period there was only one instance when considerable quantities of 3-group immatures were distributed off East and Northeast Iceland in late winter. This happened in 1986 and was due to the very large year class of 1983 of which only about 40 percent matured to spawn as 3 year olds. In the winter of 1986 there were, therefore, large numbers of immature 3 year olds of which a very considerable proportion followed the 1986 spawning stock and overwintered off East and Northeast Iceland. The same is probably true for those years in the 1969–1976 period when much immature 3-group capelin were observed in the east Icelandic area. Although acoustic assessment of stock abundance had not begun by then, the age composition of the spawning stock indicated that 3-group immatures must have been relatively abundant in most of these years. It is, however, quite possible that the presence of additional immature capelin in more offshore waters off North and Northwest Iceland in late winter may have been overlooked at that time.

As described in the previous section, it is clear that in most years of the 1978–1992 period the maturing stock of capelin undertook lengthy
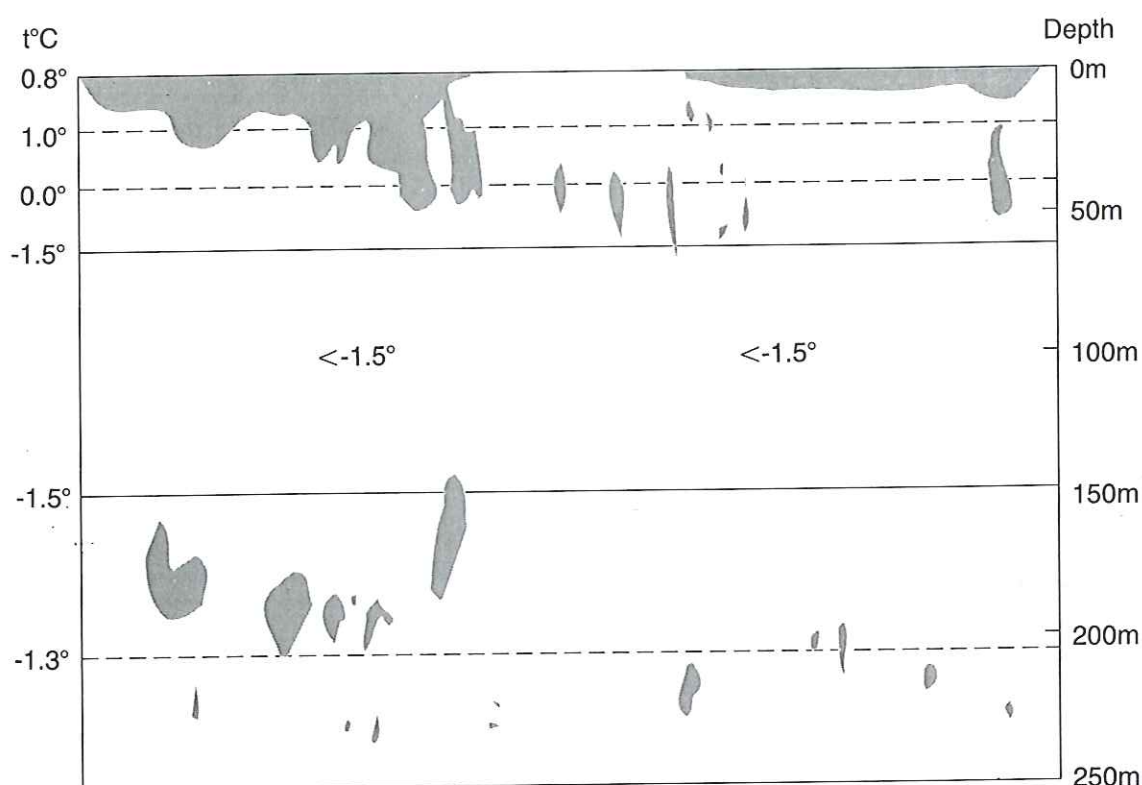
Figure 13.21. Vertical capelin distribution and temperture in the uppermost 250 m in the Iceland–Greenland Channel near position 67°30′N, 24°45′W in August 1988.

feeding migrations to the central and northern part of the Iceland Sea in summer and returned to the areas off North and Northwest Iceland in autumn. These migrations have been documented by frequent observations of capelin distribution in the July/August period and again in October/November. When comparing capelin distribution to environmental variables, it should, however, be borne in mind that actual acoustic abundance assessment has proven impossible at the height of the feeding season. This applies in particular to the central and northern Iceland Sea and is mostly due to capelin feeding in the immediate surface layers at a depth of 5–10 m where they are out of range of vertically registering echo sounders. Although this probably does not cause actual gaps in the observed capelin distribution, it may account for distribution centres not being registered where they should have been in July – August and thus to some extent give a distorted picture of the actual distribution pattern. For this reason it was decided not to attempt to present a density stratifi-

cation of the August capelin distribution shown in Figures 13.8–13.20.

With reference to Figures 13.9–13.16 it seems, nevertheless, clear that during their feeding migrations the capelin have followed the eastern boundary of the East-Greenland Current quite closely and longitudinal changes in the migration route from one year to another have been linked to changes in the distribution of polar water from the East-Greenland Current and the temperature regime of the Iceland Sea. Thus, there is for example a very large difference between the westerly distribution of capelin in the relatively warm year of 1980 and the extreme easterly capelin distribution in the very cold year of 1982, while capelin distribution was intermediate and temperatures more moderate in the central and northern Iceland Sea in 1979 (Figs. 13.9, 13.11 and 13.8 respectively). Similar displacements of capelin distribution apparently linked to large-scale changes in temperature have also been observed in the Barents Sea (Loeng 1989).

It will be noted that on some of the summer

distribution charts a considerable part of the capelin population was located in areas where the temperature at 50 m depth was below $-1°C$. This was particularly prominent in 1980, 1985, 1986 and 1988. While no specific studies have been carried out on the temperature tolerance of capelin, it seems that they are seldom consistently recorded where the temperature is much below $-1°C$. This agrees with the findings of Gjøsæter and Loeng (1987) who reported that in the Barents Sea the majority of capelin, 2 years and older, stay in waters with temperatures between $-1°$ and $+2°C$. In the Icelandic area it has been noted that when very low temperatures occur at intermediate depths in areas otherwise occupied by capelin, the fish tend to be distributed above and/or below the minimum temperature zone as shown in Figure 13.21. In all likelihood, the capelin can sustain temperatures of -1.3 to $-1.5°C$ for the short time that it takes them to traverse the area vertically in search of food in the near-surface layer or to seek deeper water for digesting the food. On the other hand, it is unlikely that they can navigate for long periods and distances through such waters. Indeed, capelin have often been observed freezing to death when fished through a surface layer with temperature between $-1.6°C$ and $-1.9°C$ in autumn. There-
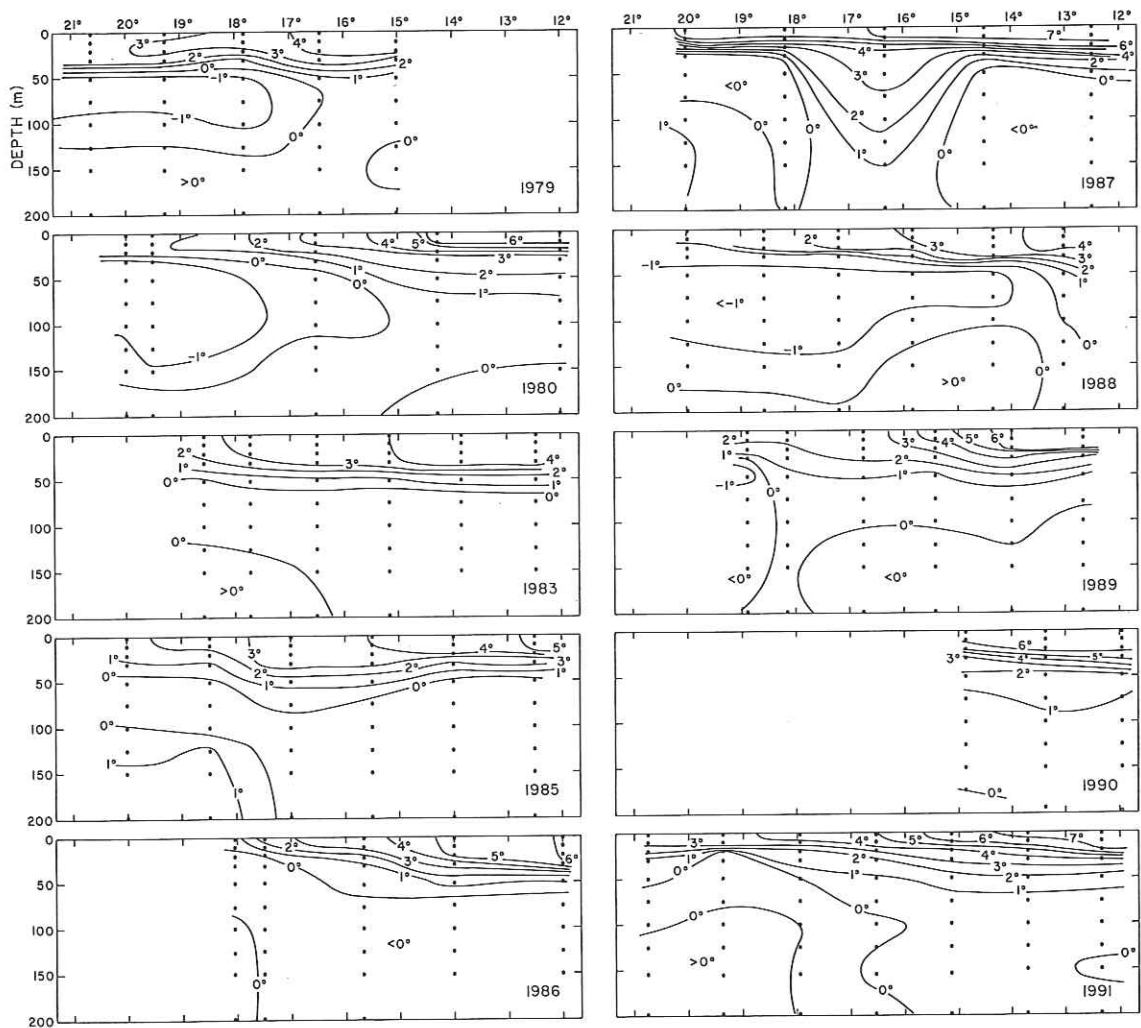
Figure 13.22. The vertical temperature distribution in the uppermost 200 m on sections along approximately 69°N in 1979–1991. Data provided by J. Blindheim.
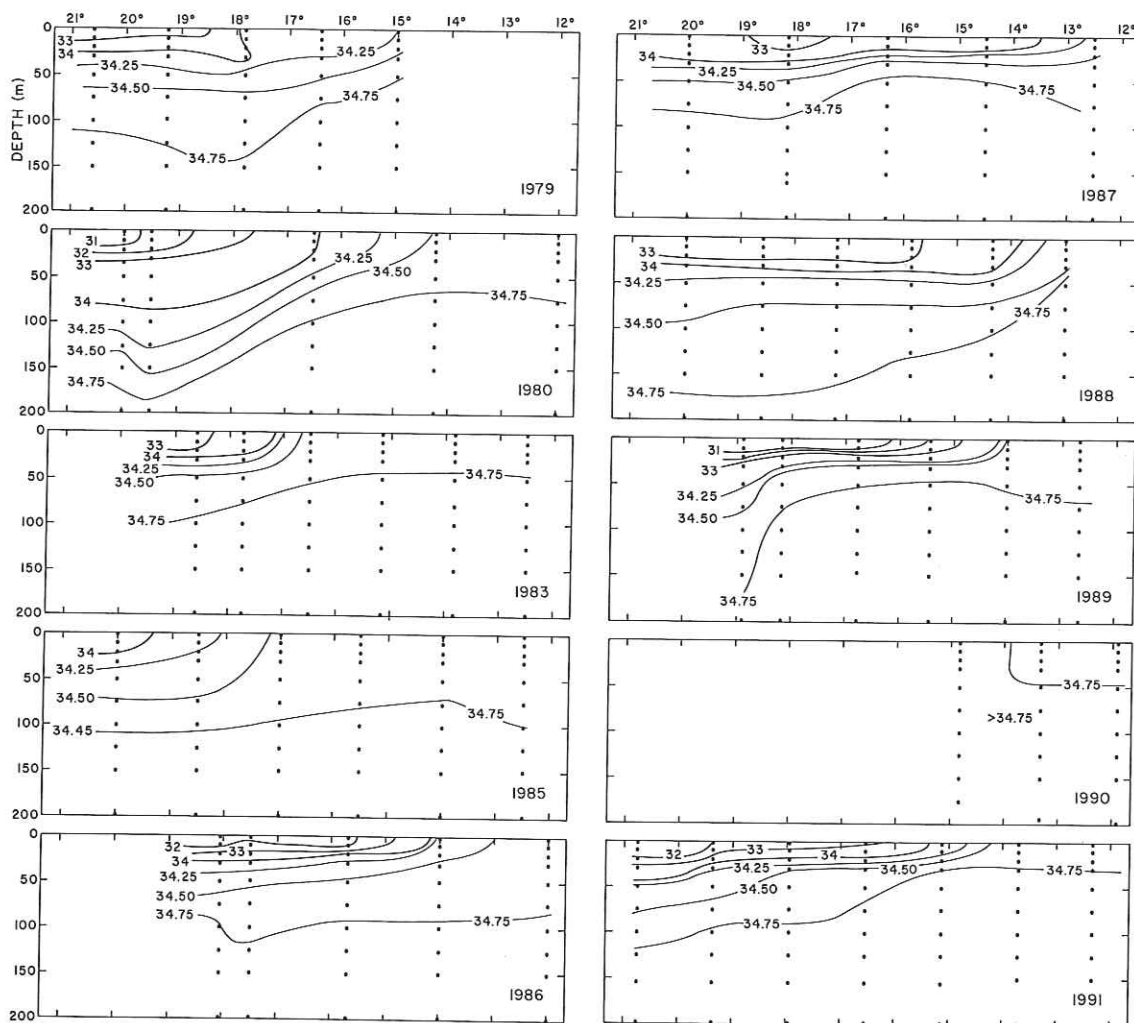
Figures 13.23. The vertical salinity distribution in the uppermost 200 m on sections along approximately 69°N in 1979–1991. Data provided by J. Blindheim.

fore, the observations of capelin in areas with temperatures much below −1°C most likely represent temporary situations and not indications of migrations for extended periods under such conditions.

As described in the previous section, no capelin migrated to feed in the central and northern Iceland Sea in 1988. In Figure 13.16 we see how a broad tongue of subzero temperatures reaches almost to 12°W in deep waters north of Iceland, with a tongue of water of <−1°C extending east to about 13°40′W, indicating extremely cold conditions in the central and northern Iceland Sea. Figures 13.22 and 13.23 further show the vertical

temperature and salinity distribution in the uppermost 200 m on a section along 69°N for those years when such data are available. Clearly, the 1988 situation when the easternmost position of the −1°C water was between 13°W and 14°W, with the 34.75 isohaline at about 170 m depth to 17°W, is extreme in comparison to that of the rest of the series. Even in 1982, when cold conditions predominated with extensive ice cover in the central and northern Iceland Sea in July – August (Fig. 13.11) the −1°C isotherm at 50 m depth was located near 15°W at latitude 69°30′N.

In migrating for feeding in the central and eastern Iceland Sea the capelin would in 1988 have

had to either traverse a wide area of inhospitable waters or circumnavigate it. With the initial westerly distribution of the adult stock in spring and early summer of 1988 neither of these choices were accepted. The hypothesis that capelin will not migrate for any length of time through waters colder than $-1°C$ is thus strongly supported by the 1988 data and explains why the normal migration pattern was disrupted that year.

In spite of drift ice, which because of prevailing winds covered quite extensive parts of the Iceland Sea for periods of time in the summer and autumn of 1989, these waters were, on the whole, relatively warm below the surface layer both in August and October. Although hydrographic data are not available for the central and northern Iceland Sea in July – August 1990, Icelandic summer and autumn data from the area south of 68°30′N indicate average or mild conditions in that part of the area. And in August 1991 the central Iceland Sea was relatively very warm (Figs. 13.19 and 13.22). So why then was the apparently normal migration pattern for feeding in the central and northern Iceland Sea not established again?

As mentioned earlier, the northward migration in early summer of 1992 was halted at about 70°N from where the capelin retraced their path to the north Icelandic area in the latter half of August. Observations of the hydrographic situation in the area north of Iceland in August 1992 (Fig. 13.20) only reached north to 68°–68°30′N. However, neither these nor hydrographic records from October of that year indicate polar influence in the central Iceland Sea which could explain the behaviour just described of the capelin in the summer of 1992 (Fig. 13.20).

While no single, concrete explanation can be offered, there may be various reasons why the capelin did not enter and remain to feed in the Iceland Sea since 1988. According to the results of surveys of capelin abundance, the stock has recently gone through a difficult period where the adult fishable part was by natural causes reduced from about 1.8 million tonnes in August 1988 to 0.8 million tonnes in August 1990. It seems reasonable that such a reduction in stock size should lessen competition for the available food and thereby the necessity to undertake wide migrations in order to satisfy the requirements of the stock. It must, however, be pointed out that when the stock suffered a similar or even greater reduction in the early 1980s, the capelin continued their northward feeding migrations into the central and northern Iceland Sea in summer. The observed difference is, however, that in the cold year of 1979 a hydrographic barrier similar to that of 1988 did not arise (cf. Figs. 13.8, 13.16 and 13.22)

As described above, the capelin did not seem to resume their extensive migrations to the area between Jan Mayen and Greenland in 1991, in spite of the fact that in August that year the adult fishable stock is estimated to have been about 1.2 million tonnes. At the time, however, the older component (3-group capelin) only amounted to about 8% by number. Considering the fact that the maturing part of the younger year class was of less than average abundance, it is clear that capelin belonging to the older conponent of the maturing stock were relatively few. A similar age composition was recorded in 1992. The older year class usually makes up the bulk of the north migrating part of the stock and, therefore, their scarcity may partly explain the apparent southern distribution of the maturing fishable stock in 1991 and 1992 when the northernmost records were well south of 70°N.

It is obvious from the fat content, recorded in catches from the north migrating part of the stock in July and August 1992, that these capelin had been enjoying abundance of food organisms. It is tempting to postulate that their sudden and unexpected return to more southern regions towards the end of August, must be linked to a sudden shortage of food owing to the supply of polar copepods from the summer generation becoming exhausted. Unfortunately, there are very limited data on feeding conditions of the Icelandic capelin in summer and early autumn (cf. chapter 12). Indeed, it seems most likely that such information is necessary to explain more fully the large variations in capelin migrations in the summer period. Thus, Jakobsson (1978, 1980) found a close correlation between concentrations of *Calanus finmarchicus* and herring in the 1960s when he was in fact often able to forecast the location of fishable herring concentrations on the basis of information about the abundance and age distribution of this copepod.
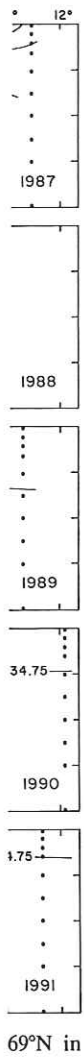
14. BIOLOGICAL VARIABLES OF THE ICELANDIC CAPELIN

14.1. Data base

Regular sampling in order to record biological variables of the Icelandic capelin began in connection with a short winter fishery in March and April 1966. Over the next few years sampling was gradually intensified and since 1970 a comprehensive sampling programme has been in operation in the period January – April, including both research vessel catches and commercial fishery.

Until the mid-1970s, biological sampling outside the winter period was only sporadic and consisted of a few capelin samples, collected by various means and parties, in the period between about mid-April and late July. Unfortunately, the situation has not improved much with regard to the spring and early summer period in later years. For studies of growth this is a definite drawback, since the spring and early summer represent the first part of the feeding season when the capelin start on their various paths of growth as immatures, maturing fish or possibly as recovering spents.

In 1975 investigations were begun in order to test the possibility of a summer and autumn fishery off northern Iceland and resulted in the opening of such a fishery in 1976. This increased the availability of adult capelin for biological sampling during the July – September period, but particularly in the months of October – December. However, the summer fishery was not always productive, resulting in few samples being available from the summer months in some years. Since 1982 this disadvantage has to a certain extent been offset by sampling of adult capelin during surveys of 0-group and juvenile capelin abundance in August. In that year the area covered by the August surveys was extended to the north and northwest in order to incorporate the juvenile 1-group capelin. Since 1978 regular autumn and winter assessment surveys of the capelin stock have also provided more comprehensive sampling in the October – February period than would have been available from the commercial catch alone.

With the above qualifications, a data base comprising about 250,000 individuals is available for age groups 1 and older. As explained above, these data are, however, neither spread evenly over the year nor the period as a whole. In addition, length and volumetric measurements of 0-group capelin are available from the July – September period with most of them, however, collected in August. Such measurements are also available from the autumn and winter months, including January and February, when the 0-age prefix is changed to 1.

All measurements were carried out on fresh specimens or capelin that had been frozen shortly after capture. However, the latter part of the material constitutes less than 15% of the total number of samples examined. Frozen samples were thawed just prior to examination, usually within one month from collection. No adjustments have been made for the slight shrinkage and loss of weight that may occur in frozen material (Monstad 1971). Almost all the commercial catch has been taken with purse seines, having a mesh size of approximately 20 mm, while research vessel samples were collected with pelagic capelin trawls of the Harstad type, having a fine mesh in the codend and a nominal opening of 14 by 14 or 16 by 16 fms. In the early 1970s there was a small trawl fishery for capelin with the same gear as used by the research vessels. This fishery was ineffective in comparison to the purse-seine fishery and soon abandoned.

Recorded fish lengths are in centimetres. These represent total lengths measured from the tip of the mandible to the end of the ventral lobe of the caudal fin. For the 1-year and older fish, lengths were recorded to the nearest ½ cm below, off a measuring board specifically con-

structed to avoid bias arising from the rounding off of length units. On the other hand, lengths of 0-group capelin were recorded in mm.

All weights are in g. With the exception of research samples, collected during abundance assessment surveys, all weights were determined in the laboratory and recorded to ¹⁄₁₀ of one g. Until recently analytical balances have generally not been available for use out at see. Therefore, the weight of capelin, caught during research surveys, were determined by volume measurements to the nearest ml (g). Such measurements have proven to be very accurate with regard to samples of, say, 100 fish. In individual cases deviations up to ± 1.0 g may, however, be observed for the largest individuals (30–40 g).

Ages were determined from the lateral, convex face of fresh otoliths mounted in water on a dark background and using a low-power binocular microscope. Ages were recorded as age groups with a fixed arbitrary date of birth on 1 January. The age of the Icelandic capelin is generally easy to determine with the possible exception of the first winter ring in some of the older fish. The method of ageing is the same as used for the Barents Sea stock (Hamre 1977; Anon. 1985b), *i.e.* to count each translucent area as a winter ring.

The sex and stage of maturity were determined visually and without the use of a microscope. The maturity scale runs from 1 to 8, where maturity stage 1 denotes immatures, stages 2–5 increasing maturity, stage 6 ripe fish with running roe and milt, stage 7 spent fish with only minor amounts of genetic products remaining and stage 8 completely spent or recovering spent fish. It is difficult to classify juvenile capelin to sex and maturity by this method, and in consequence, relatively few 1-group fish have been sex-determined. The same is true for part of the 2- and 3-group capelin in the summer months (maturity stages 1 and 2). By August the sex of most maturing fish can, however, be determined fairly accurately by a skilled worker. Sex and maturity compositions, determined during stock assessment surveys in October and November, are in close agreement with those made during assessment surveys carried out about 2 months later, *i.e.* early in the following year some 1–2 months prior to spawning (cf. section 14.6).

In the winter period (October – April) the gonad weight of female capelin in most samples handled in the laboratory, has been recorded

with a precision of ¹⁄₁₀ of one gram. The weight of the male testis is at all times only a fraction of that of the female ovary and has not been recorded as a matter of routine.

A number of samples including counts of vertebrae are available from the 1970s and the early 1980s. This was done by removing the flesh from one side of the fish and counting from the basioccipital to the hypural segment, including the latter. The process is very time-consuming and has been discontinued. No other morphometric measurements of capelin belonging to this stock have been made.

In addition to the above variables, the Icelandic Fisheries Laboratory and the State Factories have over the years gathered extensive records of the changes in fat content with time. Samples for these measurements are mainly collected from the commercial catch and, for a number of years, cover the entire capelin season. Similar information from Norwegian catches has also been made available.

14.2. Age and growth

Like other species of fish, the capelin exhibit large variations in growth rate from one year to another, depending both on changes in zooplankton abundance, year class size, *i.e.* stock abundance of the capelin, and of the physical environment (mainly temperature). In order to draw an average picture of the growth of the various components of each age group (immatures and maturing females and males) it is, therefore, neccessary to have comparable data, collected at the same time of the year and covering a fairly extensive period of time. After analyzing the available material, it was concluded that the most suitable data for the purpose of describing an average growth pattern of the various stock components, consisted of bi-monthly averages from July/August, October/November and January/February in the 1979/80–1992/93 period. The average values for individual years are given in Appendix II.1, Tables I–III, together with the grand means, standard deviations and maximum and minimum values.

In the following sections, the growth of immature, as well as of maturing female and male capelin, is traced separately over time according to the bi-monthly average values, using existing knowledge of oceanographic and biological pro-

cesses in the waters around Iceland and in the Iceland Sea, to determine the onset of growth in spring. In this way the growth of the immature part of the population is traced continuously into their third (fourth) year of life. However, the rate of growth of the maturing part of each age group starts to diverge from that of the immatures in spring and early summer, and continues to do so until spawning in March/April in the following year. At that time the high spawning mortality removes most, but probably not all, of the spawners from the population (cf. section 14.11).

14.2.1. Length at age

Age 0. Friðgeirsson (1976) reported the length at hatching for the age group 0 to be about 7 mm in his 1974 and 1975 laboratory experiments. However, Magnússon (1966) reported considerable numbers of 4–6 mm larvae in the month of May in the period 1961–1963 and similar findings were again reported off Southwest Iceland in the late 1970s (Friðgeirsson 1980). Thus, it seems that in nature the Icelandic capelin hatch at a smaller size than observed in the laboratory experiments.

Magnússon (1966) gave average sizes of 0-group capelin in the first months of their life for the period 1960–1964. These were 10.2, 14.7 and 22.0 mm for the months of May, June and July respectively. Length measurements of 0-group capelin are available from 0-group fish surveys carried out annually since 1970, mainly in August. Length measurements of 0-group capelin are also available from other surveys in the autumn (October/November) and in winter (January/February, 1-group).

From these sources it is possible to draw an average picture of the growth in length of 0-group capelin from hatching in April – May until autumn and join these observations to length measurements of 1-group capelin in January/February of the following year (Figure 14.1 and Appendix II.1, Tables I–III).

However, it should be kept in mind that growth rates of 0-group capelin are highly variable. Thus, annual weighted average lengths in the August 1970–1992 time series have varied between about 35 and 65 mm. However, variations have been somewhat smaller (38–55 mm) in the latter half of this period (Appendix II.1, Table I).

Age 1. The monthly growth in length of immature 1-group capelin is represented by the lowest curve in Figure 14.1. Since few samples were available from late winter and early spring, it is not possible to pinpoint the time at which growth is resumed after the winter starvation period. In view of the onset of spring bloom and subsequent zooplankton production in north Icelandic waters (cf. sections 6.6 and 6.7) it is, however, most probable that growth is resumed in May and is
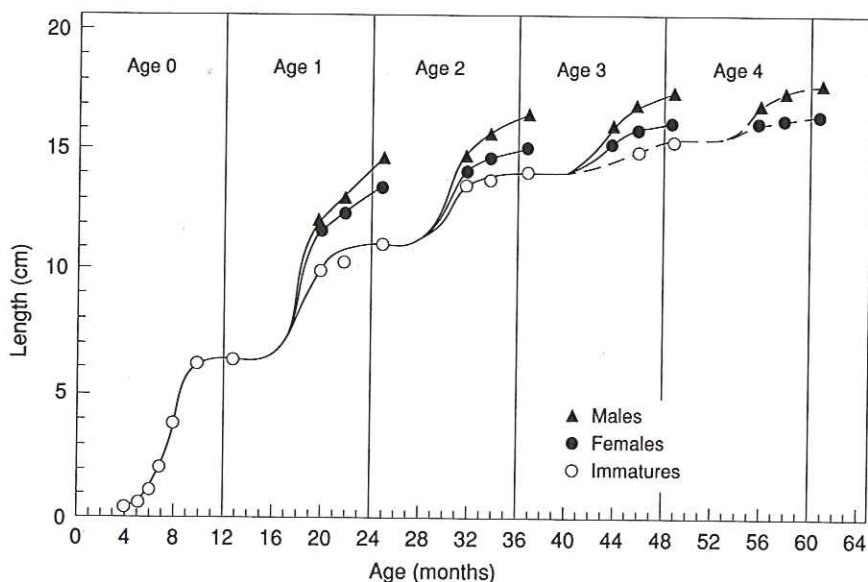
Figure 14.1. The average monthly growth in length of immature (lowest curve), female (middle curve) and male (uppermost curve) capelin in the years 1979–1993. See also Appendix II.1, Tables I–III.

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most rapid in June, July and August. From then on the growth rate of the immature 1-group capelin appears to slow down considerably. Nevertheless, this part of the stock continues to grow in length until the end of the year. It is likely that some of the observed abrupt change in the rate of growth of 1-group capelin as from August is an artifact, resulting from inadequate sampling in the autumn period. Thus, a relatively high growth rate of this stock component may well last through most of September, as indicated in Figure 14.1. This is in fact suggested by some of the available data.

A very minor part of this age group will mature and spawn as 2-group. These faster growing individuals are first recognized in the August data, but more commonly in the October/November surveys, and from then on they usually constitute a small proportion of the samples. The available but scanty data on maturing 1-group capelin indicate small size difference between the sexes until late autumn. After that the difference in length increases in favour of the males, from 0.6 cm in October/November to 1.1 cm in January/February of the following year (Fig. 14.1 and Appendix II.1, Tables II and III).

Age 2. The size of the capelin, comprising the maturing part of this age group, is uncertain in spring and early summer. This is because of inadequate sampling and also due to the fact that the maturity of these capelin was determined by direct visual observation and not using a magnifying device. The available evidence suggests that, as in the case of the 1-group, the difference in size between the sexes must be almost negligible in the beginning of the 2-group stage (0.2 cm at most). However, by July/August the average difference in length between the sexes has become approximately 0.8 cm in favour of the males. The difference gradually increases to about 1 cm in October and has become 1.4 cm in January/February of the following year (Fig. 14.1 and Appendix II.1, Tables I–III). Thus, the difference in length between the sexes continues to increase in autumn and winter.

Similar findings have been reported for the Barents Sea stock and the Newfoundland-Labrador capelin (Monstad 1971; Pitt 1958). Therefore, the maturing 2-group female and male capelin will on the average grow in length, by about 1.0 and 1.6 cm respectively from the beginning of the

feeding season until spawning some 10 months later. While most of the growth occurs during the height of the feeding season in spring and summer, a small but significant part of the length increment is added in the October – February period (Fig. 14.1 and Appendix II.1, Tables I–III).

A considerable but varying proportion of age group 2 remains immature and exhibits a much slower rate of growth than that part of the year class which matures and spawns at the age of 3 years. The growth in length of these fish is represented by the lowest curve in Figure 14.1. On the average the immature part of age group 2 grows in length only by about 0.5 cm in the period January/February – October/November. In contrast to the maturing component, very little growth has been observed in the winter months among immature 2- (3-) group capelin.

Age 3. The growth in length of 3-group male and female capelin is shown by the uppermost two curves in Figure 14.1 and is slower than that of the maturing 2- group fish. Thus, 3-group females and males grow by about 0.9 and 1.1 cm respectively, the increment being little more than half that exhibited by maturing 2-group capelin over the same period of time, *i.e.* from the beginning of the feeding season until spawning (Appendix II.1, Tables I–III).

As among the 2-group, difference in length between the sexes seems to be small (about 0.2 cm) in spring. As far as can be ascertained the difference in length between males and females has become about 0.8 cm in August. From then on it increases to 1.3 cm in January/February of the following year. Sex-linked differences in length among the 3-group, therefore, seem to develop along very similar lines as those of the maturing 2-group.

Thus, the temporal growth pattern of the 3-group capelin is quite similar to that of the 2-group. While there are very limited data available from the spring and early summer period, it seems that, like in the case of the younger age group, growth is resumed in April/May and is fastest in June, July and August. As among the maturing 2-group, growth continues in autumn and early winter, but at a reduced rate compared to that of maturing 1- and 2-group capelin.

Age 4. In the Icelandic capelin stock there are only very few individuals which do not mature and spawn until 5 years old or repeat spawning at this age (Appendix II.1, Tables I–III).

On the average, five year olds account for less than 0.5% of the spawning stock by number. In January/February, in the year of spawning, the length of 4-group female and male capelin is on the average about 16.1 and 17.4 cm respectively, *i.e.* about 1 cm in excess of that of mature 3-group capelin. The growth pattern of capelin that do not mature to spawn until at age 5 is indicated in Figure 14.1

14.2.2. Weight at age

Age 0. Volumetric measurements of different sizes of 0-group capelin have been carried out during surveys in August, October/November and January/February. A length/weight key has been established on the basis of these data and used to convert routine length measurements from these months to estimates of weights. An approximate average pattern of growth in weight from the spring until January/February of the following year has thus been established and is shown in Figure 14.2 and Appendix II.1, Tables I–III.

Age 1. On the average, the main immature part of the 1-group capelin increases in weight from about 0.6 to 4.6 g in the period January/February – October/November (Fig. 14.2) after which there is very little increase in weight throughout the winter period (Appendix II.1, Tables I–III).

As pointed out in the section on length at age, sampling in the period March – July is inadequate for accurately determining the onset of growth in weight of 1-group capelin. This is especially true for the small part which matures and spawns at age 2. However, these individuals grow at a much faster rate than the immature component. Apparently, they continue to do so for the rest of the year and the males indeed until February in the following year (Figure 14.2, and Appendix II.1, Tables II and III).

The sex-linked difference in weight appears to be negligible during the first half of the year. In July/August the males have, as far as can be ascertained, become about 0.6 g (about 10%) heavier than the females. After that the differ-ence in weight between the sexes continues to increase and has reached 1.6 g (about 20%) by October/November. The difference in weight between the sexes culminates in January/February (2-group) at 3–4 g (about 30%). However, the extremely high growth rate in the winter period, in particular among the females, seems unlikely, since in relative terms it far exceeds that observed of the older age groups. In this context, it should be noted that data on maturing 1-group capelin are very limited in comparison to data on the older age groups. For this reason, possible mistakes in age reading could have altered the picture considerably.

Age 2. Among this age group growth in weight of maturing female and male, as well as immature 2-group capelin (Fig 14.2), probably begins to diverge by spring or early summer. The difference in weight between the sexes has become well established by July/August when it amounts to about 20% (Appendix II.1, Table I).

The fast growing maturing males continue to increase in weight in autumn and winter at only a slightly reduced rate as compared to the summer months. The females, on the other hand, show a much smaller increase in weight after October/November. Consequently, the difference in weight between mature male and female of this age group is at its peak of about 7 g in January/February, just before spawning, when the weight of the males exceeds that of the females by about 40% (Figure 14.2 and Appendix II.1, Tables I–III).

Immature 2-group capelin seem to grow at a fast and steady rate from early spring throughout summer, apparently reaching their maximum weight by August. However, as mentioned before, this is most likely an artifact resulting from some of the faster growing maturing 2-group capelin being mis-classified as immatures in the July/August samples. There seems to be no increase in weight in the fall and winter period among the immature 2-group capelin.

Age 3. Once again the available data indicate little difference in weight between the sexes among this age group in the beginning of the year and for the first 3–4 months of the year (Fig. 14.2, Appendix II.1, Tables I–III). However, by July/August the difference in weight between the sexes has become 5–6 g (about 30%). This size
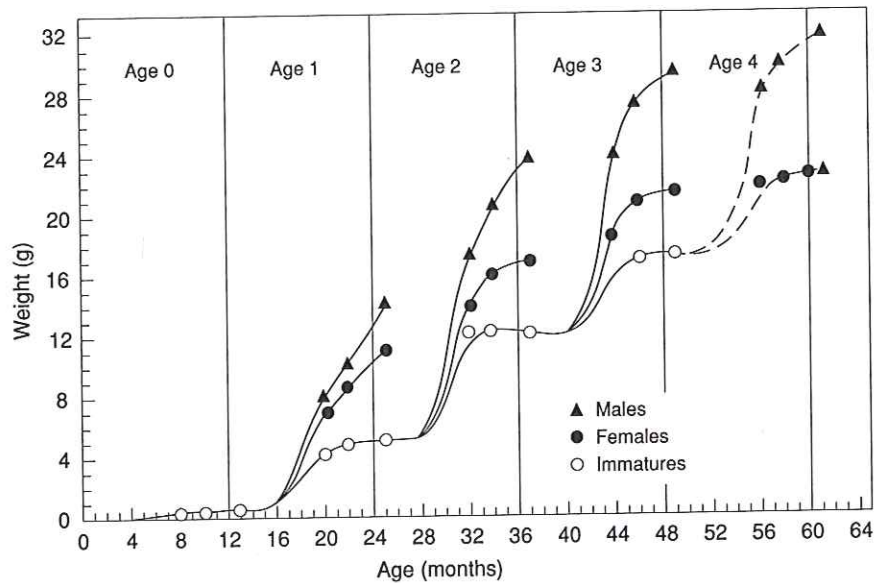
Figure 14.2. The average monthly growth in weight of immature (bottom curve), female (middle curve) and male (uppermost curve) capelin in the years 1979–1993. See also Appendix II.1, Tables I–III.

difference is much greater than observed for the 2-group fish, both in the absolute and relative sense, and could imply that the size difference between the sexes exceeds that observed among these fish at the immature 2-group stage.

Otherwise, the growth in weight of this age group follows the same pattern as observed for the maturing part of age group 2, with the males increasing their weight until spawning, while growth among the females has practically ceased by October. Consequently, the sex-related difference in weight continues to increase from 5–6 g in July/August to 6–7 g in October/November and culminates at about 8 g in January/February, when the average weight of males exceeds that of the females by about 40% (Fig. 14.2 and Appendix II.1, Tables I–III).

Age 4. As mentioned in a previous section, this age group comprises a very insignificant part of the stock and is rare in the samples. In January/February in the year of spawning (age 5) the average weight of female and male capelin, belonging to this age group, is about 22 and 31 g, respectively, or slightly greater than that of maturing females and males belonging to the preceding age group. However, the difference in weight between the sexes is about 40%, or the same as in the younger age groups.

14.2.3. Discussion

When studying the growth of the Icelandic capelin, it must be borne in mind that conditions may be quite different in the various parts of the area between Iceland, Greenland and Jan Mayen in summer and autumn. Also, due to variations in behaviour pattern and external variables such as drift ice, some of the stock components may not be available for sampling in numbers proportionate to their abundance. Difficulties in establishing valid estimates of growth parameters at various times in different years, may also result from gear selection and distribution of the capelin in relation to environmental variables such as food and temperature. Much of the variability encountered in the data, when compiling the above growth parameters for the Icelandic capelin, will be due to these problems as well as insufficient sampling in parts of the year, as described in the beginning of this chapter. The problem is further aggravated because of the sexual dimorphism exhibited by the capelin which makes it necessary to distinguish between sexes, an undertaking that is not easy when dealing with immature fish or fish in their early stages of maturity. Due to the sexual dimorphism, sampling effort must also be much greater in order to obtain a similar degree of confidence as for species where biological variables are not sex-linked.

Due to inadequate data from spring and early

summer, the onset of growth of the various components of the capelin stock cannot be determined accurately. But as described in sections 6.6 and 6.7, the spring bloom of phytoplankton in the north Icelandic area probably does not start until early May in most years, reaching a maximum around the middle of the month. The subsequent spring increase in zooplankton production is, therefore, not to be expected until in late May or June except in the colder and more stratified polar waters farther to the north and west where stratification of the surface waters occurs at a slightly earlier date.

The onset of growth among the Icelandic capelin is generally assumed to be in May. However, for the reasons pointed out above, the timing need not be exactly the same for all stock components. Thus, the larger individuals among the 2- and 3-group fish, which generally overwinter in the outer shelf area off the western north coast of Iceland, tend to migrate north into the cold water off the shelf in early spring. Therefore, these fish may have access to a more plentiful food supply at an earlier date than those parts of the stock which remain in the mixed waters of the north Icelandic plateau.

As described in chapter 12 there are very limited data on the feeding intensity of capelin in the area between Iceland, Greenland and Jan Mayen, both as regards the main feeding season during May – September as well as during other times of the year (cf. chapter 12). It is clear, however, that the intense and more or less continuous feeding activity, which must take place among all age and maturity groups wherever food is available in summer, largely ceases in autumn and early winter. This is reflected in difficulties frequently encountered in the processing of summer capelin for meal and oil. At this time of year, the capelin have often ingested large amounts of redfeed (mostly copepod stages of calanus-type crustaceans). Due to the presence of excessive digestive fluid, such a situation induces self-digestion unless the catch can be processed quickly. Following the reduction of available zooplankton, feeding activity seems to become more sporadic and limited to such occasions when autumn and winter migrations pass through patches of zooplankton, usually consisting of overwintering euphausiids. By September, problems in the reduction process due to food contents in capelin stomachs are usually not en-

Table 14.1. The mean weight (g) of the two main age groups in the maturing stock, recorded when acoustic surveys were carried out both in the autumn (October/November) and in winter (January/February) of the same season over the period 1979–1993.

Season	Autumn		Winter	
	Age 2	Age 3	Age 3	Age 4
1979/1980	15.7	23.0	19.3	26.7
1980/1981	19.3	26.7	22.2	27.2
1981/1982	19.4	22.0	19.7	27.0
1982/1983	16.5	24.1	18.5	24.2
1983/1984	16.8	22.6	19.3	25.8
1984/1985	15.8	25.8	19.1	27.2
1986/1987	18.1	24.1	19.2	25.0
1988/1989	15.5	23.5	18.6	24.9
1990/1991	18.1	25.5	20.1	27.6
1991/1992	16.3	24.3	17.9	25.8
1992/1993	16.5	22.6	19.6	29.4
Average	17.1	24.0	19.4	26.4
SD	1.41	1.49	1.11	1.48

countered and certainly not in the period October – March. But in winter, lower air and sea temperatures will, naturally, help preserve the capelin after they have been caught.

Nevertheless, the adult part of this capelin stock continues to grow in the months of November – January. Thus, when comparing autumn and winter acoustic estimates of stock abundance in the 1980s, it gradually became clear that the winter estimates produced consistently higher biomass values than expected from the autumn estimates. Since these estimates were comparable in numbers of fish, when adjusted for catches and natural mortalities, the observed increase in biomass could only be explained by an increase in individual weights (Anon. 1987, see also section 15.4.1).

For the period 1979–1993 there are 12 pairs of data on average lengths and weights available for each of the two main age groups in the spawning stock obtained in autumn (October/November) and winter (January/February) from acoustic surveys. The weight increase for each age group is highly significant (Table 14.1). A regression analysis of the autumn data on those from the winter surveys results in an $R^2 = 0.85$ and $P < 0.01$ (Fig. 14.3). This comparison indicates that there is a somewhat larger increase in weight of smaller fish than larger ones. However, the most common mean weight in the maturing stock in autumn is about 20 g. According to the regression just referred to, the average weight in-

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Figure 14.3. A regression analysis of the mean weights recorded in autumn surveys on mean weights from the winter surveys in the period 1979/80–1992/93.

$$y = 0.92x + 3.96$$
$$R^2 = 0.85$$
$$P < 0.01$$
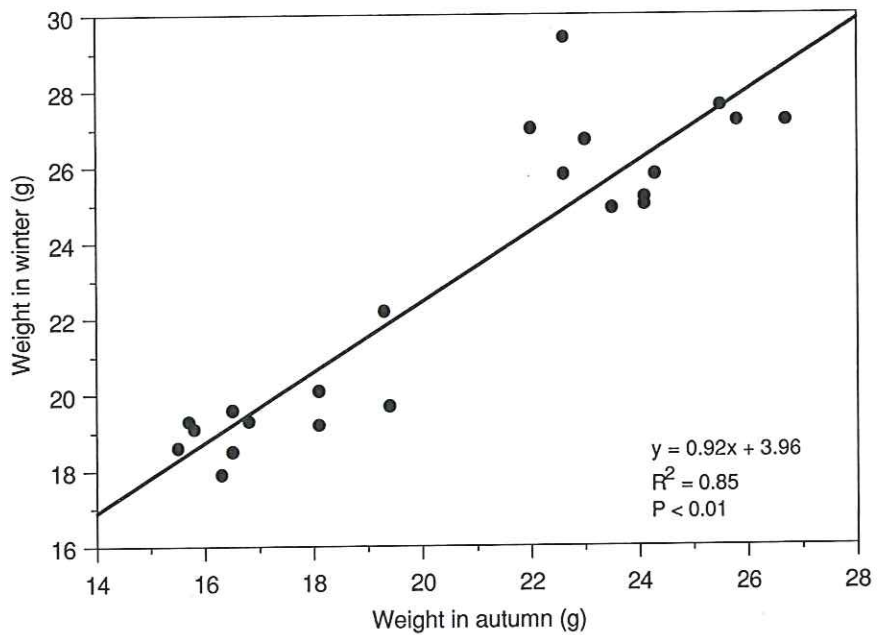
crease of a 20 g maturing capelin in the two months period October/November – January/February is just over 2 g. Therefore, a weight increase of 10 percent is most often used when projecting stock abundance measured in October/November forward in time for the purpose of calculating the total allowable catch (TAC) for the rest of the fishing season and the targeted remaining spawning stock in March – April of the following year (cf. section 17.3).

The continuation of growth of adult capelin is also well demonstrated in the average growth curves for length and weight, shown in Figures 14.1 and 14.2 respectively. There is a considerable variance in the autumn and winter mean lengths of both sexes in the period 1979/80 – 1991/92 (Appendix II.1, Tables II and III), and the correlation between autumn and winter mean lengths and weights of the same year classes is less than that observed in the acoustic stock assessments, where data on size in the various parts of the distribution area are weighted by abundance. Feeding conditions are, as a rule, quite variable within the area occupied by this capelin stock. Such variations may have fairly large effects on growth rates. The studies of growth should, therefore, preferably include some measure of the distribution of abundance within the area occupied by the stock.

Unfortunately, such information is only available for each age group as a whole and not divided according to sex. However, information on sex related growth in winter is available from samples of catckes taken from the stock at large, collected in October/November and January/February (Appendix II.1, Tables II and III). Among the mature part of the population, the increase in length and weight is highly significant for males of all age groups. Among the female part of the population, on the other hand, there is a significant increase in length among the two younger age groups while the observed increase in weight is significant only in case of the youngest age group (Table 14.2). Obviously, the large and continuously increasing difference in length and weight between the sexes themselves is highly significant. As shown in Table 14.2, the increase in length and weight of immature capelin in the autumn/winter period is not significant. From this it must be concluded that the winter growth, exhibited by the adult Icelandic capelin, is real but mostly takes place among the male part of the population.

Some of the winter growth in length of adult capelin belonging to this stock could derive from accumulations of fat that were deposited in the preceding months of high feeding activity. However, this store of energy is mainly used for fuel-

Table 14.2. Significance tests for the increase in length ($l_2 - l_1$) and weight ($w_2 - w_1$) from October/November until January/February in the following year, as given in Appendix II, Tables II and III. Significance at the 99% level is denoted by *.

Sex (age groups)	Length			Weight		
	l_2-l_1	d.f.	t_{obs}	w_2-w_1	d.f.	t_{obs}
Immature (0–1)	0.18	26	0.77	0.03	26	1.13
Females (1–2)	1.18	21	4.67*	3.42	21	5.24*
Males (1–2)	1.77	21	6.48*	5.46	21	5.49*
Immature (1–2)	0.60	25	2.20	0.63	25	1.39
Females (2–3)	0.34	26	2.65*	0.95	26	1.94
Males (2–3)	0.79	26	5.64*	3.03	26	4.57*
Immature (2–3)	0.28	26	1.96	0.19	26	0.41
Females (3–4)	0.23	26	1.70	0.75	26	1.27
Males (3–4)	0.47	26	3.47*	2.46	26	4.01*

ing migration, the development of sexual products and the maintenance of physical condition in general. As described in section 14.8, the energy stored from the summer feeding period is gradually used up during December – March. On the other hand, the increase in weight during the winter months can not be accounted for by the utilization of internal energy reserves. There seem to be two possible ways in which to account for the observed increase in weight during the October/November – January/February period.

First, the winter growth might result from increased total water content of the fish due to the development of eggs in the female ovary and the development of external spawning ridges on the males which will tend to retain some water and thus increase recorded weights. Since neither the female ovary nor the male spawning ridges have reached an advanced stage of development by the time at which the winter assessment surveys are carried out, this explanation is hardly satisfactory.

A second and more likely explanation for the winter growth of adult capelin is continued feeding. The sparse data on stomach contents of capelin during the winter months suggest that feeding also takes place in that period, at least intermittently, among adult capelin. The main food item is euphausiaceans which are particularly abundant near the edge of the north and east Icelandic shelf. And this is indeed the most frequent location of the winter migrations of adult capelin on their way to the spawning areas. At the same time, feeding frequency seems to be much lower among the juvenile than the mature

part of the stock, and as shown in Figures 14.1 and 14.2, these young capelin do not increase their length or weight in the winter months. Instead, the juveniles must use their limited amount of stored energy reserves purely for the purpose of migration and to maintain themselves until the following spring. The most likely reason for the practical starvation of juvenile capelin in winter, is that the 0- and 1-group capelin, as well as the smaller individuals among the 2-group, are unable to cope with the relatively large and agile euphausiids.

It is, however, the difference in growth rates between the two sexes, the members of which apparently have had the same or similar opportunities for feeding and storage of energy reserves, that is most interesting. There is no evidence of a winter feeding activity being limited to the male part of the population. On the contrary, the collection of female capelin with roe for the Japanese market has often been temporarily halted due to food contents in their stomachs. In the absence of specific studies to throw further light on this phenomenon, the most reasonable explanation seems to lie in the difference in sex-linked characteristics that are gradually being established during the winter period. Apart from the external spawning ridges, these characteristics of the male are mainly manifested in somatic changes, *i.e.* the formation of muscle tissue, while in the female case most of the energy must be converted to sexual products that are much more voluminous than those of the male. In winter the female must, therefore, spend much of its stored or acquired energy on the formation and maintenance of sexual products while much less energy is presumably required for corresponding processes in the case of the male.

14.3. Weight-length relationships

14.3.1. Weight at length

Data from which the weight-length relationship of the Icelandic capelin can be calculated, are not available on a monthly or bi-monthly basis over the whole year. For this stock there is, however, a fairly extensive collection of data covering the period from July until February in the following year, *i.e.* from the mid- and latter part of the main feeding season until just prior to the spawning season of the following year. A smaller

Table 14.3. The number of capelin on which calculations of weight at length by sex and season in 1976–1992 were based.

Season	Immatures	Females	Males
July/August	14,685	3,883	3,046
October/November . . .	18,767	20,145	15,529
January/February	11,817	29,028	23,973
March/April	–	1,566	1,113

set of data is available for spent or recovering spent capelin from the months of March and April. A summary of the data set used in the following calculations of the weight-length relationship is given in Table 14.3.

In order to investigate seasonal changes in the weight-length relationship among the Icelandic capelin, bi-monthly regressions of weight on length, representing July/August, October/November and January/February separately, were computed from commercial and research vessel samples for immature as well as female and male capelin respectively, spanning the 1976–1993 period. A regression of weight on length for spent female and male capelin was obtained from commercial samples collected on the actual spawning grounds in March/April and in addition some research vessel samples of spent and apparently recovering females taken 10–50 naut. miles from the nearest known spawning grounds in March/April.

The seasonal relationships between weight and length for each sex and the immature part of the stock are shown in Figure 14.4. The regression coefficients for each sex and season are given in Table 14.4 using the basic equation

$$w = \alpha l^\beta \qquad (14.1)$$

where w and l are the weight (g) and length (cm) respectively, and α and β are coefficients determined by regression techniques.

Since the regression coefficients α and β may be variable according to sex and season, models were fitted to the data to test for significance. The variance of the weight distribution increases with length and the weight has a gamma-type distribution for each length. Therefore, a generalized linear model (McCullagh and Nelder 1989) was used with a gamma density and log link, so that weight and length are linearly related on a log scale. Although a log-log regression could be used, this would result in biased weight predictions, and hence the current approach was taken.

The adequacy of the model was tested with respect to season and sex. It was found that a full model with all interaction terms is needed, *i.e.* both regression coefficients, α and β, are different for the different sexes and seasons as shown in the analysis of variance table based on these deviances (Table 14.5). Since β is not a constant equal to 3.0, the usual condition factor, w/l^3, varies according to length and has little meaning as a measure of condition. For describing variations in the condition of capelin, measured as weight at length, it is therefore necessary to calculate weights at fixed lengths for each sex as well as the immature part of the stock. This has been done for the modal lengths of the main stock components, *i.e.* for 1- and 2-group immatures as well as mature male and female capelin. The resulting seasonal changes in weights are given in Table 14.6. Furthermore, the data indicate that maturing males are slightly heavier than females at any given length.

Measured in this way, there are obviously fundamental differences in changes in condition with time between the immature part of the population on one hand and that of the mature capelin on the other (Table 14.6). The immatures seem to be in their prime condition in August but to lose weight in autumn and winter. A change of

Table 14.4. Length/weight regression coefficients for Icelandic capelin by season and sex using the basic equation $w = \alpha l^\beta$ as described in section 14.3.1.

	Immatures		Females		Males	
Seasona	$\alpha \cdot 10^{-3}$	β	$\alpha \cdot 10^{-3}$	β	$\alpha \cdot 10^{-3}$	β
July/August	1.015	3.594	1.718	3.380	0.663	3.742
October/November . . .	0.596	3.762	0.745	3.698	0.420	3.913
January/February	0.640	3.697	0.871	3.632	0.746	3.700
March/April	–	–	2.592	3.103	1.821	3.382
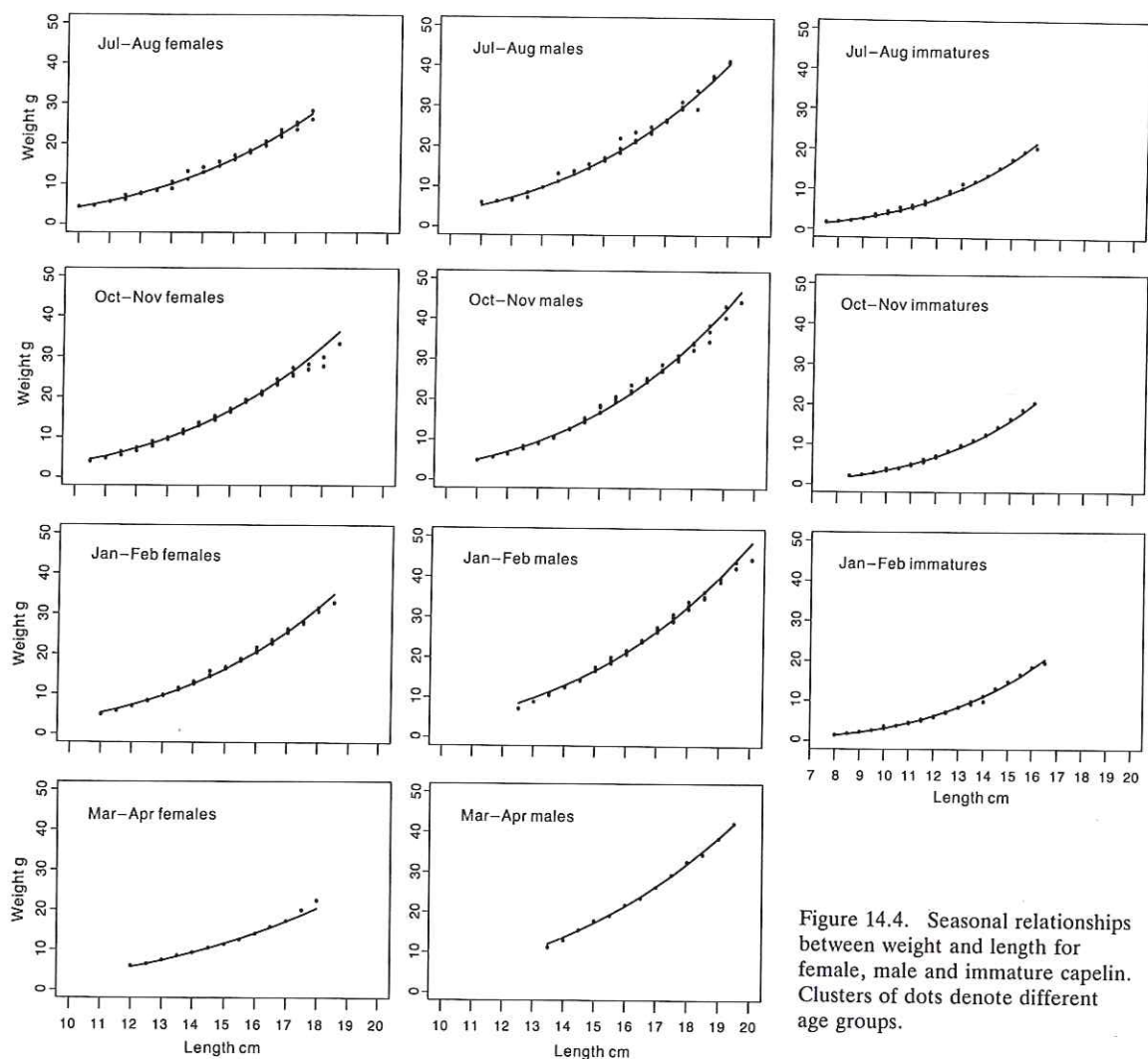
Figure 14.4. Seasonal relationships between weight and length for female, male and immature capelin. Clusters of dots denote different age groups.

almost 20% occurs in weight at length over the 5 month period September – January. On the other hand, the condition of the maturing part of the stock improves in the autumn months but has by January/February fallen to the late summer level again. These changes are much smaller than among the immatures and amount only to some 2–2.5% of the body weight. However, a comparison between the condition of immature capelin in mid-winter on one hand, and that of maturing fish in July/August some 5 months later on the other, indicates an improved condition, as measured by the increase in weight at length, of 15–20%.

Table 14.5. Analysis of deviances in the model $w = \alpha l^\beta$ for Icelandic capelin.

Terms	Residual DF	Residual deviance	Model DF	Deviance	F-value	P
Log (length)	345	645.2				
Log (length) + season + sex . .	340	320.3	5	324.9	239.9	<0.01
Log (length) * season + sex . .	337	210.7	3	109.6	134.8	<0.01
Log (length) * sex * season . .	325	88.1	12	122.7	37.7	<0.01

Table 14.6. The calculated weight (g) at length for Icelandic capelin by season and sex where I, F and M denote immatures, females and males at the most frequent lengths of 10.0, 12.5, 15.0 and 16.5 cm, respectively.

Season	I_{10}	$I_{12.5}$	F_{15}	$M_{16.5}$
July/August	3.98	8.89	16.23	23.86
October/November .	3.44	7.98	16.64	24.40
January/February ..	3.19	7.27	16.27	23.85
March/April	–	–	11.56	23.87

There has never been a special effort to sample Icelandic capelin in the final phases of the spawning season or immediately afterwards, in order to study the condition of the spawners. However, an examination of samples of completely spent fish from commercial and research vessel catches in March and April, indicates that the weight at length for males has remained almost the same as observed in January/February, while that of the females has dropped drastically to just over 70% of the January/February level (Figure 14.4, Table 14.6). Most of this difference is easily explained by the sudden loss of roe, which may account for up to 30% of the total body weight of the female just prior to spawning. Such a large change in the male condition would, on the other hand, not be expected on account of the loss of reproductive material, since the weight of the ripe male testes is only a fraction of that of the female ovary and, consequently, of the total body weight.

14.3.2. Discussion

The relation between fish length and weight is much used in fisheries biology for converting catch weights to numbers of fish for further use in stock prognoses and projections. Furthermore, as growth may be defined as change in length and weight with time, these parameters are interrelated and often used in attempts to describe the physical state or condition of the fish.

The generally accepted form of the growth equation is the power curve expression, where $w = \alpha l^\beta$. When $\beta = 3$, growth is isometric, *i.e.* the weight increases as the 3rd power of the length. Deviations from this indicate allometry or different growth rates of different parts of the body (see *e.g.* Jones 1976). Among the capelin, allometric growth can obviously be expected as a result of the accumulation of fat in the feeding season, the formation of some of the secondary sex-linked characteristics of the male as well as

the development of sexual products before the spawning season. Sex- and maturity dependent β-values may, therefore, be expected with variations over the biological year, and this is indeed observed.

The changes in the condition of maturing Icelandic capelin from late winter/early spring until January in the following year, as described by the weight-length relationship, are in conformity with observed changes in fat content over the same period (cf. section 14.8). Thus, there is a large increase in fat content from the beginning of the feeding season in spring to August. The fat content continues to increase at a reduced rate until November, when it begins to fall off again. Furthermore, the reduction in weight at length from August onward, observed among both the 1- and 2-group immatures, coincides with the practical cessation of feeding activity among the juvenile stock component in autumn and winter.

There are no specific data that suggest differences in the diet or feeding intensity of maturing female and male capelin, and indeed there is a fairly close correlation between variations in weights at length in autumn over the 1979–1992 period, of these stock components. Not surprisingly, these variations do not correlate with those observed among the juvenile part of the stock. On account of their inferior size, the juvenile capelin is dependent upon a different size category of prey from that of the larger capelin. In addition, the juveniles are more frequently distributed in or near the Icelandic shelf area, where they feed on a zooplankton community different from that constituting the diet of the maturing stock, which in summer tends to be distributed farther north in the colder waters of the Iceland Sea. The physical condition of capelin in autumn is probably in the main a reflection of feeding conditions during the preceding summer, even among the older age groups. The availability of food is of course the main determinant of growth. However, feeding conditions are both determined by the absolute zooplankton abundance, which is the result of the state of the physical environment and plant production, and also by the abundance of capelin year classes competing for the available food. The effect of temperature *per se* on growth is well known. Unfortunately, the available information on environmental variables of the Iceland Sea and the North Icelandic area is not detailed enough to explain observed inter-an-

nual variations in the condition of the Icelandic capelin.

There seem to be few studies available in the literature of changes in the weight-length relationship among capelin. Winters (1970) gave weight/length regression coefficients for capelin overwintering in Trinity Bay in Newfoundland and Winters and Campbell (1974) for pre-spawning female and male capelin on the Grand Bank. Monstad (1971) has given similar information on capelin in the Barents Sea. According to these studies, Icelandic capelin are somewhat lighter for a given length than those from the Barents Sea and the Grand Bank, but considerably heavier than the coastal spawners of eastern Newfoundland. Furthermore, Winters and Campbell (1974) reported decline in body condition among Grand Bank capelin of both sexes from the pre-spawning to the ripe condition, that was more pronounced in females than in males. On the other hand, using the condition factor $(w/l^3 \cdot 100)$, Monstad (1971) found a general improvement in the condition of Barents Sea capelin of both sexes from the maturing to the ripe condition. Following this, there was a large decline in the condition of the female part of the stock, associated with the spawning in April.

Nyholmen and Hopkins (1988) carried out a monthly study, over a period of one year, of the condition of one year class in an apparently isolated stock of capelin in the Balsfjord on the northwest coast of Norway. In this study, a seasonal and frequently significant variation in β-values was observed for each sex as well as between sexes in all months but one. There was a general improvement of condition, as measured by the power factor (β), during the feeding season that fell off gradually in winter with a sudden drop at and immediately following spawning in June. Thus, from May to June the β-value fell from 3.196 to 2.994 for females but from 3.550 to 1.980 in the case of the males. As most of their June data derived from spent fish, the authors drew the conclusion that spent males were in a worse condition than spent females and could, therefore, be expected to suffer higher spawning mortalities than the latter.

The results of the present study agree with the observations made by other authors of different ß-values for the sexes as well as a clear and continuous improvement in condition over the feeding season, followed by a slow decline in the immediate pre-spawning period. The extremely low ß-values, recorded for spent males in the Nyholmen-Hopkins study, are not found in the Icelandic data nor in those on the capelin of the Grand Bank and the Barents Sea. Indeed it appears that in the Icelandic case, females come away from the spawning process in a much worse physical state than the males, as judged by the weight-length relationship. It has been pointed out, however, that according to the present study a model of the length-weight relationship, including both the regression coefficients α and β, is needed to adequately describe changes in condition among both sexes as well as the immature capelin.

The above observation of a good condition of the males throughout the spawning season, is contrary to the view held by many, if not most capelin biologists, that due to their prolonged attendance on the spawning grounds, repeated matings and greater expenditure of energy in general, males will afterwards be in a worse physical condition than the females and, consequently, suffer a much higher spawning mortality (cf. Templeman 1948; Prokhorov 1968; Dragesund et al. 1973; Jangaard 1974; Friðgeirsson 1976; Nyholmen and Hopkins 1988). Consequently, the present author shares the view that the spawning mortality of male capelin is in all likelihood much higher than that of the females. In the absence of any evidence of males in the process of reverting to the pre-spawning condition, it even seems likely that, for all practical purposes, male spawning mortality of capelin belonging to the Icelandic stock is total.

However, judging by the condition of males in the Icelandic capelin stock at the end of and after the spawning season, as measured by the weight-length relationship, it seems unreasonable to assume a much higher spawning mortality among the males than the females as a result of physical exhaustion. Therefore, the weight-length relationship does not, at least in this specific case, seem to measure physical condition in the usual sense. A likely explanation for the mass mortality of male capelin is that suggested by Friðgeirsson (1976). In his aquarium observation of post-spawning male and female capelin, he noted that after the spawning activity had subsided the males showed no sign of reverting to the appearance of pre-spawning capelin. Since 5–6% of the females but no males were still alive when the experiment was terminated some 6 weeks after

spawning, Friðgeirsson concluded that the very marked physiological changes, which the males must undergo in order to become able to execute their role in the mating process, are probably irreversible. Although the lacerations and sores, received during spawning, seemed to heal, the males apparently could not live with their spawning condition for any length of time and died soon thereafter.

In the Icelandic stock this is supported by frequent catches of spent or even dead males on or near the spawning grounds during and just after the spawning season, and the almost total absence of such records elsewhere at that time of year or later. On the contrary, spent females are usually not caught in quantities on or near the spawning grounds but have indeed been taken some distance away 2–3 weeks after spawning (cf. Vilhjálmsson 1974a). This would seem to suggest that in spite of their apparently poor
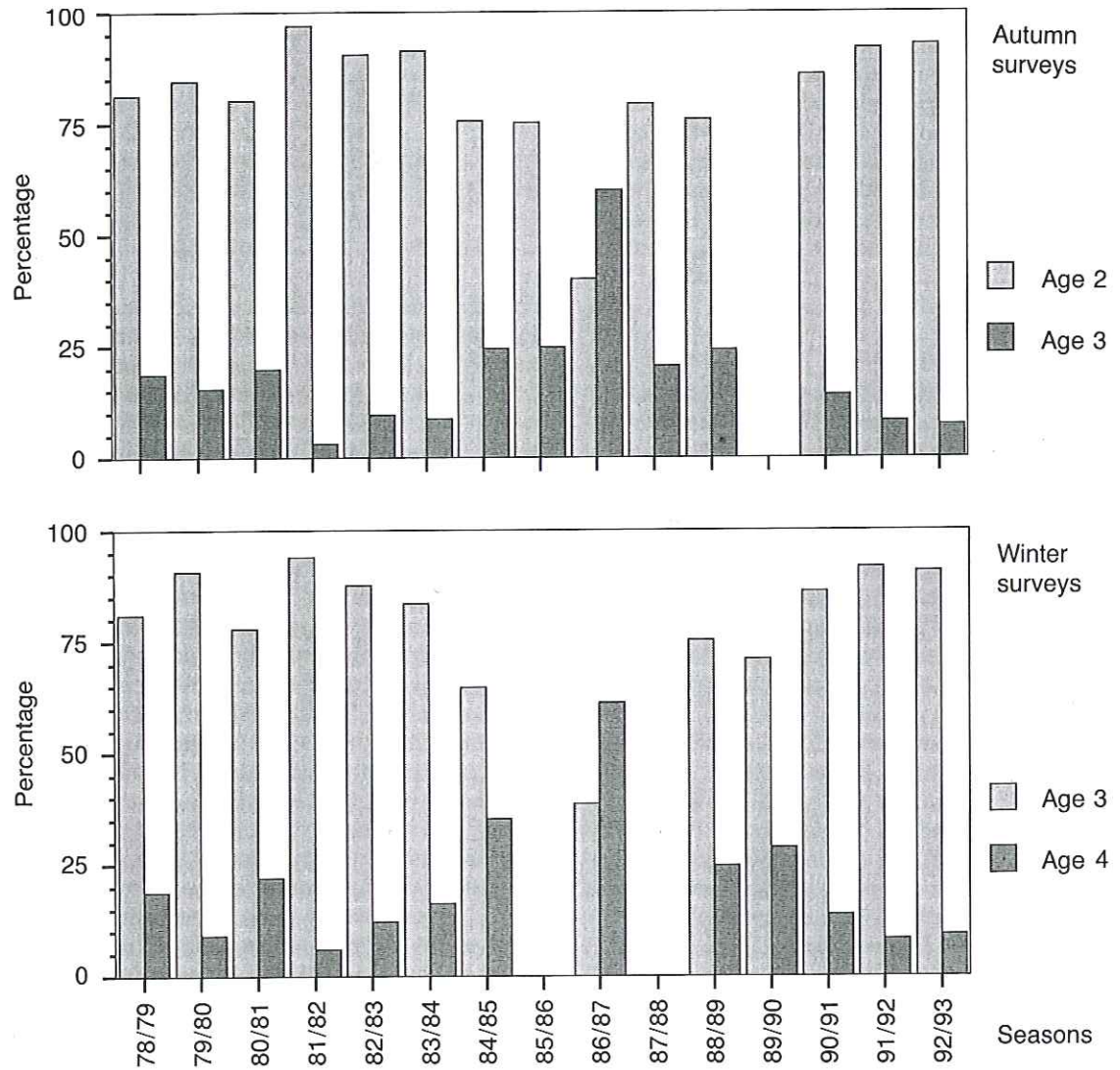

Figure 14.5. A comparison between the distribution of the two main age groups in the spawning stock in autumn (October/November) and winter (January/February) as recorded during acoustic surveys of stock abundance in 1978/79–1992/93.

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physical condition, the females are at least able to move off the spawning grounds and may survive to some extent, as will be further discussed in section 14.11.

Although high spawning mortality is certainly one of the principal features of the capelin, this need not be of the same magnitude among all capelin stocks. It is for example reasonable to assume that second or third time spawning is more common among capelin belonging to the stocks at Greenland and in the Newfoundland – Labrador area, where 5, 6 and even 7 year old fish may constitute an important part of the spawning stock, than among such stocks as the Icelandic one where 5-group fish and older are practically nonexisting. Similarly, sex-linked differences in spawning survival rates may vary between stocks. Thus, Nakashima (1992) has found that returns of tagged capelin indicate that there may not be much difference in spawning survival between female and male capelin, spawning on the beaches of the east coast of Newfoundland.

14.4. Length at maturity

The length at which 50% of individuals are mature is a commonly used reference in fish biology when dividing stocks into their mature and immature parts. In calculations of capelin biomass from acoustic survey data, collected in October/November, the stock has been split into its mature and immature components, using 13.5 cm as the length at which 50% of individuals are mature. In general terms, maturity seems to occur within a short length range, and no large deviations from the above working maturity length have been observed.

The stage of maturity of the Icelandic capelin has been determined visually without the aid of magnifying devices. As a test of the reliability of such a determination of maturity in the autumn period, a comparison was made between age distributions of the spawning stock as measured in October/November, on one hand, and January/February in the following year on the other. The underlying idea is that if there were severe difficulties in the determination of maturity in the autumn period, these should be reflected in an increased contribution by the younger age group (smaller fish) when autumn samples are compared to winter samples. As shown in Figure 14.5, this is not the case, and the correlation

Table 14.7. The mean length (cm) at maturity of female (F) and male (M) capelin and both sexes combined (All) as measured in October/November 1981–1992. Standard errors and confidence intervals are given for each mean and for the mean difference in maturing length between the sexes (M-F).

Year	F	M	All	M-F
1981	13.11	14.74	13.22	1.63
1982	13.21	14.62	13.35	1.41
1983	13.30	14.79	13.85	1.49
1984	12.67	14.29	13.77	1.62
1985	12.90	14.50	13.82	1.60
1986	13.00	14.50	13.76	1.50
1987	12.64	14.38	13.36	1.74
1988	12.78	14.29	13.36	1.53
1990	12.74	14.10	13.22	1.36
1991	13.00	14.28	13.70	1.28
1992	12.44	14.32	13.55	1.88
Mean	12.89	14.44	13.54	1.55
SE	0.08	0.06	0.07	0.05
Upper 95%	13.06	14.58	13.71	1.66
Lower 95%	12.71	14.29	13.38	1.43

between these data sets is indeed quite high. Furthermore, failure to identify in autumn the usually small sized late maturing spawners would cause a reduction in mean lengths and weights at age in January/February in the following year, when it has become a very easy task to differentiate between mature and immature fish. This is contrary to observation, as immediately obvious when consulting Figures 14.1 and 14.2 and Appendix II.1, Tables II and III.

A comparison of the October/November maturity data, covering the 1981–1992 period, shows some inter-annual variations with the length at maturity for both sexes combined varying between 13.22 and 13.85 cm (Table 14.7). However, for the 1981–1992 period the overall mean length at maturity is 13.54 cm with a standard error of 0.07, resulting in a 95% confidence interval ranging from 13.38 to 13.71 cm (Table 14.6). It seems, therefore, that for this capelin stock the process of maturity is indeed fairly closely related to increase in length, and that the relationship does not change in any drastic manner from one year to another within the October – November time span. Judging by past biomass calculations, a variation of 0.25 cm around the mean maturing length, could in the worst case have resulted in some 30–40 thous. tonnes, or 5%, being misplaced with either the immature or the maturing stock component.

M-F
2	1.63
5	1.41
5	1.49
7	1.62
2	1.60
6	1.50
6	1.74
6	1.53
2	1.36
0	1.28
5	1.88
4	1.55
7	0.05
1	1.66
8	1.43

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Figure 14.6. Average maturity ogives in the 1981–1992 period for females, males and both sexes combined.
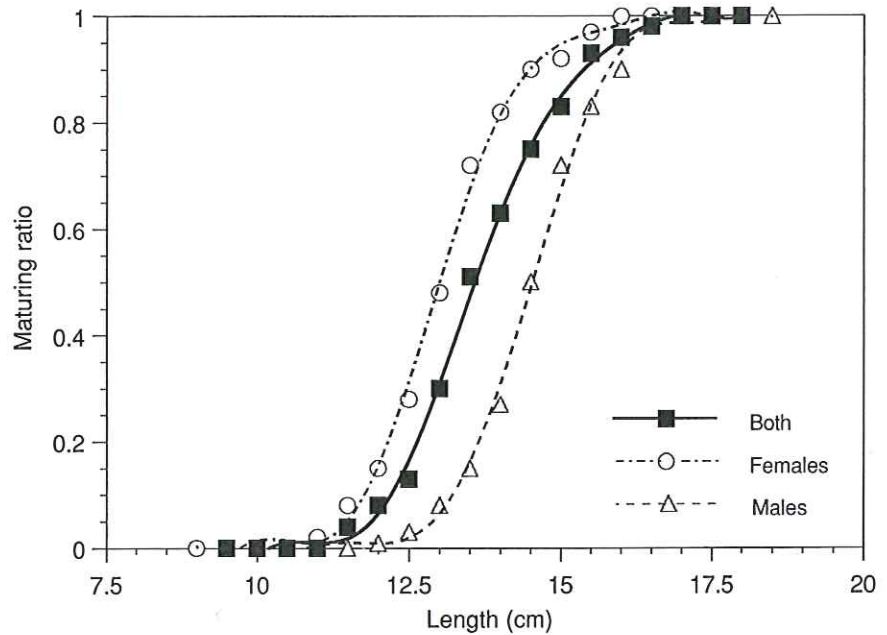
The maturity ogives, compiled from the October/November data in the 1981–1991 period for both sexes separately as well as combined, are shown in Figure 14.6. For the females the annual 50% maturity length has varied between 12.44 and 13.30 cm, while that of the males ranges from 14.10 to 14.79 cm. The overall mean 50% maturity length is 12.89 and 14.44 cm for females and males respectively. In the case of the females, the standard error is 0.08 but 0.06 for the males, resulting in a 95% confidence interval ranging from 12.71 to 13.07 for the females and 14.29 to 14.58 for the males. On the average, therefore, females mature at a size which is 1.55 cm smaller than that of the males.

The difference in length at maturity is larger than that observed between the mean lengths of maturing 2- and 3-group males and females in October/November in the same period (1.0 and 1.1 cm, see Appendix II.1, Table II). The implication of this is that not only do the females belonging to the Icelandic capelin stock become mature at a smaller size but also at a younger age than the males. This phenomenon was observed by capelin biologists long ago and seems to be universal (cf. Templeman 1948; Prokhorov 1967). Further description and discussion of sex distribution within age groups is given in section 14.6.

14.5. Maturing ratio

As described in the following section, only a very small proportion of each year class in the Icelandic capelin stock matures and spawns as 2 year old. In comparison with the older age groups, the number of 2 year old spawners must be judged insignificant in the propagation of this stock, and the same is true for 5-group spawners which always have been very rare in the samples.

The ratio of each year class that matures to spawn at age 3 has been estimated. This has been done for the 1976–1989 year classes by back-calculating winter and/or autumn abundance estimates of 3- and 4-group spawners by number, taking account of catches, and assuming an average natural mortality rate of $M = 0.035$/month (cf. section 14.10). Figure 14.7 shows the estimated total number of 2-group capelin of the 1976–1989 year classes in August and that part of each year class which matured and spawned at age 3. Apparently, the maturing ratio is related to year class size and, excluding the 1983 year class, a regression of the number maturing to spawn at age 3 on total abundance yields an $R^2 = 0.75$ with $P < 0.01$, the slope and intercept being 0.70 and 1.60 respectively. Thus, the average proportion of the 1976–1989 year classes maturing to spawn at age 3, is about 0.70. In this
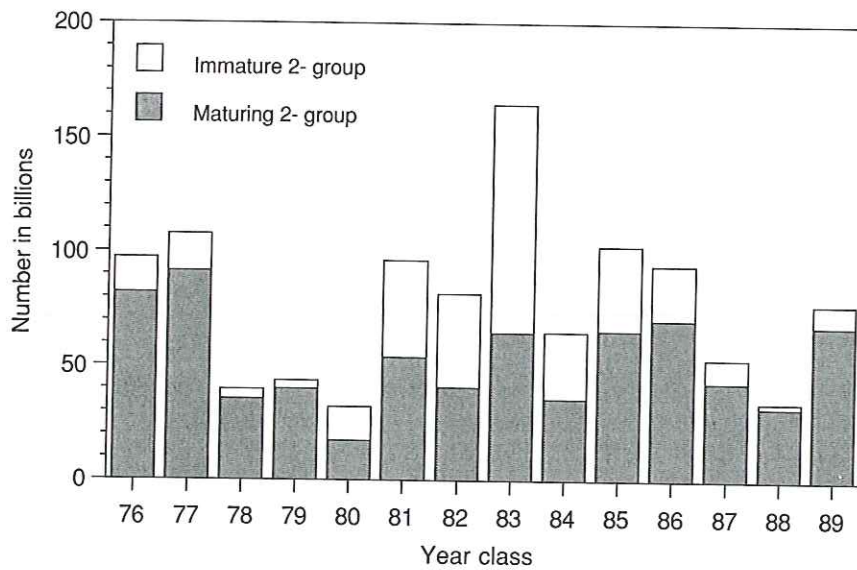
Figure 14.7. The division by maturity at age 2 of year classes 1976–1989.

short series, the 1983 year class is a case apart, due to its superior abundance in comparison to other year classes, leading to an exceptionally low maturing ratio.

The variance in the maturing ratios is most easily explained by competition for food which is linked to year class abundance. However, whether an individual capelin will mature to spawn at 3 years of age instead of 4 years, is no doubt also dependent upon the state of the physical environment as well as the availability and amount of suitable food, possibly not only in the last feeding period before maturity and spawning, but depends also to some extent on conditions during the 1-group stage. While such variations are known to have occurred in the North Icelandic area in the past years, the available information is insufficient for studies of their effect on maturing ratios of different capelin year classes.

However, a striking feature of temporal variations in the estimated maturing ratios is the very large drop in the maturing ratio of the 1980 year class and the relatively low ratios among the subsequent 4–5 year classes, followed by a rapid rise again (Fig. 14.8). One of the sources of such variance might be difficulties in determining the stage of maturity until in autumn or early winter. For this reason, back-calculations of year class abundance may overestimate the proportion of maturing 2-group capelin, when large catches consisting of mixed mature and immature fish are taken in the summer period. It is very likely that the changes in fishing pattern, which took place in the 1980s, may account for some of this difference. Iceland is responsible for about 80% of the total catch from this capelin stock. In the late 1970s, and until the fishing ban in the early 1980s, the Icelandic fishing fleet used to take a large part of its quota in summer and early autumn in areas where both the maturing and non-maturing parts of age group 2 were feeding. From 1983, when the summer fishery was resumed after the stock collapse in the early 1980s, practically all the Icelandic catch has been taken in the November – March period or in the central Iceland Sea from concentrations consisting mostly of maturing fish. Since 1990, however, there has been a certain trend to revert to the earlier fishing pattern, as a result of reduced migrations by the adult stock to feed in the central Iceland Sea in summer. It is of course also quite possible that natural mortality may vary much more than what appears from comparisons between acoustic abundance estimates, after fishing mortalities have been accounted for.

With the present lack of detailed knowledge of temporal variations in living conditions, it does not seem possible to carry the discussion of maturing ratios much further. As stated above, the most frequent maturing ratio among year classes in the Icelandic capelin stock seems to be about 70%, with a 95% confidence limit of about 15% for an average size year class counting 70–
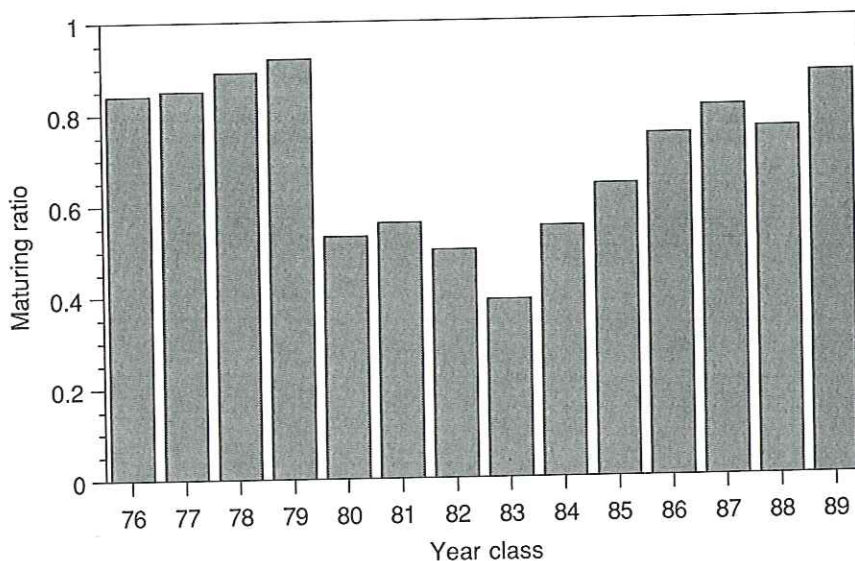
Figure 14.8. The maturing ratio of year classes 1976–1989.

100 billion 2-group recruits. In extreme cases of high abundance this ratio may, however, be much lower as the example of the 1983 year class illustrates.

14.6. Distribution of age groups and sexes in the spawning stock

14.6.1. Age distribution

The relative annual proportion by number of age groups in the maturing part of the stock has been calculated from samples taken in deep waters off East and Northeast Iceland in January/February. The time of year and locality was chosen both with respect to the large material available and also because there is less segregation by sex and size at this time of year and in these locations than observed in the shallow coastal waters when spawning approaches. Due to the lack of stock abundance data for most of this period, the samples were not weighted by stock in numbers in this calculation. However, the available information does not indicate large deviations in such cases when age distribution, calculated directly from the samples, can be weighted by stock abundance.

The proportion of age groups in the spawning stock, calculated in the above manner for each year of the period 1970–1993, is shown in Figure 14.9. In these years the spawning stock has overwhelmingly consisted of age groups 3 and 4 with

relatively insignificant contributions of 2 and 5 year old fish. Averaging the age distribution, reveals that by number, age groups 3 and 4 have contributed about 70% and 27% respectively in the 1970–1993 period. The remaining 3% are almost completely accounted for by 2-group fish (about 2.9%), while age group 4 is responsible for less than 0.1%. The detailed breakdown of the age distribution is given in Appendix II.1, Table IV.

14.6.2. Sex distribution

As stated in section 14.4, the female part of the Icelandic capelin stock not only matures at a smaller size but also at a younger age than the male part of the stock. Assuming an initial 1:1 sex ratio (cf. Winters 1966; Prokhorov 1967) it follows that one would expect a higher proportion of females than males in the younger age group of the maturing stock (2-group) and, given a high spawning mortality, a reversal of the situation among the older age group (3-group).

The distribution of sexes in the adult stock in January/February 1970–1993 was calculated from the same samples as the distribution of age groups and is shown in Figure 14.10. Obviously, females form a majority among age groups 2 and 3 as expected, while males are dominant in age groups 4 and 5. Due to the relativly low number of 2-group spawners which were available at times, the somewhat unlikely 100% contribution
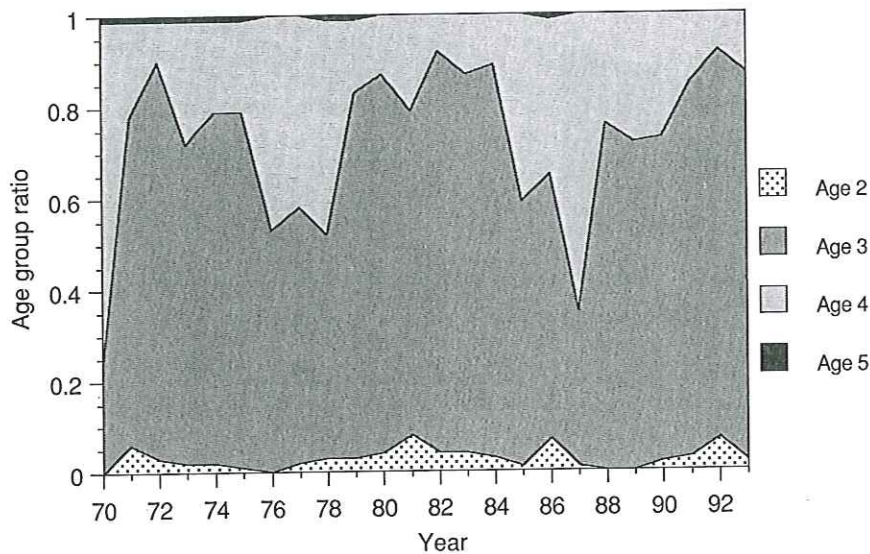
Figure 14.9. The age composition of the spawning stock in 1970–1993. See also Appendix II.1, Tables IV.

of females is observed in some years. For the same reason, the variance in observed sex ratios among age group 5 is unrealistic.

Details of the distribution af sexes within the age groups are given in Appendix II.1, Table V. Over the 1970–1993 period, the average contribution of females in age groups 2, 3, 4 and 5 was 79, 60, 40 and 26 in that order. As stated above there are large variations in the distributions of sexes in the youngest and oldest age groups. Although there are also considerable deviations from the mean value among age groups 3 and 4, these are much smaller (Appendix II.1, Table V).

14.6.3. Discussion

In the 1970–1993 period there have been large annual variations in the contribution of the two main age groups to the spawning stock (Fig. 14.9). Nevertheless, there are two instances of an exceptionally large contribution by 4 year olds to the spawning stock, *i.e.* in 1970 and in 1987. The reasons for this are probably not the same in both cases. In 1987 spawning stock abundance was high on account of the remainder of the very large 1983 year class, less than half of which had matured and spawned in the year before. The 1970 case is more uncertain since accurate information on stock abundance and year class size was not available at the time. However, evidence from the fishery and the fact that in March 1970

the capelin utilized only a small part of their normal spawning area, suggest that spawning stock abundance was low in that year. Consequently, the high contribution of 4 year olds was then most likely the result of poor recruitment by the 1967 year class rather than due to a super-abundance of the year class from 1966.

In the absence of stock abundance data, little can be said about the relatively large contribution of 4 year old spawners in 1976–1978 (Figure 14.9, Appendix II.1, Table IV). As explained in the previous section, it seems possible that in the beginning years of 1976 and 1977 the Icelandic summer and autumn fishery, which was mainly conducted off Northwest Iceland and in the Iceland-Greenland Channel, could have selectively reduced the numbers of 2-group capelin in comparison to the older year class, the majority of which was probably feeding farther north at the time. On the other hand, the fairly high contribution of 4 year olds in 1985 and 1986 must primarily have been due to larger than average year classes from 1981 and 1982.

Throughout the 1970–1993 period, the percentage contribution by the number of 3-group females has consistently been in excess of 50% but varied between 51 and 73%. On the other hand, there are only two instances of females being in majority among the 4-group spawners, *i.e.* in 1977 and 1983. Otherwise, there is a complete dominance (53–73%) by males in this age group. With the exception of those two years,

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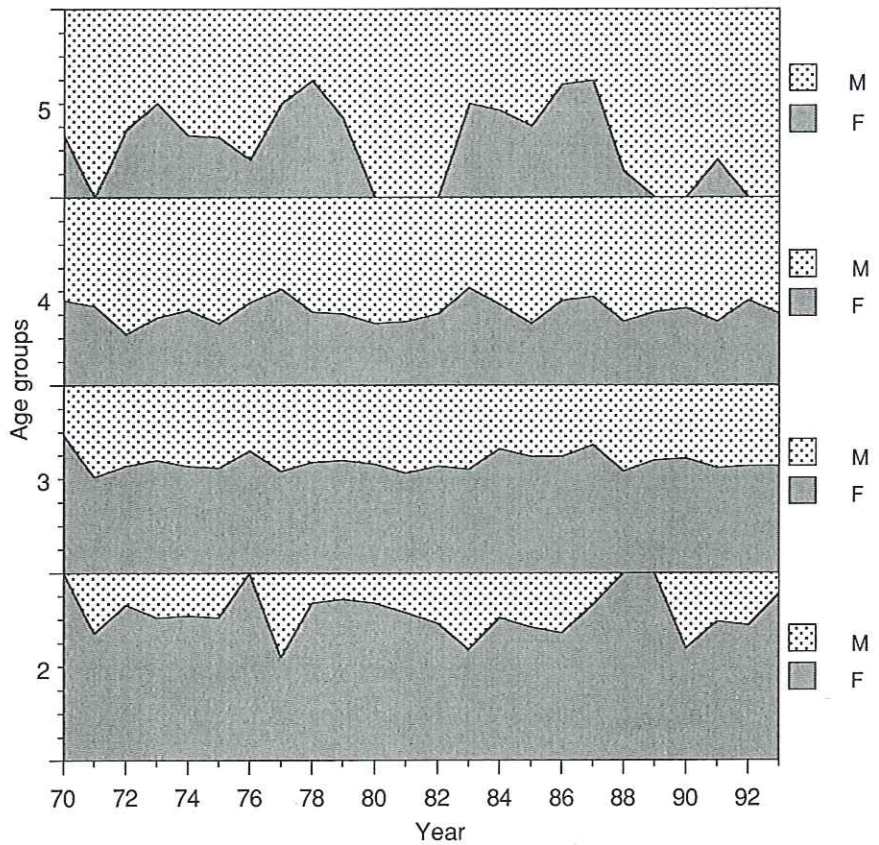
Figure 14.10. The distribution of sexes within each age group of the spawning stock in 1970–1993. See also Appendix II.1, Tables V.

this observation is in agreement with the expected sex composition of the main age groups in the spawning population, considering the earlier maturation of the female part of the stock and the high spawning mortality.

14.7. Mean lengths and weights of capelin in the spawning stock

In the spawning stock of the 1970–1993 period the overall average lengths of 3-group females and males, measured while this part of the stock was still in the deep water area off East and Northeast Iceland, were 15.0 and 16.4 cm, and those of the 4-group females and males 16.0 and 17.3 cm respectively. Average weights for the same age groups and sexes are 16.5 and 23.4 g and 21.9 and 28.5 g respectively.

However, the annual mean lengths and weights of mature 3- and 4-group capelin, recorded in January/February during the above period, have been quite variable as shown in Fig-

ure 14.11. After the initial 2–3 years of small mean lengths and weights, sizes increased suddenly to a record high in 1974 and 1975. In general, there was a decline in size over the next several years culminating in 1980 and followed by an immediate recovery in 1981. After that lengths and weights generally remained at a fairly high level until in the late 1980s when growth again dropped sharply. Thus, annual variations of up to or even exceeding 1 cm in average lengths and 4–6 g in average weights, are not uncommon among the mature part of the Icelandic capelin stock, with maximum variations approaching twice the above figures. The larger variations in size, observed among the 2- and 5-group spawners, are probably not realistic but the result of inadequate sampling or the misinterpretation of growth zones when reading ages from otoliths. Further details of the data underlying Figure 14.11 are given in Appendix II.1, Tables VI and VII.

Referring back to Figure 14.11, the similarity
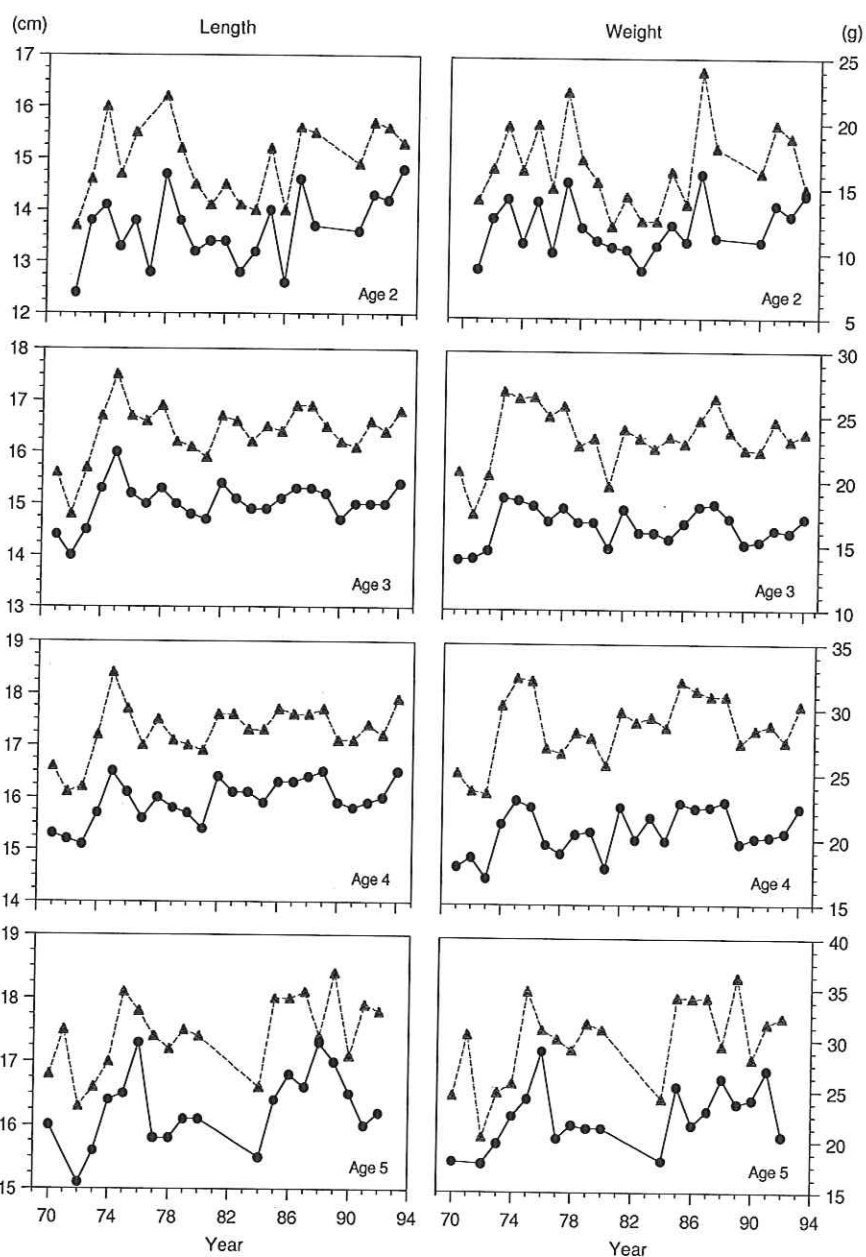
Figure 14.11. The mean length and weight of mature 2-, 3-, 4- and 5-group capelin in January/February 1970–1993. Circles denote females, triangles denote males. See also Appendix II.1, Tables VI and VII.

between growth patterns of both sexes and the main age groups (3 and 4) will be noted. Regressions of annual mean lengths and weights of males upon those of females belonging to the same age group, result in R^2 values of 0.83 and 0.89 for age groups 3 and 4 respectively. However, similar regressions comparing males and females of different age groups, result in much lower coefficients, R^2 of 0.50 and 0.62.

It is known that in any year the rate of growth may vary considerably within the feeding area of the maturing stock (*e.g.* Vilhjálmsson 1974a, 1974b). The high degree of correlation between sexes within the same age group, therefore, indicates that the winter sampling of the stock has in most cases been representative. The observation of a somewhat different growth pattern of the two age groups is reasonable, since the size of the

4 year olds will not only depend on conditions during the last feeding season but also on those in the previous year.

The available information on growth conditions in the feeding area of the adult part of the Icelandic capelin stock, is dismally small. As pointed out in chapter 6, data on oceanographic conditions and plankton production are for the most part limited to the Icelandic shelf area and waters immediately adjacent to it, *i.e.* to more southern regions than those occupied by adult capelin in summer which are partly populated by different plankton communities. It is, therefore, not surprising to find that data on annual zoo-plankton abundance north of Iceland in spring do not correlate with variations in mean weights and lengths of adult capelin in the following autumn or winter.

However, when variations in winter weights and lengths of adult capelin, belonging to the two main age groups (3 and 4), are plotted against deviations in temperatures and salinities (Fig. 14.12), observed in the shelf area off the central north coast of Iceland in spring in the preceding year (Ólafsson 1985; Anon. 1993a), a different picture emerges. Regressions of these variations in temperature on the corresponding average weigths of capelin, belonging to the two main age
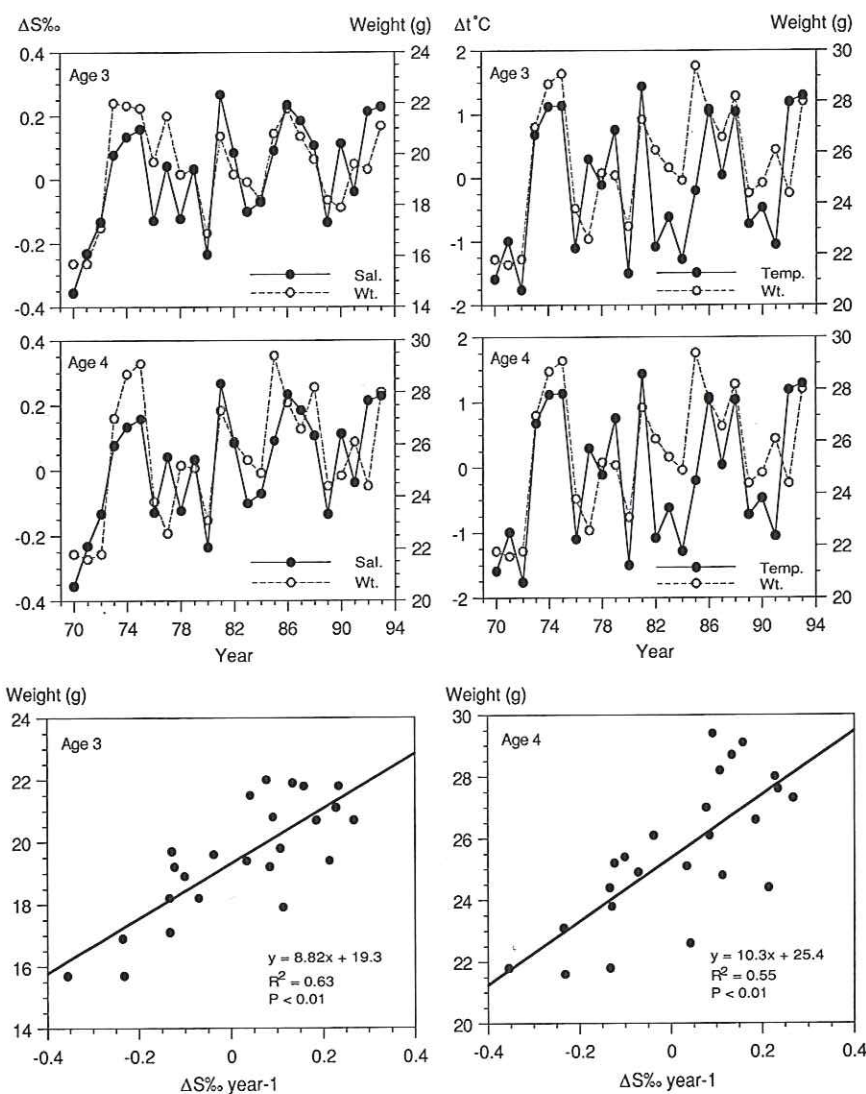
Figure 14.12. Variations in winter weights of adult 3- and 4- group capelin and salinity deviations in May of the preceding year.
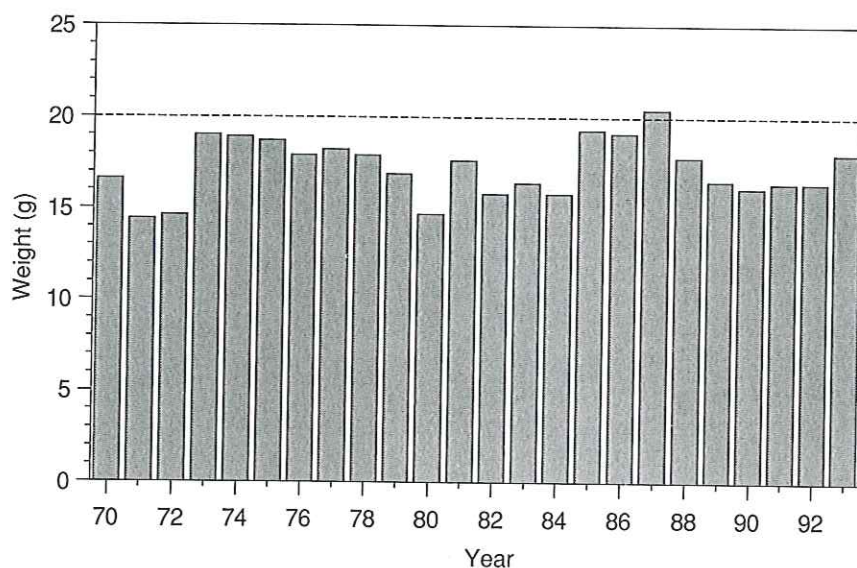
Figure 14.13. The mean weight of females in the spawning stock of 1970–1993.

groups in the spawning stock, result in an R^2 of 0.55 and 0.46 respectively. Regressions of salinity variations on these mean weights give an R^2 of 0.63 and 0.55. In all four cases P <0.01. The basic data for these comparisons are given in Appendix II.1 Table VIII. Thus, variations in the mean weights of 3- and 4-group mature capelin in winter are positively correlated to variations in the physical environment observed in May/June of the previous year. Favourable growth conditions in the area north of Iceland usually coincide with a strong influx of relatively warm and saline Atlantic water. As described in chapter 6, the presence of Atlantic water tends to prolong primary production due to improved mixing conditions and induce increased zooplankton abundance, while the presence of polar water has the reverse effect. Although much of the adult stock generally feeds in the Iceland Sea, sometimes as far north as 70°N–73°N, it seems likely that increased northward extension of Atlantic water in the north Icelandic region provides much more favourable conditions in the oceanic area just north of the Icelandic shelf, *i.e.* in a considerable part of the feeding area of adult capelin in summer.

Due to a long-standing market demand in Japan for large female capelin with high roe content, a continous sampling programme to determine the size of such capelin in the last 2–3 weeks before spawning has been in operation since 1968. The results of such sampling are shown in

Figure 14.13. In the period 1970–1993 the mean weight of females with roe content of 10–25% of the total body weight is 17.5 g and over the last 24 years the "magic" (high price) mean weight in excess of 20 g (*i.e.* <50 individuals/kg) has been attained only once. In this period, the proportion of 4 year old spawners has, nevertheless, exceeded 40% on six occasions and twice been over 60% (see Fig. 14.9).

It seems, therefore, that to attain an overall mean weight of females in excess of 20 g, without sorting or using selective fishing methods, requires a very high percentage of 4 year olds in the spawning stock as well as reasonably favourable conditions in the preceding feeding season. Exceptions to this are such cases as that of 1993 when the largest and oldest fish, which often enter the spawning grounds ahead of the rest of the stock, remain separate until at or just before spawning.

14.8. Fat content

14.8.1. Changes in fat content

The price of the capelin catch going into the production of meal and oil usually depends to a large degree upon the fat content of the fish. In Iceland this has until 1987 been measured by an independent, publicly financed institute, the Icelandic Fisheries Laboratory (IFL). The fat content of all capelin landed by Icelandic vessels

was reported in a series of technological reports (Tækniíðindi) issued by the IFL and expressed as percent fat of the total catch landed on a weekly average basis for all seasons from the winter of 1973 until 1985, with the exception of the period of no fishing in the early 1980s (Guðmundsson 1973, 1974; Martinsdóttir and Kristinsson 1975; Martinsdóttir 1976, 1978; Martinsdóttir *et al.* 1977, 1979; Martinsdóttir and Pálsson 1979; Bergsdóttir *et al.* 1980, 1981; Dagbjartsson *et al.* 1982, 1984, 1985; Einarsson 1988). In addition, the State Factories (Síldarverksmiðjur ríkisins) have kindly supplied comprehensive data on the fat content of capelin, measured in their own laboratories since the summer/autumn 1987 season. Thus, the available information on changes in fat content with time covers part or all of 20 winter seasons and 14 summer and autumn seasons in the period 1973–1993 (Appendix II.1, Table IX).

By averaging the weekly values of fat content, a graph of the changes in percent fat of the Icelandic capelin catch was compiled, spanning the period from the beginning of July until the end of the spawning season in March/April in the following year (Fig.14.14). It should be noted that in practical terms the catch consists exclusively of 2- and 3- group capelin (3- and 4-group after the turn of the year) while immature capelin, belonging to age groups 1 (2) and 2 (3), constitute only a minor proportion of the catch in summer and autumn and are not taken at all in the winter season.

No direct measurements are available on the fat content of immature capelin in winter and early spring. However, the first attempt to fish capelin in summer, made around mid-July 1975, yielded only 5,000 tonnes which consisted mostly of immature 1- and 2-group capelin. When this catch had been processed to meal and oil, the products amounted to about 675 tonnes of fishmeal and 95 tonnes of oil or 13.5 and 1.9% of the catch, respectively. From this information it may safely be assumed that the actual fat content of this capelin can not have been more than 3–4%. From this it is concluded that the fat content of immature capelin, as well as that part of the stock which is starting on the path to maturity and spawning, must be very low before the beginning of the feeding season in May/June.

14.8.2. Discussion

Judging by the above information on the fat content of juvenile capelin in summer and measurements of fat in Icelandic catches of maturing capelin in the summer/autumn season, there is a rapid accumulation of body fat from May/June

Figure 14.14. The mean weekly changes in the fat content of capelin in the commercial catch from early July until early April of the following year. Black dots represent average values recorded in the Icelandic catch and the outlines of the hatched area represent minimum and maximum values. Crosses are average values from Norwegian catches. See also Appendix II.1, Tables IX and X.
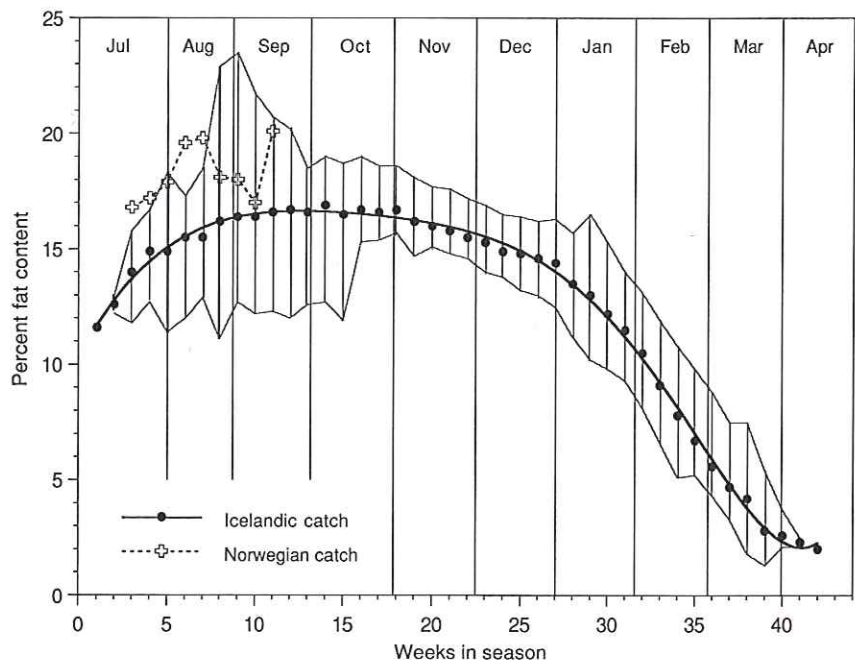
(<3–4%) until July/August (about 15%) continuing at a slower rate to late September. There follows a period of no change lasting throughout October, but after that there is a slow and fairly steady decline for the rest of the year from about 17% to 14%. Towards the end of January the fat content is 11–12% and the rate of decline starts to fall off more rapidly, dropping steadily until the final stage of the spawning season is reached in the latter half of March and early April (2–4%) as shown in Figure 14.14.

Norwegian vessels have fished for capelin in the Iceland Sea since 1978, mainly in the latter half of July and in August between 69°N and 72°N. Information on the weekly mean fat content of capelin of the Norwegian catches, kindly supplied by the Directorate of Fisheries, Bergen, Norway, is given for each year in Appendix II.1, Table X. The mean percent fat in the 1980–1992 period is shown by the uppermost curve in Figure 14.14 and is generally much higher than that recorded for the Icelandic catch at the same time of year. The difference in fat content of capelin from Icelandic and Norwegian catches may conceivably in part be due to different measurement techniques. However, the main reason no doubt is that when capelin migrate to feed in the central and northern Iceland Sea in summer, the fastest growing and largest fish arrive there first. The Norwegian fishery primarily exploits these fish, while most of the time the Icelandic summer capelin fishery has taken place much farther to the south and west and thus exploited the slower growing part of the stock. Because it has proven impossible to assess capelin abundance in August and September, the fat content, recorded in the different areas in the first 6–8 weeks of the summer season, cannot be weighted with stock abundance. However, in the light of the available information, the fat content, recorded in the Icelandic capelin catch in the period July – September, is an underestimation of the fat content of the fishable stock as a whole. Since the capelin, which feed in the northern part of the Iceland Sea, usually have returned to the area north and northwest of Iceland by October, the fat content recorded in the Icelandic catch after that time (late October) is believed to represent the true situation.

The above changes in fat content of the capelin are of course closely linked to the general biology of the maturing part of the stock. The summer and early autumn is a period of intense feeding when the energy from the food is partly stored as fat while the remainder is converted to somatic growth and to some extent to reproductive material. From October there is little somatic growth among the female part of the population while the males exhibit considerable growth, both in length and weight, in the following months (cf. sections 14.1 and 14.2). It has been suggested that this is necessary in order to enable the males to carry out their role in the mating process, and it explains, at least partly, why the male capelin is so much larger than the female.

During the period November through January sexual products are slowly developing to reach the ripeness appropriate for the onset of the last leg of the migration to the spawning grounds. At this time the capelin are still in the relatively cold border area between the waters of the East Icelandic Current and the mixed water covering the continental shelf off North and East Iceland. On entering the warm, Atlantic water off Southeast Iceland, usually sometime in the first half of February, the maturing rate and migration speed increases greatly. This requires increased amounts of energy which is reflected in the rapid decline in fat content in the following weeks.

Unfortunately, there is no comparative information on the accumulation of body fat among immature capelin in the feeding season. The available evidence suggests that it is much lower and may sometimes be as low as 2–3% in July–August among the 1-group (Anon. 1976). Furthermore, Winters (1970) reports that among Newfoundland capelin the fat content of juveniles is much lower than among mature fish and that no decline is evident in late winter and spring. It seems, therefore, that juvenile capelin convert food directly to somatic growth and that large reserves of energy in the form of fat are only accumulated after the process of maturation sets in.

The fat content of adult Icelandic capelin is subject to large temporal and spatial variations. Thus, the highest annual weekly average in the Icelandic catches was 19% in early October 1978, while the lowest annual high (15.7%) was recorded in late October of the following year (Appendix II.1, Table IX). The large difference between minimum and maximum fat content in the summer – early autumn period (Fig. 14.14), as well as the difference in fat content of capelin from Icelandic and Norwegian catches described

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earlier, are reflections of the variations in growth rates in the different parts of the feeding area of the adult stock as well as inter-annual changes. As shown in Appendix II.1, Table IX, the minimum fat content, recorded at this time of year in the period 1976–1981, derives from the 1976 data on one hand and from those of 1979 on the other. In the first case, the Icelandic summer capelin fishery mainly took place off the western north coast of Iceland and in the strait between Iceland and Greenland where growth conditions seem to be much inferior to those farther north and east. On the other hand, the summer of 1979 was one of the coldest in the period in question, resulting in extremely low zooplankton indices (Ástthórsson *et al.* 1983) as well as slow growth rates of capelin.

As described above, capelin caught in the more northern part of the distribution area in summer and early autumn tend to have a much higher fat content than that part of the fishable stock which feeds at more southerly latitudes, *i.e.* between Northwest Iceland and Greenland. However, it is obvious from Norwegian data on fat content (Appendix II.1, Table X) that feeding conditions in the northernmore part of the summer distribution area are not equally good in all years. Cases in point are the years 1988–1992, when the fat content was on average 3–4% lower than in other years in the 1980–1992 period.

14.9. Development of sexual products and external sex-linked characters

The disproportionate size of gonads of male and female capelin is well known. This phenomenon is one of the specific characteristics of the species and has been noted by earlier authors (Templeman 1948; Winters 1966; Prokhorov 1967). Furthermore, the weight of the female ovary may become more than 30% of the total body weight in the last stage of maturity before spawning, while the weight of the male gonads is negligible in comparison.

Accurate ovary weights are available from samples taken during the traditional Icelandic winter capelin fishery (January – April) from 1973 and from the late autumn catch (November – December) in the last one and a half decade. These observations are continuous over the season with the exception that there are few data available for the last two weeks of the year and

the first week of the following year. From these data weekly averages were compiled, ranging from the week beginning on 30 October until mid-April. These average values of roe content, expressed as percentage of body weight, are plotted against time, together with the maximum and minimum values (Fig. 14.15a).

In late October – early November the roe content of the female is low or about 2%. The rate of maturation rises slowly and the roe content usually does not exceed 5% of the body weight at the end of the year. During this time the maturing capelin are usually migrating slowly eastwards off North or Northwest Iceland and tend to stay in or close to the cold mixed or possibly polar waters carried by the East Icelandic Current.

In January, when these capelin have in most years reached the area off Northeast or East Iceland, a slight increase in maturity rate is observed while the roe content increases to about 10–12%. This stage is normally reached late in January or in the first half of February at the cold/warm water boundary off the southern east coast. The increase in roe content from 2–12% has thus taken 13–14 weeks.

On entering the warm Atlantic waters, however, the maturation rate increases dramatically. The graph shows that on the average a roe content of 25% is reached in 4 weeks upon which spawning begins as indicated by the subsequent fall in roe content. The rebound of the roe content in early April (Fig. 14.15a, 23rd week) is the result of a late migration that sometimes arrives after the main spawning season.

Figure 14.15a is the result of the pooling of many years of data. Although this approach gives a general idea of the maturation process, some important details are lost, especially in the last stages. This is due to the fact that the timing of the spawning runs varies from one year to another and there may also be two or more spawning runs entering the spawning grounds one after the other within the same year. These occurrences tend to indicate a longer period of time, spent by individual capelin in the warm south coast waters before spawning, than what is the case in reality. A fairly accurate rule of thumb is that on the average each group of spawners spends about 3 weeks off the south and southwest coasts of Iceland before spawning actually begins. This is about one week less than indicated in Figure 14.15a.
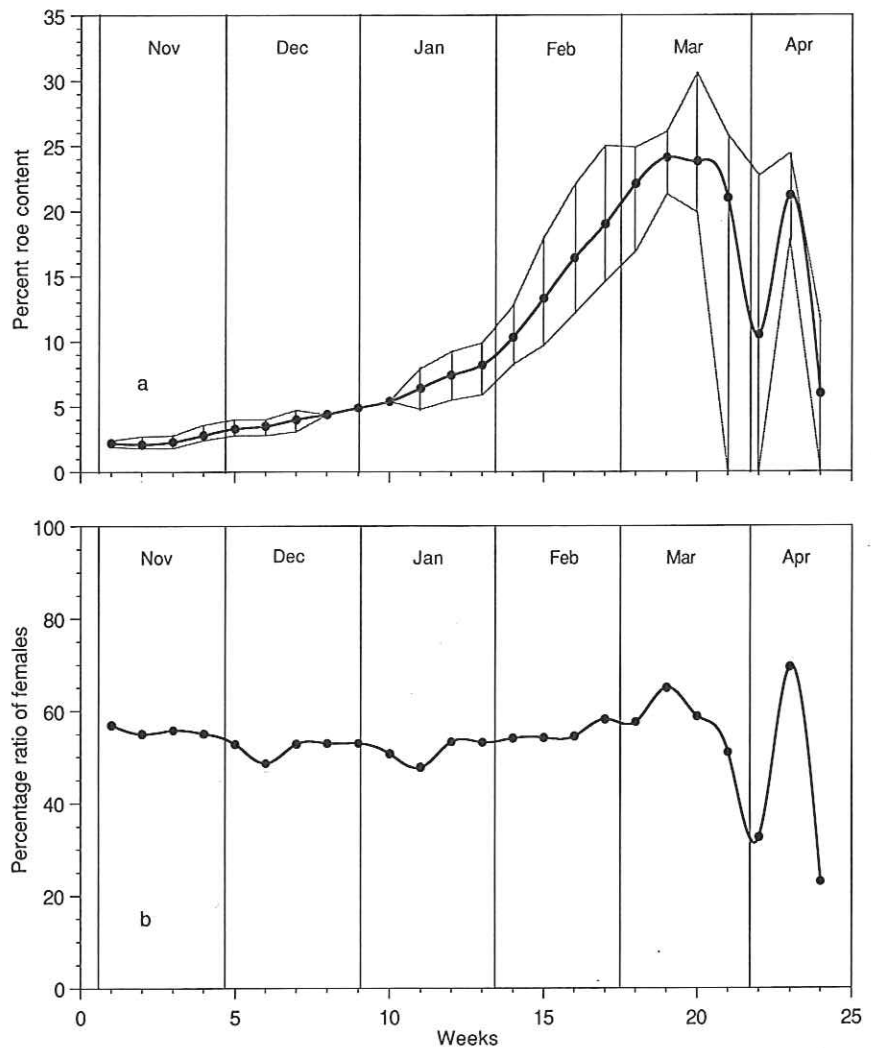
Figure 14.15. a) The changes in average roe content of female capelin, expressed as percentage of total body weight, in the period from October until spawning in March/April of the following year. The hatched area denotes minimum and maximum values. b) The changes in the proportion of females in the catch over the same period.

It is also clear that the highest average roe content of about 25% in Figure 14.15a is an underestimate. Most samples are from purse-seine catches that are pumped from the net and collected on arrival at the landing stage. Ripe females may in many cases have lost some of their roe during this handling. In the large collection of samples there are in fact some instances where the measured roe content has reached 30–35%. This is indicated by the two maxima (Fig. 14.15a) and is probably closer to the natural situation than the average value. The different behaviour of the sexes during spawning was described in chapter 9. A characteristic feature is the continued attendance of the males at the spawning site while the females move to other locations. This phenomenon is illustrated in Figure 14.15b, which shows the diminishing ratio of females in the March samples as the main spawning progresses, as well as the sudden increase in the proportion of females with the arrival of the last spawning run which often is quite separate from the main spawning in time.

As stated above, the sexual products of the male capelin constitute a much smaller proportion of total body weight than those of the females. The weight of the testes has generally not been determined, and consequently, information on their development in relation to the female ovary are not available for the Icelandic

capelin. However, Winters and Campbell (1974) noted that the male testes do not increase in volume from the pre-spawning to the spawning condition and Prokhorov (1967) reported that the weight of the testes constituted about 1.5% of the total body weight of male Barents Sea capelin.

Although fairly readily distinguishable from females by superficial examination in October – November, the male capelin do not acquire their striking secondary sexual characteristics in full until later. By January, about 8–10 weeks before spawning, the thickening of the abdomen as well as the base of the anal fin and the beginning of the formation of the typical spawning ridges along the lateral line on either side can easily be seen. The development of the spawning ridges does not, however, seem particularly advanced until shortly before the capelin enter the warm Atlantic waters south of Iceland or 4–6 weeks before spawning. The timing of these developments is similar to that observed among Newfoundland capelin (Templeman 1948; Pitt 1966 and Winters 1966).

14.10. Natural mortality

It would be expected that natural mortalities among the Icelandic capelin are quite variable depending on stock components and the different migration and distribution patterns exhibited by them. During the summer feeding season and in early autumn, most of the adults and part of the juvenile 1- and 2-group fish are distributed in the cold oceanic area between Iceland, Greenland and Jan Mayen. While remaining in that area

these capelin may be pursued by whales (mainly humpbacks and minkes) but are out of reach of most of their major fish predators. In late autumn and winter when these capelin start assembling on the wintering grounds near and over the outer shelf area off northwest and north Iceland and especially during the spawning migration in January – March, the adult capelin become easily available as food for cod and other large fish.

There are no data available to describe mortalities of 0-group capelin. Among this age group, mortalities are doubtless high but variable as pointed out in an earlier section. Due to the small size of 1-group capelin, the same would be expected for this stock component. However, on the basis of the available information, it seems that after the first winter, natural mortalities among age group 1 have become much more stable and are perhaps not very different from those experienced by the older age groups. This is indicated by the positive relationship between direct acoustic estimates of 1-group abundance and later estimates of year class strength (cf. section 15.5.1).

A measure of natural mortality of the adult fishable capelin may be obtained by comparing successive and reliable abundance estimates of the same stock components, taking into account the catch in the intervening periods (cf. Dommasnes 1981). For the Icelandic capelin there are 8 such pairs of estimates, resulting from autumn surveys on the one hand and winter surveys on the other, available from the 1978/79–1988/89 seasons (see section 15.4.2). The relevant esti-

Table 14.8. Natural mortality rates of Icelandic capelin as calculated from successive acoustic estimates of spawning stock abundance and catch (both main year classes combined). The first and second acoustic estimates are denoted by t_1 and t_2; N is the estimated stock abundance by number (billions); C is the catch by number in the intervening period; Z and M denote the total mortality and fishing mortality respectively, and M/Mon. is the monthly natural mortality rate.

Periods	t_1	t_2	N_{t1}	N_{t2}	C	e^{-z}	Z	F	M	M/Mon.
1.	01 Nov 1978	01 Feb 1979	74.9	54.7	12.4	0.730	0.32	0.20	0.12	0.040
2.	01 Nov 1979	01 Feb 1980	59.2	45.5	9.4	0.769	0.26	0.18	0.08	0.027
3.	01 Nov 1980	01 Feb 1981	24.3	15.4	7.6	0.634	0.46	0.34	0.12	0.040
4.	01 Dec 1981	01 Feb 1982	12.5	8,2	3.3	0.656	0.42	0.32	0.10	0.050
5.	01 Nov 1982	01 Feb 1983	16.6	15.5	0.0	0.934	0.07	0.00	0.07	0.023
6.	01 Nov 1983	01 Feb 1984	64.3	43.2	13.1	0.672	0.40	0.25	0.15	0.050
7.	15 Nov 1984	01 Feb 1985	42.5	32.7	7.3	0.769	0.26	0.19	0.07	0.028
8.	01 Nov 1988	15 Jan 1989	70.5	46.6	20.2	0.661	0.42	0.35	0.07	0.028
									Mean	0.035
									SD	0.011

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mates and the catch in the period between them, both expressed as numbers of fish, are given in Table 14.8. The two year classes that constitute the spawning and fishable stock have, in this instance, been pooled. The reason for this is that small deviations in age structure have sometimes been observed between corresponding estimates. These deviations are believed to be due to inadequacies in sampling rather than actual differences in stock structure with regard to age or size groups. Since there seem to be no obvious reasons to suspect different natural mortality rates of the two age groups in the mature stock, the abundance of the two age groups may be pooled for the purpose of calculating mortality rates.

For calculations of mortality coefficients we use the method described by Beverton and Holt (1957). First we find Z, the total mortality coefficient:

$$N_2 = N_1 \cdot e^{-Z} \qquad (14.2)$$

and thus:
$$Z = \ln \frac{N_1}{N_2}$$

where N_1 and N_2 denote the first and the second stock abundance estimates and Z is the total mortality coefficient.

Having thus calculated Z, the total mortality coefficient, we may proceed to divide it into its two components, F and M, *i.e.* mortalities due to fishing and natural causes respectively, using the formula:

$$\frac{C}{N_1} = (1 - e^{-Z}) \frac{F}{Z} \qquad (14.3)$$

By rearranging we obtain:

$$F = \frac{C \cdot Z}{N_1 \cdot (1 - e^{-Z})}$$

where N_1 and Z are as above and C denotes the catch taken in the time elapsed between the first and the second abundance estimate.

M, the natural mortality coefficient, is simply the difference between Z and F. Finally, the rate of mortality is found by dividing the relevant mortality coefficients by the desired time unit.

The results of calculations of mortality coefficients in the November – January period, carried out in the above manner for the eight seasons when comparable estimates of abundance have been obtained in autumn and winter, are given in Table 14.8. Judging from these calculations there are no signs of a large increase in predation in the period of low capelin abundance in the early 1980s. This is curious, since it is without doubt that capelin abundance in the main predation period (December – March) in the 1980/81–1982/83 seasons was only a fraction of what it was before and has been since then. This can not be explained by unusual migration routes of capelin in these years since the observed variation in mortality certainly did not render the capelin inaccessible to the cod. However, mean weights at age of the Icelandic cod declined dramatically (20–30%) in the years 1981–1983 (Anon. 1984) as did the calculated consumption of capelin by cod (Magnússon and Pálsson 1989, 1989a). Therefore, it seems likely that under conditions of low capelin abundance, predators such as the cod, find it much more difficult than otherwise to locate this prey and take advantage of it.

Natural mortalities, calculated in this way for the Icelandic capelin, indicate a much lower removal rate than that appearing from calculations of the consumption of capelin by the Icelandic cod stock, based on digestion rates and samples of cod stomach contents taken off North and East Iceland in the 1980s (Magnússon and Pálsson 1989, 1989a). One explanation of such a discrepancy could simply be that the measurements were independent of each other and not conducted at the same time of year. A research programme has now been designed in order to obtain more accurate estimates of the predation by cod on capelin and relate the findings to assessments of the capelin abundance.

14.11. Sex ratios and spawning survival

As explained in section 14.6, the female capelin become mature at a smaller size and younger age than the males, causing disproportionate sex distributions in the two main age groups of the spawning stock. Thus, a preponderance of females among age 3 spawners has been found in all 24 available cases and of males among the 4 group in all cases but one (23), the female/male ratios being on the average approximately 60/40 and 40/60 for age groups 3 and 4 respectively.

It is generally presumed that for capelin, as well as other fish, the initial sex ratio is geneti-

cally determined as 1:1. If that is the case, the sexes should occur in equal numbers in the immature part of the stock, at least at the 0- and 1-group stage. Unfortunately, this has not been tested in the case of the Icelandic capelin and limited information appears to be available from other stocks. Winters (1966) microscopically determined the sex of Newfoundland capelin larvae, 7–9 cm in length, and found a 1:1 ratio of males to females. Similarly, Prokhorov (1967) found that among 1-group Barents Sea capelin one half were males and one half were females. Both authors conclude that sexes are most likely distributed in equal numbers in the immature stock. While no corroborative evidence is available in the case of the Icelandic capelin, there seems no reason to suspect uneven initial sex distribution in that stock either.

Given that there are no great differences in natural or spawning mortalities between the sexes, it would, therefore, be expected that the overall sex ratio of a year class, as estimated from maturing fish only, would be 1:1. In order to check this, the year classes from 1976–1988 were considered. The total abundance by number of capelin belonging to these year classes has been assessed by acoustic methods and back-calculated to a fixed point in time (1 August) as maturing 2- and 3-group fish (cf. section 15.6.2). These abundance estimates have been taken and divided by sex according to the sex distribution observed in the relevant seasons in the shelf area off

East and Northeast Iceland in January/February. The resulting division of year class abundance by age and sex is given in Table 14.9.

Assuming a fixed natural mortality rate of $M = 0.035$/month the estimated numbers of 3-group capelin by sex were then projected backwards over one year, $i.e.$ to 1 August at age 2. The total numbers of females and males were thus found for each year class at this age and are given in Table 14.10. Obviously, there is a clear majority of females among all year classes but one (1980), the average positive deviation from a 1:1 ratio (50% females, 50% males) being 3.58%. A test of significance gives a standard error of 0.57, resulting in a 95% confidence interval ranging from 2.34–4.81%. Among the 1976–1988 year classes females have, therefore, outnumbered males in the Icelandic capelin stock by a significant margin. Theoretically, this deviation could be produced by a variety of reasons.

It is known that both the purse seines and trawls with which capelin samples are taken, are selective in favour of the older and larger fish. This is very pronounced when immature 1-group capelin occur together with older year classes and seems to be present to some extent in the case of small immature 2-group fish. However, such selection effect does not seem to occur in the case of maturing males and females of either age group 2 or 3, neither in autumn nor in winter (age groups 3 and 4). Some tests to determine differential escape of size groups from capelin trawls

Table 14.9. The division of the abundance of the mature part of the 1976–1988 year classes by number (billions) and sex at ages 2 and 3 with reference to 1 August (cf. section 15.6.2).

Year class	Age 2				Age 3		
	N_{all}	N_{mat}	N_{f2}	N_{m2}	N_{mat}	N_{f3}	N_{m3}
1976	97.2	81.9	48.9	33.0	10.1	2.6	7.5
1977	107.7	91.3	53.6	37.7	10.3	3.3	7.0
1978	39.6	35.4	19.9	15.5	2.8	1.2	1.6
1979	43.3	39.7	22.8	16.9	2.4	1.1	1.3
1980	32.1	17.1	9.4	7.7	9.8	4.2	5.6
1981	96.2	53.7	35.5	18.2	27.9	9.3	18.6
1982	81.6	40.7	25.2	15.5	26.9	12.2	14.7
1983	164.6	64.6	37.7	26.9	65.0	30.2	34.8
1984	65.0	35.6	23.5	12.1	20.0	8.5	11.5
1985	102.6	65.4	37.2	28.2	24.4	10.6	13.8
1986	94.3	70.3	41.6	28.7	15.8	6.1	9.7
1987	53.1	42.8	25.3	17.5	6.8	2.4	4.4
1988	42.2	31.9	17.3	14.6	6.7	3.3	3.4
Total	1,019.5	670.4	397.9	272.5	228.9	95.0	133.9

Table 14.10. Division of the total abundance by number (billions) of the 1976–1988 year classes by sex on 1 August at age 2. Deviations from zero (1:1 ratio) and the standard error of the mean are also given.

Year class	N_{ftot}	N_{mtot}	Δ_0
1976	52.8	44.4	4.32
1977	58.6	48.4	4.77
1978	21.7	17.9	4.80
1979	24.5	18.9	6.45
1980	15.8	16.2	−0.62
1981	49.7	46.5	1.66
1982	43.8	37.9	3.61
1983	83.7	79.9	1.16
1984	36.4	29.6	5.15
1985	53.3	49.2	2.20
1986	50.9	43.5	3.92
1987	29.0	22.7	6.09
1988	22.3	19.8	2.97
Total/Average	542.5	474.9	3.58
SE			0.57

were carried out in the autumn of 1991, but the results were inconclusive and have not been reported. In any case the female capelin is smaller than the male, and gear selection for the larger fish would lower the female/male ratio.

Segregation into schools with uneven distributions of sexes irrespective of age is well known among capelin stocks (cf. Templeman 1948; Bakke and Bjørke 1973; Friðgeirsson 1976). On the other hand, this phenomenon seems to be limited to the spawning process itself and a relatively short period immediately leading to it. In order to avoid this problem, no samples taken later than 3 weeks before spawning were included in the data on which the division of sexes within age groups is based.

There are no sex-specific estimates available of the instantaneous natural mortality of capelin, *i.e.* death from natural causes other than spawning. Since the sexes migrate together around the distribution area at all times of the year, it seems reasonable to assume similar instantaneous mortality rates for both. During periods of low food abundance, competition may of course arise and lead to increased mortality rates among individuals that for some reason, such as inferior size, are less competitive in the chasing of prey animals. However, due to the smaller size of the females, such conditions would in all probability favour the males and contribute to a situation that is contrary to observations.

Therefore, the remaining reason to account for the observed preponderance of females in the mature part of almost every year class in the Icelandic capelin stock, is that some of the fish will survive the spawning process and that the magnitude of this survival rate is sex dependent favouring the females. Considering the evidence of spawning survival of the Icelandic as well as most other capelin stocks, it is concluded that spawning survival among the male part must be negligible. Assuming zero spawning survival for males belonging to the Icelandic capelin stock, a spawning survival rate of 3-group females, belonging to the 1976–1988 year classes, can be calculated as follows.

Having obtained the total number of capelin by sex at age 2 for each year class, addition gives an overall surplus of females. Thus, the total difference of $N_f - N_m = 67.6$ billion fish for all 13 year classes together (Table 14.10). If this is explained as spawning survival of females, with all males dying as a result of spawning, then the number of females observed as maturing 3-group on 1 August (Nf3 in Table 14.9) should have been (Beverton and Holt 1957);

$$N_{f3} = (N_{mtot} - N_{f2})e^{-M} \qquad (14.4)$$

where N_{f3} denotes the number of females observed as maturing 3-group on 1 August, N_{mtot} the total number of males back-calculated to age 2 in August, N_{f2} the total number of females maturing at age 2 and M the natural mortality over one year = 0.42.

From Tables 14.9 and 14.10 we get;

$$N_{f3} = (474.9 - 397.9)\ e^{-0.42} = 50.6$$

The observed total number of females at age 3 was 95.0 billion fish. Hence, a total of some 95.0 − 50.6 = 44.4 billion females belonging to the 1976–1988 year classes were preparing to spawn for the second time, which represents about 47% of the total. To observe 44.4 billion recovering females in August we need a total of $44.5\ e^{1.15} = 51.1$ survivors at the time of spawning in March in the same year in order to explain the observed surplus of females. Since this figure represents a total of 13 years, it is concluded that on the average some 3.9 billion females have survived the spawning process per annum.

On the average about 16.1 billion capelin

Table 14.11. Vertebral frequencies among year classes 1967–1979 in the Icelandic capelin stock.

Year class	Females			Males		
	Count	Average	SD	Count	Average	SD
1967	38	69.55	0.69	30	69.53	0.79
1968	115	69.08	0.58	33	69.06	0.83
1969	170	69.11	0.84	170	69.06	0.87
1970	752	69.17	0.95	499	69.10	0.87
1971	1,144	69.19	0.90	675	69.27	0.85
1972	475	69.30	0.91	327	69.35	0.90
1973	194	69.54	0.98	116	69.42	0.92
1974	193	69.28	0.98	148	69.53	0.92
1975	163	69.25	0.82	226	69.19	0.89
1976	803	69.25	0.82	596	69.24	0.83
1977	473	69.17	0.91	288	69.21	0.93
1978	180	69.14	0.89	143	69.28	0.91
1979	102	69.17	0.98	47	69.21	0.84
Total/Average	4,802	69.23	0.90	3,298	69.25	0.88

(340,000 tonnes) have spawned annually at Iceland over the last 13 years. Of these, about 8.9 billion fish have belonged to the female part of the spawning stock, where 7.3 billion belonged to age group 3 and 1.6 billion to age group 4. If some 47% of the 4-group females were actually spawning for the second time, they have numbered 0.75 billion fish on the average or just over 8% of the female part of the spawning stock by number, assuming similar natural and fishing mortalities for all of the adult stock.

The primary purpose of the exercise just described is to point out the apparently anomalous sex distribution within year classes in this capelin stock, which this author is at present unable to explain except in terms of different spawning survival of the sexes. As mentioned above, there are other possible explanations in theory, although from the present state of knowledge, they do not seem plausible. However, if there is a spawning survival of 3-group females as suggested in the above paragraph, this considerably alters the present picture of the biology of the Icelandic capelin stock. Thus, it is implied that by number about one half of the 3-group female spawners may survive on the average, and that the majority of these will then, either become part of the fishable stock during the next season, or spawn again at age 4. For the time being, this proposition should, however, be considered as an unresolved hypothesis to be answered through future research.

14.12. Vertebral counts

Vertebral counts were carried out on a regular basis in the 1970s and early 1980s. The data, comprising 4,802 females and 3,298 males in all, were arranged by year class and sex as shown in Table 14.11. The number of vertebrae varies from 67–72 with the most frequent counts being 69 and 70. The grand average is 69.23 for females and 69.25 for males, the standard deviation being 0.90 and 0.88 respectively. Year class averages ranged between 69.08–69.55 for females and 69.06–69.53 for males.

The present overall means for both sexes differ considerably from those reported previously. Thus, Friðriksson (1943) found an average of 69.44 and 69.59 for females and males respectively, and Vilhjálmsson (1968) reported averages of 69.49 and 69.44 for the sexes in that order. The earlier averages were based on much fewer counts, or 714 males and 59 females in the former case and 623 each, males and females, in the latter. In all cases inter-annual variations were reported of sufficient magnitude to explain a difference of 0.2–0.3 in averages of overall vertebral counts. No significant sexual dimorphism is found in vertebral counts of Icelandic capelin.

In fisheries research, meristic and morphometric characteristics are often used in attempts to distinguish between populations or sub-groups within a stock. Successful subdivisions by this method must, however, usually depend on a combination of many characteristics as de-

Table 14.12. Number of vertebrae in capelin (including the urostyle) from different areas where method of counting has been asserted.

Location	Female	Male	Source	
British Columbia	66.13±1.02	66.59±0.95	Hart and McHugh (1944)	
Bay of Fundy	66.86	67.03	Tibbo & Humphreys (1966)	
Gulf of St.Lawrence				
Coudres Islands	64.45	66.89	Arsenault (1979), in Stergiou (1989)	
Grande Riviere	68.50	66.16	—	—
Natashquan	66.57	66.87	—	—
Seven Islands	67.07	66.56	—	—
Newfoundland (offshore)				
Grand Bank	66.60±0.85	66.48±0.81	Pitt (1958)	
Grand Bank	66.480.77		Carscadden and Misra (1980)	
Newfoundland (inshore)				
West coast	66.51±0.87	66.43±0.88	Templeman (1948)	
South and SW-coast	66.72±1.00	66.56±0.95	—	
East coast (south)	66.60±0.92	66.56±0.95	—	
East coast (north)	66.64±0.96	66.45±0.93	—	
Labrador	66.58±0.93	66.53±0.97	—	
West coast	66.35±0.95		Carscadden and Misra (1980)	
St. Pierre-Green Bank	66.47±0.81		—	
N-Grand Bank-Avalon	66.38±0.91		—	
Labrador	66.51±0.93		—	
Greenland (west coast)	68.20±0.61		Hansen (1943)	
Greenland (east coast)	68.27±0.58		—	
Iceland (spawn. grounds)	69.44±0.91	69.59±1.17	Friðriksson (1943)	
— —	69.49±1.00	69.44±1.00	Vilhjálmsson (1968)	
— (various regions)	69.22±0.90	69.25±0.88	This paper	
Barents Sea (western part)	69.31±0.72	69.33±1.11	Prokhorov (1967)	
— (eastern part)	69.16±0.82	69.23±0.94	—	
— (spring)	69.56	69.53	Khokhlina (1957), in Prokhorov (1967)	
— (summer)	69.31	69.58	—	—

monstrated for capelin in the Gulf of St. Lawrence and off Newfoundland and Labrador (Sharp *et al.* 1978; Carscadden and Misra 1980). The reason for this is that small changes in these genetically determined characteristics may take place from year to year and are generally believed to be caused by environmental changes which, nevertheless, do not necessarily affect all characteristics in the same way. On its own, vertebral counts are, however, of interest when studying the possible relationship between geographically well separated capelin populations (cf. McAllister 1963; Stergiou 1989).

Vertebral counts from various parts of the capelin distribution, corrected for the inclusion or omission of the last segment, the urostyle, are given in Table 14.12. There seems little doubt that the Barents Sea stock at large and the stock in the Iceland – East Greenland – Jan Mayen area are composed of fish with essentially the same average number of vertebrae (69.16–69.59). On the other hand, all stocks in the Labrador – Newfoundland – Gulf of St. Lawrence area, as well as those of the eastern North Pacific, have vertebral averages generally ranging from 66.30 to 66.80. Such a difference of about 3 vertebrae is highly significant, and the two major capelin stocks in the Northeast Atlantic proper must have been isolated from the rest of the capelin complex for long enough time to become distinct.

The number of vertebrae in capelin population(s) inhabiting the fiord system of the west coast of Greenland as well as the Ammassalik area on the east coast seems to be intermediate between those of the Icelandic and Newfoundland-Labrador stocks. Thus, Hansen (1943) gives averages, based on 6 samples of 100–164 fish each, ranging from 68.07–68.32, with a weighted average of 68.21. Although Hansen does not

state whether he included the urostyle in his counts, it must be presumed that he did. He quotes Friðriksson's (1943) average of 69.45, which certainly included the urostyle, as being much different from his own. These two researchers must have been in personal contact since Friðriksson's results on vertebral counts were published in the same year as those of Hansen's.

The West-Greenland capelin are beach spawners and in that sense closely resemble the Labrador-Newfoundland stocks. It is well established, however, that varying amounts of 0-group capelin drift across the strait from the west coast of Iceland to the banks off East-Greenland almost every year. Although the fate of these larvae is not known, it seems likely that at least some of them will end their lives by joining the Greenland stock(s) and thereby affect stock variables such as vertebral counts.