SAITHE ON A SHELF

Two studies of *Pollachius virens* in Icelandic shelf waters

I. Food and feeding of saithe (*Pollachius virens*) at Iceland

and

II. On saithe (*Pollachius virens*) migrations to Iceland

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titilblaðs

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Thesis submitted in partial fulfillment
of the degree Cand. scient.

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Reykjavík, April 1996

Sigurður Þór Jónsson

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SYNTHESIS

1. Introduction

The saithe is a resident of the North Atlantic. It occurs on both sides of the ocean, but is more abundant and widely distributed on the eastern side. The western Atlantic stock is found between the Gulf of St. Lawrence and Georges Bank and strays have been observed as far south as Chesapeake Bay and north to Davis Strait. On the eastern side of the Atlantic there are a number of stocks units, *i.e.* around Iceland, off the coast of Norway reaching north into the Barents Sea, in the northern part of the North Sea, and north and west of the British Isles. In the eastern Atlantic there are individual records of saithe in the Bay of Biscay or even farther south (Reinsch 1976; Anon. 1995a).

The saithe has been decribed as both pelagic and demersal, and also as a strong facultative schooler (Partridge *et al.* 1980). Observations have been made of saithe feeding on prey schooling close to the surface suggesting that the saithe may cooperate when foraging. Thus, Sæmundson (1926) observed that "in spring and summer [the saithe] often school at the surface in varying numbers, especially when preying on euphausiids, moving so swiftly and with such violent jumps, that the sea resmbles a boiling cauldron." And Misund (1993) states that "schools of large saithe hunted the schools of small herring, and occasionally forced them to the surface where a heavy predation, both by saithe and seabirds, was observed." Thus it is even possible that the saithe are capable of herding behaviour similar to that exhibited by some baleen whales when feeding on euphausiids.

In the literature saithe is generally described as a voracious predator, feeding to some degree on demersal, but mainly on pelagic prey species, such as euphausiids and various species of fish (*e.g.* Wagner 1959; Gislason 1983; Pálsson 1983; Sunnanå 1984; Daan 1991; Nicolajsen 1993).

The two most comprehensive recent studies of the feeding of commercially sized saithe were carried out in the northern North Sea. According to these studies there can be large variations in the diet of the saithe within a fairly small geographical area. Thus, to the west of Scotland fish completely dominated the diet with crustaceans contributing less than 10% of the estimated consumption, while east of Scotland crustaceans, mostly euphausiids, amounted to one third of the diet (Du Buit 1991). Off the southwest coast of Norway, Bergstad (1991) found the euphausiid contribution to be close to 80% for saithe smaller than 50-60 cm, while larger saithe consumed mostly fish prey.

For management purposes, the International Council for the Exploration of the Sea (ICES) has defined five separate saithe stock assessment units in the NE-Atlantic. These stock units, their average fishable and spawning stock biomass, and spawning stock as percentage of fishable stock in 1990-1994 are given in the text table below:

Stock	ICES subareas	Fishable stock (tonnes)	Spawning stock (tonnes)	SSB %
Northeast arctic saithe	I and II	540 000	127 000	24
North Sea saithe	III and IV	409 000	87 000	21
Saithe west of Scotland	VI	60 000	16 000	27
Faroese saithe	Vb	156 000	75 000	46
Icelandic saithe	Va	420 000	215 000	51

Sources: Anon. 1995, 1995b, 1996, 1996a

Average total annual landings of saithe from these stock units in the same period were 360 thousand tonnes. In addition, some landings have been reported from subarea VII, *i.e.* the waters surrounding Ireland, but these saithe have not been included in any assessment. The average fishable saithe biomass in ICES statistical areas I-VI has thus been approximately 1.5 million tonnes in the 1990s. This may be compared to the estimated cod biomass of 3 million tonnes in the same area, two thirds of which are the Northeast arctic cod (Anon. 1995, 1995b, 1996, 1996a). Northwest Atlantic saithe are regarded as one stock unit by Canada and the USA (Anon. 1995a).

Fisheries scientists are well aware of the limitations of such a division for migratory species like saithe. A number of studies have attempted to take account of migrations between different units when assessing the NE-Atlantic saithe stocks (*e.g.* Jakobsen 1981; Anon. 1983; Hastie 1995) and on one occasion a joint VPA was run for all the stocks (Anon. 1974).

The proportion of total stock biomass, estimated to be mature, is remarkably variable and twice as high at Iceland and the Faroes as in the other areas. On the other hand, the proportion removed annually by the fishery lies in the range of 20-30% of fishable biomass for all five stock units. The variability in the proportion of mature fish is probably for the most part due to the different harvesting strategies employed. The most recently recruited saithe year classes west of Scotland, in the North Sea and off the coast of Norway are subjected to intense fishing pressure. Thus, the easternmost saithe stocks can, to some extent, be characterized as growth overfished (Anon. 1995a). However, a possible supplementary explanation could be net immigration of adult saithe to Icelandic and Faroese waters from the eastern part of the distribution area. Such a migration would conform with the observation that the whereabouts of adult North Sea saithe are poorly known for large parts of the year (Reinsch 1994).

Thus, at least two important aspects of saithe biology merit further study. On the one hand, the variability in the results from feeding studies suggests a certain degee of opportunism in the saithe's feeding behavior. This behaviour must therefore be carefully studied before the species can be properly placed in a multispecies modelling context. On the other hand, tagging studies have revealed movements of saithe between managment units. Indeed, such studies have shown that saithe are highly migratory, and methods must be developed to monitor their movements in order to improve stock assessment. The following two studies were carried out with the purpose of answering questions relating to these two aspects of the biology of saithe at Iceland.

In the food study, the diet of the saithe at Iceland is analysed in a descriptive sense, with the main emphasis on saithe predation on capelin and euphausiids. These prey categories are very abundant in Icelandic waters and make up the largest part of the diet. In the fashion of many diet studies, variability in the diet in relation to such factors as year, season, predator size and time of day is described.

In the migration study, indications of saithe migrations to Iceland are investigated, mainly on the basis of mean-length-at-age and catch-at-age data. The observed anomalies in mean-length-at-age might have alternative explanations, such as reduced growth or much delayed recruitment. However, when these indications are placed in the perspective of historical saithe data and tagging results, they seem to lend support to an hypothesis of immigration of saithe to Iceland from the 1984 year class in 1991. The magnitude of this migration is estimated.

Before the results of the two studies are summarized, a short introduction of the hydrobiological environment of the Icelandic shelf will be given, followed by a general description of the species, as well as results from various saithe studies and information extracted from the saithe data base at the Marine Reasearch Institute, Reykjavík (MRI).

2. The Icelandic shelf environment

Most of the saithe, which are the object of the following studies, were caught on the Icelandic shelf. A short description of this area, its bottom topography, circulation and water masses, and aspects of its temperature-salinity regime, primary and secondary production, will be given here based mainly on recent reviews (Vilhjálmsson 1994; Ástþórsson and Gíslason 1995).

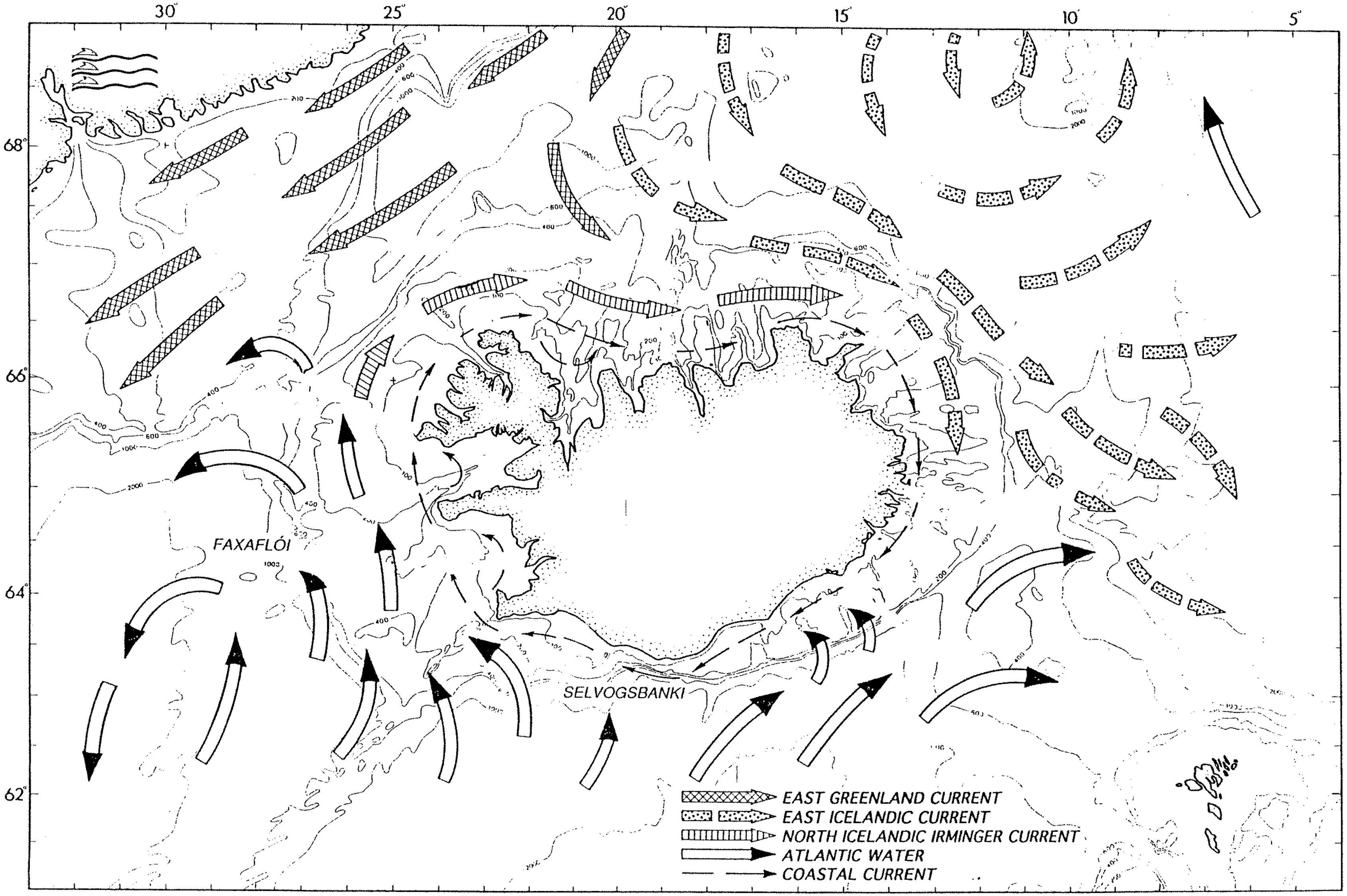


Figure 1. Ocean currents around Iceland (from Ástþórsson and Gíslason 1995).

The shelf surrounding Iceland breaks roughly at a depth of 400-500 m. Thus, the Icelandic groundfish survey (IGFS) covers the area within the 500 m depth contour, amounting to some 61 500 square nautical miles or 210 000 km^2 (Pálsson *et al.* 1989). This may be compared to 1.4 million km^2 for the entire Barents Sea (Sakshaug *et al.* 1992). The shelf is narrowest in the south where the slope plunges to a depth of 1 500 m or more, only a few miles off the coast. It is broader east, north and west of Iceland, in most places reaching a width of 60-90 nautical miles. Several submarine ridges are connected to the shelf. These are the Reykjanes Ridge in the southwest, the Iceland-Greenland Ridge in the northwest, to the southeast lies the Faroe-Iceland Ridge, and, though less distinct, the Kolbeinsey Ridge extending due north from the central north coast and the Jan-Mayen Ridge which touches the northeastern part of the Icelandic continental shelf.

The ocean current system around Iceland is shown in Figure 1. As a result of this current pattern, the Icelandic shelf can be divided in two with regard to water masses. To the south and west, warm and saline Atlantic water predominates with a seasonally varying admixture of coastal runoff. To the north and east, on the other hand, conditions are more variable. A tongue of Atlantic water of varying extent mixes with water from the coastal current and arctic water from the East Icelandic Current. Thus, the strength of the East Greenland Current, the prevailing wind force and direction and variability in the coastal runoff are all factors known to have affected recruitment to the Icelandic cod stock (Vilhjálmsson and Magnússon 1984; Jakobsson 1992; Ólafsson *et al.* 1993) and, by analogy, although fewer analyses have been undertaken, other fish stocks at Iceland as well.

South of Iceland, runoff from the rivers has a direct effect on the establishment of stratification and thereby on the supply of nutrients, in particular, that of silicate. Wind pattern is a factor in determining the spread of the low salinity coastal water, southerly winds leading to increased stratification in the productive Faxaflói, while northerlies have the opposite and, on the plant production, negative effect. There have been large fluctuations in the inflow of Atlantic water onto the shelf area to the north and northeast of Iceland, with consequences for the nutrient supply to the otherwise nutrient poor and stratified arctic water there. At times, the strength of the East Greenland Current is such that it forms a barrier to the North Icelandic Irminger Current, causing much reduced productivity on the northern shelf, and on occasion directing the drift of larvae, from the spawning grounds off SW-Iceland, towards Greenland.

The primary production around Iceland is highest in areas where Atlantic waters predominate. There are two "hot spots" off the south coast, one in the southwest in the region of Selvogsbanki and another in the southeast, and a third in Faxaflói. In these areas the average annual primary production exceeds 200 g C m^{-2} $year^{-1}$. The general area off the south and west coasts is more productive and stable with regard to primary production than the northern and eastern areas. Variations of one order of magnitude have been observed north of Iceland, depending on Atlantic influx to the northern shelf (Þórðardóttir 1984). Gíslason *et al.* (1994) timed the peak in the phytoplankton spring bloom to the southwest of Iceland in 1990-1992 and observed the highest concentrations in chlorophyll *a* in late May 1990, early May 1991 and early in June or even later in 1992. A close association between the spawning of *Calanus finmarchicus* and the spring bloom was observed, which is in agreement with findings from other areas.

Variations of zooplankton biomass in Icelandic waters in spring are described by Ástþórsson and Gíslason (1995). In summary, they found the spring biomass, in terms of volume measurements converted to dry weight per square meter of ocean surface, to range generally from 2 to 4 g m^{-2}, somewhat lower nearshore in the northeast and east, while some stations had persistently higher values, *i.e.* close to 10 g m^{-2}. The highest values were found in the southwest on Selvogsbanki, an important spawning ground for many fish species at Iceland, and in the arctic waters of the East Icelandic Current off the northeastern part of the shelf. *C. finmarchicus* is the dominant species, in particular to the south. The other main components of the plankton are cirrepede and euphausiid larvae close to shore while arctic species such as *C. hyperboreus*, *C. glacialis* and *Metrida longa* become abundant off the northeastern part of the shelf. Zooplankton biomass indices from stations in the Atlantic waters show a significant positive correlation with 0-group cod abundance.

3. General biology of the saithe

The saithe is one of the larger gadids. Lengths of up to 127 cm and weights close to 21 kg have been recorded at Iceland and the oldest saithe on record, among the year classes since 1959, belonged to age group 22. There are German records of a saithe 135 cm in length as well as of a 27 year old individual (Reinsch 1976). However, the bulk of the commercially caught saithe at Iceland are in the length range of 50-100 cm, weigh some 1,5-8 kg and the majority are less than 15 years old.

Svetovidov (1948; in Patterson and Rosen 1989) is the classic work on gadiform systematics. However, later work, where cladistics have been applied to fish systematics, indicates that there is need for a revision of the Gadidae, and indeed of the order Gadiformes and the higher taxonomic grouping they belong to, the doubtfully monophyletic superorder Paracanthopterygii (Patterson and Rosen 1989; Nelson 1994). Thus, Dunn (1989) places the genus *Pollachius* in the new gadid subfamily Eleginae along with the genera *Merlangius*, *Melanogrammus*, *Trisopterus* and *Eleginus*, based on a cladistic analysis of selected osteological characters. On the other hand, Nolf and Steurbaut (1989) place *Pollachius* in the tribe Gadini, along with *Eleginus*, *Gadus*, *Melanogrammus*, *Microgadus* and *Theragra* on the basis of similarities in sagittal otolith structure.

3.1 Spawning

Of all the gadids at Iceland, the saithe spawn earliest (Jónsson 1992). In the NE-Atlantic they spawn at temperatures of 5°-10°C and salinity close to 35‰. Spawning of saithe in the NE-Atlantic begins already in January and peaks in February, except at higher latitudes where it is delayed (Reinsch 1976). Their cousins on the western side of the Atlantic spawn at lower temperatures and salinities and can perhaps be characterized as mid-winter spawners, the spawning beginning already in October and continuing until March in this area (Svetovidov 1948; in Reinsch 1976).

At Iceland, ripe spawners are rare in January and February, but present in samples throughout March and April in substantial numbers. In comparison, the spawning of cod has just begun at the end of March and peaks in late April or early May (Marteinsdóttir and Pétursdóttir 1995). The main spawning areas are Selvogsbanki and Eldeyjarbanki, southwest of Iceland, with a secondary but substantial spawning taking place off the southeast coast.

3.2 Eggs and larvae

In a plankton study of the area off SW-Iceland, Gíslason and Ástþórsson (1991) observed eggs, judged to be saithe eggs from their diameter, in late March 1991. Magnússon (1966) observed saithe larvae at stations to the west of Iceland in May and June of 1961-1964 and saithe larvae have also been observed in Faxaflói and on Selvogsbanki at the same time of year (Anon. 1994; K. Þórisson, MRI, pers. comm.). On the other hand, saithe have only been observed sporadically in very low numbers in the MRI 0-group surveys, conducted in July and August since 1970 (*e.g.* Anon. 1972, 1973; Magnússon *et al.* 1987).

Saithe fry of unknown origin have been observed drifting towards Norwegian waters at 63°-64°N near the zero meridian, in late April and early May (Bjørke and Sætre 1994; Nedreaas and Smedstad 1995). If they stemmed from spawning at Iceland, the easternmost spawning ground would seem the most likely origin and the larvae would have drifted a distance of at least 500-600 nautical miles. To cover that distance in a period of 45-60 days, drift speeds of 20-30 cm s^{-1} are necessesary, or close to the maximum current speeds given for the North Atlantic Drift (Stefánsson 1994). Furthermore, the possibility of continued import to Norwegian waters at a later date can not be ruled out, *i.e.* later in May or perhaps in early June. Although a survey in one year fails to detect saithe postlarvae, such results do not eliminate the possibility of their arrival at that time in a different year.

The diet of the 0-group saithe while in the plankton is mainly composed of calanoid copepods. During the first life-stages, the saithe diet is similar to that of other gadids which have been studied (Nagabhushanam 1965; Robb and Hislop 1980; Economou 1991).

3.3 Juveniles and nursery areas

During early and mid-summer, the first 0-group saithe can generally be observed settling in the littoral area (*e.g.* Nagabhushanam 1965; Lie 1961; Clay 1989; Godø *et al.* 1989). Throughout the distribution area of saithe, the 0-group has vanished from the plankton in July-August (*e.g.* Clay *et al.* 1989; Godø *et al.* 1989; Nedreaas and Smedstad 1995).

In general, the juvenile saithe reside in the littoral and sublittoral zones during the first 1-2 years of their life, but are often forced into deeper waters by the cooling of the surface layer in winter (Reinsch 1976; Clay *et al.* 1989). As they grow the saithe will gradually move away from the coast (Jakobsen 1981), but the juveniles often take up residence on nearshore reefs and shallow banks (*e.g.* Nedreaas 1987). Experiments conducted on acoustically tagged saithe at such locations have shown them to undertake short daytime feeding excursions from a home area where they spend the night (Smith *et al.* 1993; Sarno *et al.* 1994).

The importance of the kelp forest as a nursery for the juvenile saithe has recently been pointed out (Høisæter and Fosså 1993; Sarno *et al.* 1994a; E. Hjörleifsson, MRI, unpubl. mat.) and *Laminaria* is sometimes mentioned in descriptions of study areas where juvenile saithe have been studied (Ojeda and Dearborn 1991) These authors and others have also reported on the diet of juvenile saithe in their respective areas and generally found them to feed on a variety of littoral organisms and fish but, in some cases, mainly on planktonic prey (Nagabhushanam 1965; Salvanes and Noreide 1993).

Nedreaas (1987) found the diet of 2 year old saithe at two exposed locations on the west coast of Norway to be dominated by abundant planktonic organisms, such as copepods and euphausiids, but when these prey became scarce they were substituted by other available prey, either fish or benthic organisms, the latter probably least preferred.

3.4 Recruitment

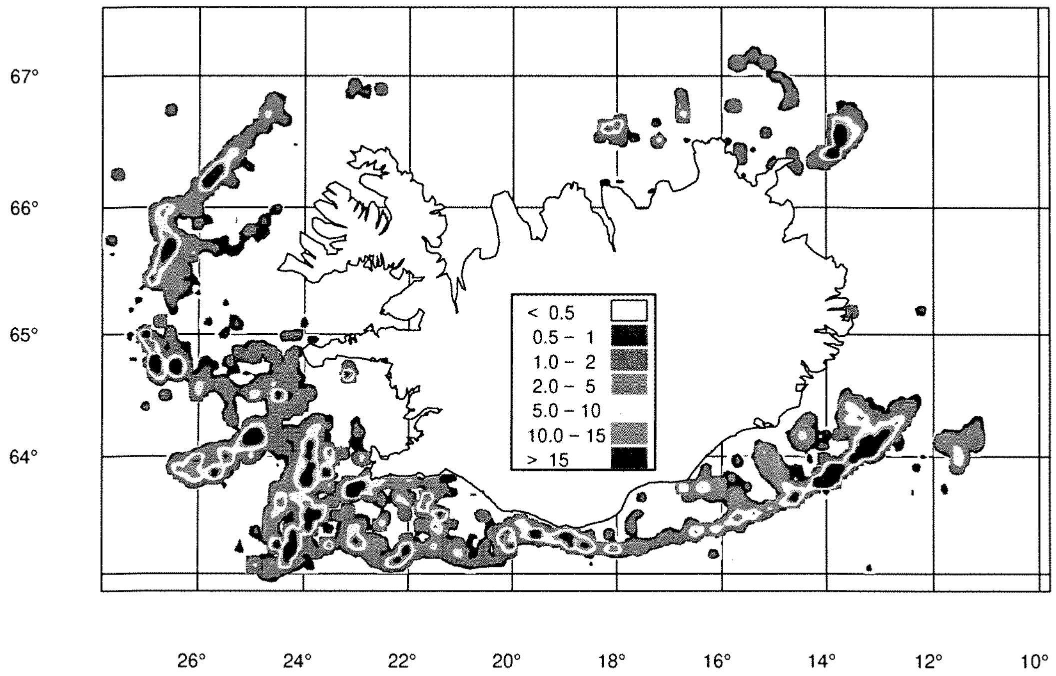
At Iceland, the saithe generally recruits to the fishery as age group 3 or 4 and is in most cases fully recruited at the age of 5. However, as will be shown in Paper II, the 1984 year class appeared not to have recruited fully until 1991, as age group 7, and other such anomalous examples can be found in older VPA tables (Anon. 1993). To the knowledge of this author, only one study has been carried out of saithe in the nearshore habitats (E. Hjörleifson, MRI, unpubl. mat.) and none of the transition from the juvenile coastal phase until the fish appear in the commercial catches in the Icelandic area.

In Icelandic groundfish surveys, observations of age group 2 and 3 saithe are most frequent on the shelf area off Vestfirðir, the northwest peninsula of Iceland, indicating the importance of this area as a nursery ground. It is also clear that the saithe in this area prefer locations farther west and thereby in warmer waters than cod of the same age (Pálsson *et al.* 1993).

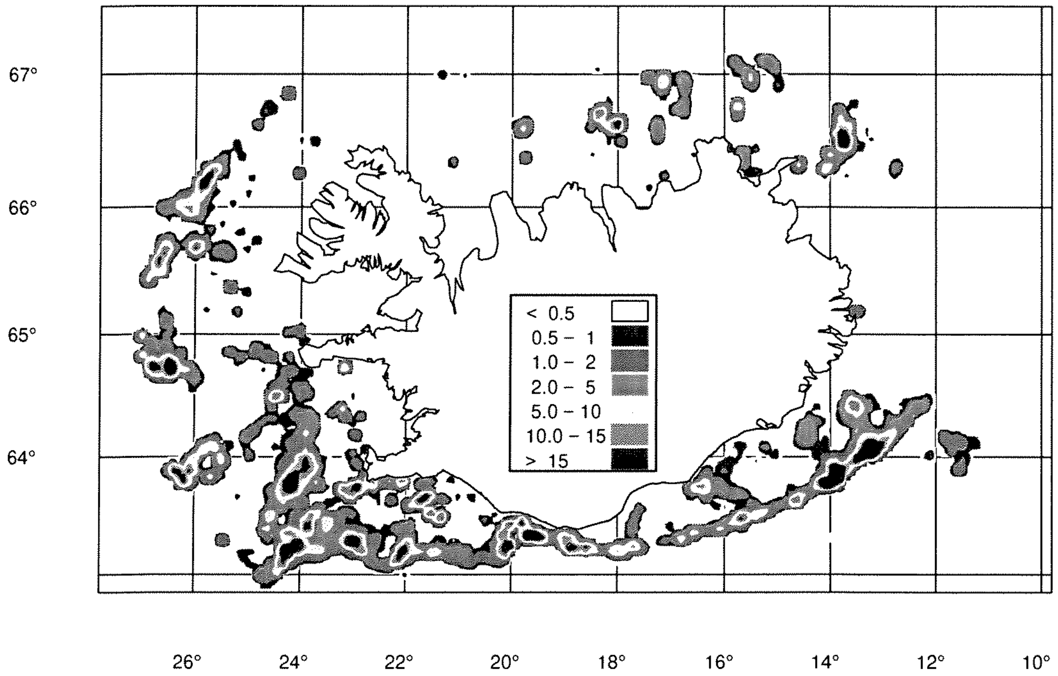
On the basis of data from the International Bottom Trawl Survey (IBTS), it has been observed that North Sea saithe of age groups 2 and 3 are to be found in highest concentrations on the western slopes of the Norwegian Deep (Reinsch 1994).

3.5 Adult saithe and the saithe fishery at Iceland

The distribution of adult saithe at Iceland, as reflected by the commercial catch in 1991-1994, is shown in Figure 2. The catches are summed over a fine grid and smoothed slightly for cosmetic purposes (H. Björnsson, MRI, pers. comm.). A decreasing trend is apparent, the total catch was reduced by approximately 50% in the period, and the saithe fishery at present is at a low level. The catches are distributed throughout the year and lie mainly in the relatively warm Atlantic waters to the south and southwest of Iceland. The predominant gear types are gill nets and bottom trawl. In the 1990s in the range of 10-40% of the annual landings were taken in gill nets, for the most part during the winter and spring fishery on spawning concentrations. For all intents and purposes, the remainder was caught by trawlers, their fishing effort more evenly distributed over the year. The size and age distributions in the Icelandic catches clearly show that younger and smaller saithe are caught in the bottom trawl than in gill nets. This is a reflection both of selection due to the difference in minimum mesh size between these two types of gear (155 mm for bottom trawl; 152-178 mm for gill nets) and the fundamental difference in fishing method.



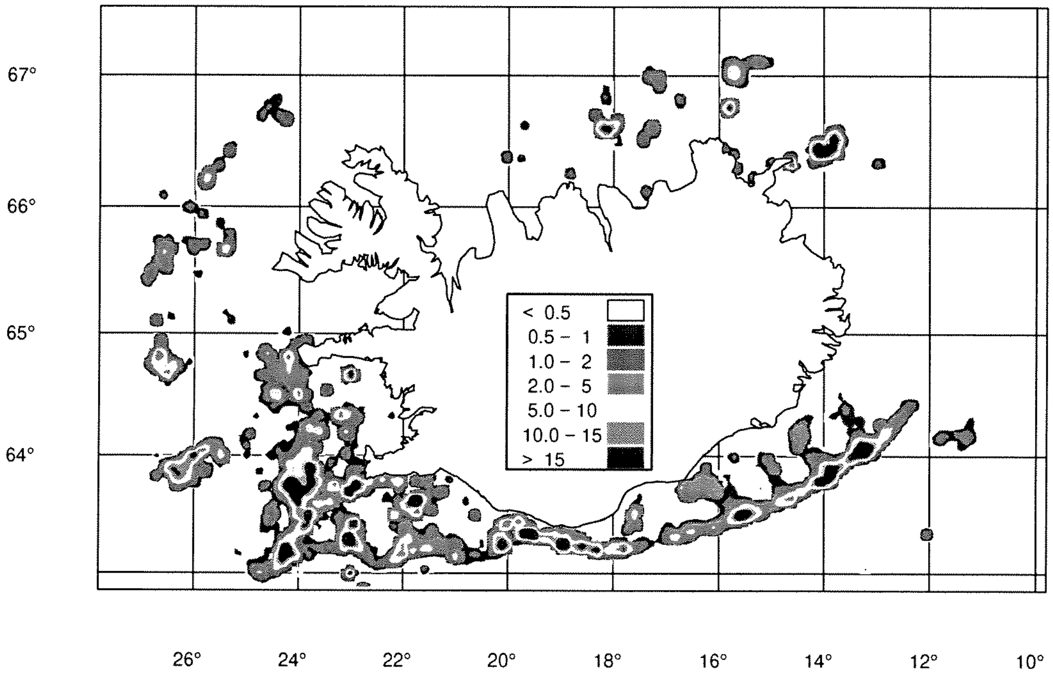
1991



1992

Figure 2. Saithe catches in bottom trawl and gill nets around Iceland in 1990–1994 in tonnes/square mile. Based on records from fishing vessel log-books.

1993



1994

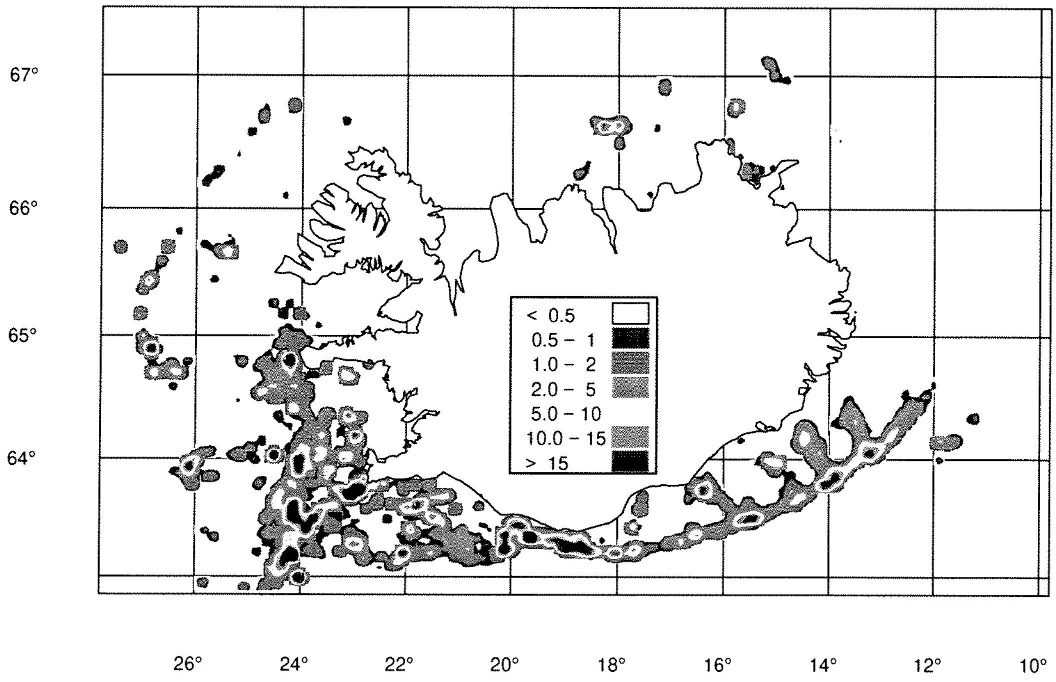


Figure 2 (continued).

A simple study of the catch per unit fishing effort (CPUE) of the Icelandic bottom trawlers reporting saithe, showed pronounced diel variation in the saithe catches throughout the year. The catch rates peaked at night and there was an early afternoon minimum corresponding to 50% of the CPUE at night. This phenomenon merits further study and a more complete analysis should be undertaken, especially of data from trawlers directing their effort at saithe and taking account of trawling depth and geographic location.

As stated earlier, tagging experiments have shown that saithe are highly mobile. As an example, saithe tagged at Iceland have been recaptured at the Faroe Islands and off the coast of Norway (Jones and Jónsson 1971), and Norwegian tags, have regularly shown up in catches taken at Iceland (Jakobsen and Olsen 1987).

Mean lengths of saithe in German trawl catches from the North Sea, calculated on a quarterly basis, show a fairly regular decrease from spring to summer and autumn as the saithe migrates out from the coast (Reinch 1994). No trend was apparent in quarterly mean lengths in saithe samples from Icelandic trawlers since 1980. This is probably a reflection, on the one hand of the schooling nature of the saithe, and on the other of variable fishing effort allocated to saithe by the Icelandic trawlers, depending *i.a.* on their cod quota status. Before making too much of Reinsch's observation, it must be noted that it is possible that outside of the spawning season, the largest saithe are more agile and better capable of avoiding the gear used by commercial trawlers. At a speed of 1.25 ms^{-1} or 2.5 knots, a 50 cm saithe has been shown to endure 30 minutes of swimming. Furthermore, extrapolating from the empirical relationship established for maximum sustained swimming speed, a 70 cm saithe can swim for prolonged periods at 2.5 knots (He and Wardle 1988). This indicates that saithe, 70 cm and larger, could endure swimming for some time at 4 knots, the common towing speed in the commercial fishery.

4. Main results and conclusions from the present investigations

4.1 Food and feeding

At Iceland, capelin was found to be the main constituent of the saithe diet in March 1990-1992. This is probably also true for February and April, *i.e.* the period when capelin are available in large amounts in the main distribution area of saithe, south and west of Iceland. The amount of capelin observed in the saithe stomachs varied in proportion to capelin stock abundance during the study period. Like in the case of capelin, the krill feeding level in summer seemed to be related to krill biomass in the area (Á. Gíslason, MRI, pers.comm.).

Euphausiids seem to be the staple diet of the saithe. The krill dominated in the summer stomach samples and were present in considerable quantities in spring and late autumn. These results conform well with previous studies of saithe feeding in other areas (*e.g.* Du Buit 1991; Bergstad 1991).

Seasonal and interannual variability in the saithe's feeding appeared to be considerable. The data indicate that feeding level is lowest in autumn, while inter-annual variations in spring and summer are large, and mainly a reflection of capelin and krill feeding level, respectively.

Diel variations in stomach fullness indices for capelin and krill in spring suggest nocturnal, or perhaps crepuscular, predatory activity by the saithe. Such variations conform with the general observation that both of these prey categories are more available in the pelagic layers during the hours of darkness than in the daytime.

4.2 Saithe migrations

Tagging experiments have demonstrated that saithe migrations across the NE-Atlantic are commonplace (Jones and Jónsson 1971; Jakobsen and Olsen 1987). Using a modification of the mixture model, for estimating the proportions of the components in a mixture of two distributions (James 1978; Shepherd and Pope 1993), it was estimated that in 1991 some 10-20% of age group 7 saithe at Iceland had immigrated from other areas. An approximation of the variance of the mixture proportion estimate is discussed.

A comparison was made of data used in virtual population analyses of the Icelandic saithe and the literature on saithe taggings. In some of the years, when it has been suggested that large migrations to Iceland have occurred, it was found that cach-at-age from certain year classes peaked later than normal. Thus, the well tagged Norwegian saithe year classes of 1962 and 1964 gave numerous returns from Icelandic waters (Reinsch 1976; Jakobsen and Olsen 1987) and had catch-at-age curves at Iceland similar to that of the 1984 year class.

A comparison of a re-analysis of the only saithe tagging experiment conducted at Iceland with saithe taggings on the eastern side of the Atlantic, does not indicate any difference in saithe traffic east or west across the Norwegian Sea. In other words, on the basis of the available information, emigration from and immigration to the Icelandic area are just as likely.

In view of previous evidence as well as that presented in these studies it would seem that the boundaries, used in the present management of NE-Atlantic saithe stocks, are, at least at times, by no means clear.

4.3 Coupling of the two papers

The feeding study does not lend any obvious support to the migration hypothesis. On the contrary, it seems likely that low capelin biomass in 1990 and the apparently poor feeding conditions in that year could have resulted in retarded growth, thereby casting doubt on the validity of the mixture model results. However, cod at Iceland, which are notorius capelin eaters, do not seem to have suffered any reduction in growth in 1990 and 1991 (Anon. 1995).

A necessary prerequisite for the application of the mixture model for estimating migrations is an approximate size distribution for the resident fish. In this study that variable had to be roughly estimated by ANOVA methods. This approximation could be improved by growth modelling, where one key component naturally is the abundance of the main prey groups. The present feeding study indicates that capelin and krill should be included in a growth model for the Icelandic saithe, at least for age groups 3 and older.

Due to low number of stations and different vessels used, the material collected in the summer and autumn stomach sampling surveys was much less complete than the spring material. This, together with the semi-pelagic behavior of saithe, makes it difficult to draw any firm conclusions from the feeding study in support of a migration hypothesis. However, the summer diet was dominated by euphausiids, with a significant contribution of both mesopelagic fish and blue whiting. A common characteristic of all these prey species is their wide distribution throughout the N-Atlantic. Low saithe occurrence in the samples taken on the Icelandic shelf in summer could be a reflection of the saithe's foraging expeditions off the shelf, *e.g.* in pursuit of blue whiting. Such a feeding strategy would be comparable to that of the Atlantic salmon.

5. Future research

5.1 Recruitment studies

Although outside of the main scope of these studies, it is clear that further recruitment studies of saithe are called for. For the North Sea saithe, a recruitment index is established from the IBTS and used in stock assesments. In all other VPA assessments of saithe in the NE-Atlantic an average recruitment is assumed. At Iceland, no studies of juvenile saithe have been attempted, with the exception of their ecological position in the kelp forest (E. Hjörleifsson, MRI, unpubl. mat.).

A survey of the distribution of postlarvae off the coasts of Norway was conducted in the period 1985-1992. The predictive value of the results was found to be low, and the programme is under reconsideration (Nedreaas and Smedstad 1995). In light of the coastal distribution of juvenile saithe, it seems reasonable to attempt some sort of monitoring of the strength of incoming saithe year classes while still in the nearshore habitat. In Norway, the development of a recruitment monitoring programme for predicting the development of the adult stock is still at the experimental stage (Aglen 1995; Smedstad 1995). At Iceland, a simple first step could be to single out some key locations, and study the development of a few successive year classes, using different sampling methods.

5.2 Incorporating the saithe into multispecies models

The comparison of the biomass of saithe and cod in ICES statistical areas I-VI makes one thing clear. Assuming similar energetic demands, as ecosystem components the two species are, at present, on an almost equal footing except in the Barents Sea. The distribution and predatory behaviour of cod is such that they are probably more serious competitors to man for commercially utilized species, *e.g.* cod, redfish, capelin and northern shrimp. However, saithe at Iceland are obviously important predators on capelin in winter and spring. Consequently, they compete for that resource with cod and man and must be taken account of. Although saithe prey on euphausiids for most of the year, also when feeding heavily on capelin, the state of knowledge of euphausiid distribution and abundance at Iceland must be improved to allow further speculation. It has been suggested that saithe, along with other zooplanktivorous fish, could exert a controlling effect on euphausiid populations in the North Sea area (Bergstad 1991a)

5.3 Monitoring saithe migrations

In light of the indications of saithe migrations, it seems reasonable ask for more frequent sampling, although the samples need not necessarily be as large as those presently collected from the saithe landings. It has been shown that such a sampling strategy can improve precision of survey abundance estimates, the estimation of biological parameters of fish being surveyed (Pennington and Vølstad 1991, 1994; Bogstad *et al.* 1995) and also improve the estimation of age and length stucture of fish populations from trawl catches (Horppila and Peltonen 1992).

In attempting to estimate the size of a saithe migration, a more direct approach than that possible with a joint VPA and related methods, should be taken. It seem reasonable to ask for better tagging evidence, especially with respect to a possible emigration from Iceland. Morphological and genetic characters should be studied in order to determine whether such characters can testify to the origin of a saithe.

Fish otoliths and scales have been used to differentiate stock units of marine species (*e.g.* Easey 1978; Rätz 1990; de Barros and Holst 1996). No observations have been made of different types of otoliths in Icelandic saithe samples since the suspected immigration in

1991 (Þ. Viðarsson, MRI, pers. comm.), but it is possible that differences unnoticed by the a human age reader might be detected by modern image analysis systems applied to fish age determination. Observations of otolith type differences between saithe stocks that might merit further study have been made (Olsen 1959). Methods and systems for this type of image analysis are under development but have not yet reached the stage of routine application (*e.g.* Troadec 1991).

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PAPER I

FOOD AND FEEDING OF SAITHE (*Pollachius virens*) AT ICELAND

ABSTRACT

The diet of saithe at Iceland, as observed from stomachs collected in sampling programmes in early spring, summer and late autumn 1990-1992, is described. Euphausiids and fish prey, mostly capelin in spring, dominated the diet. Of the prey groups encountered, shrimps and the larger fish prey occurred more frequently in the stomach contents of the larger saithe. The size of capelin and euphausiid prey did not show a general increase with predator size. However, due to differences in overlap between components of the capelin and saithe populations, only the smaller saithe preyed on the smallest capelin. Data on the two most abundant prey groups in spring, *i.e.* capelin and euphausiids, showed signs of crepuscular peaks in the feeding activity of saithe. Saithe and cod appear to be about equal in their ability to prey on capelin. The monthly consumption of capelin by the saithe stock at Iceland in spring 1992 is estimated at 100 thousand tonnes.

1. Introduction

In the arcto-boreal ecosystems of the North Atlantic the saithe (*Pollachius virens*) is one of the most abundant of the piscivorous predatious fish and an important fisheries resource (*e.g.* Reinsch 1976; Bergstad *et al.* 1987; Anon 1995, 1995a, 1996, 1996a). Nevertheless, saithe of commercial size (age 3+) has not been given the attention it deserves in the considerable work on multi-species interactions carried out since the 1980s. This is probably to some extent due to the lesser commercial value of saithe relative to the cod (*Gadus morhua*) but for the most part because of various sampling problems, mainly connected to variable behaviour, catchability and migrations of the saithe (*e.g.* Gislason 1983; Pálsson *et al.* 1989, Grástein 1992, Anon 1995a).

The saithe has been described as a voracious predator (Du Buit 1991) and is, due to its active behaviour, likely to have a higher metabolic rate and require a higher daily food ration than an equally sized cod. However, the opposite has also been suggested, *i.e.* that saithe may have a lower daily ration than cod (Gislason and Helgason 1985). The number of published reports on the food and feeding of adult saithe is limited (Wagner 1959; Gislason 1983; Pálsson 1983; Sunnanå 1984; Bergstad 1991; Du Buit 1991; Daan 1991).

The present study was carried out as part of the Icelandic multi-species project (IMSP). The main purpose of the IMSP is to increase present knowledge of marine biology and ecology of the Icelandic shelf ecosystem in order to improve management of living resources in these waters (Stefánsson and Pálsson 1995). For fishery-economic reasons, the analyses of interactions between cod and capelin have been given top priority (*e.g.* Stefánsson *et al.* 1994) followed by the predation of cod on the valuable northern shrimp (*Pandalus borealis*) (Stefánsson *et al.* 1994a). However, the IMSP has also provided the material for several single-species diet studies carried out by university students (Sólmundsson 1994; Valtýsson 1995; Óskarsson 1996).

The most comprehensive data collection for diet studies of demersal fish, including saithe, was carried out in 1992. Prior to this, considerable sampling effort had been devoted to saithe in 1990 and 1991. The present study is based on these data.

In recent years, much effort has been devoted to studying the cod-capelin interaction in the Arcto-Boreal ecosystems of the North Atlantic (Mehl 1989; Magnússon and Pálsson 1989, 1991; Lilly 1991, 1994; Bogstad and Gjøsæter 1994). The saithe-capelin relationship is only seldom mentioned because of limited resources and the sampling problems mentioned above. However, it is likely that the saithe are important predators of capelin at Iceland and that this importance might be out of proportion to the relative stock sizes of saithe and cod. Two points in support of this view are:

i. The saithe is a fast swimmer, known to traverse great distances, and must therefore have high energy demands.

ii. The saithe spawns earlier than the cod. For that reason, most of the saithe can devote themselves to capelin as forage, when the capelin spawning migrations reach the southwestern part of the Icelandic shelf. At this time, spawning of the cod is much less advanced (Marteinsdóttir and Pétursdóttir 1995) and they are, therefore, to a larger extent otherwise preoccupied.

Saithe and cod generally have different distribution patterns, the saithe occupying somewhat warmer waters (*e.g.* Bergstad *et al.* 1987). At Iceland, the cod are more widely distributed to the north and east than the saithe, especially the juvenile cod (Pálsson *et al.* 1993). This leads to different overlap of cod and saithe with the capelin. The cod is more closely associated with the immature and maturing capelin over the outer part and the edge of the shelf north of Iceland, while the saithe tend to occupy the Atlantic waters south and west of Iceland and will, therefore, mainly have access to adult capelin in winter and spring.

This study has the primary objective of documenting the diet of the saithe at Iceland as observed by the analysis of stomach contents collected in surveys in 1990-1992. In addition, descriptive analyses of some aspects of the saithe's feeding will be undertaken.

The spatial distribution of the most important prey groups will be shown and interannual and seasonal variations in feeding level explored. Variations in frequency of occurrence and average stomach contents of selected prey are analysed with respect to predator size and compared to previously described size dependencies in saithe predation. An analysis of diel variations in the saithe's feeding is attempted. Prey size distributions for capelin and the krill, *Meganyctiphanes norvegica*, the two most important prey species, are explored. Finally, a comparison is made of cod and saithe as predators on capelin. A null hypothesis of no difference between the two species is tested.

2. Material and methods

2.1. Sampling

Saithe stomachs were collected from bottom trawl catches taken in early spring, summer and late autumn in 1990-1992. Commercial trawlers were chartered for carrying out the Icelandic groundfish survey (IGFS) in spring. The summer and autumn surveys were conducted with research vessels of the Icelandic Marine Research Institute (MRI) using fishing gear similar to that used in the IGFS.

Table 2.1 gives an overview of the timing of the surveys and the type of vessel used. Figures 2.1-2.3 show the grid of stations by season for the years under study. The fishing gear used in the surveys was usually the standard gear of the IGFS surveys, a trawl with a heavy groundrope, vertical opening of 2-3 metres and a codend lined with a fine meshed (40 mm) net (Pálsson *et al.* 1989). Sampling was carried out around the clock on most trips. An exception was the smaller r/v Dröfn, which used a trawl of smaller dimensions and was operated only during the daytime. The standard tow length was fixed at either 3 or 4 nautical miles, depending on the survey.

Table 2.1 Survey times and vessels

Season	Survey vessels	Period
Spring 1990	F/v Arnar, Bjartur, Ljósafell, Rauðinúpur, Vestmannaey	March 5 - 21
Summer 1990	R/v Dröfn	July 6 - 16
Autumn 1990	R/v Dröfn	November 6 - 18
Spring 1991	F/v Arnar, Bjartur, Hoffell, Rauðinúpur, Vestmannaey	March 5 - 23
Summer 1991	R/v Dröfn	June 14 - 25
Autumn 1991	R/v Dröfn	November 5 - 20
Spring 1992	F/v Arnar, Bjartur, Ljósafell, Rauðinúpur, Vestmannaey	March 4 - 18
Summer 1992	R/v Bjarni Sæmundsson	July 10 - 29
Autumn 1992	R/v Árni Friðriksson and Bjarni Sæmundsson	November 12 - December 2

Trawl stations in March were more or less the same as those set out prior to the beginning of the IGFS in its present form in 1985. The survey area, the Icelandic shelf within the 500 m isobath, was divided into strata according to catch-by-area statistics for cod. The sampling intensity in each stratum was set in proportion to a calculated catch index. Stations were allocated to strata in two ways. One half was chosen by skippers who took part in the organisation of the first co-ordinated bottom trawl survey in 1985 and the other half was picked at random by computer. In this way the position of about 600 trawl stations was fixed, thus making the 1985 survey semi-random stratified. In subsequent surveys, however, the same stations have been revisited, with changes only to allow for adverse bottom conditions. From 1986 onwards these surveys can, therefore, be described as systematic stratified (Pálsson *et al.* 1989).

In summer and autumn, special surveys have been undertaken with the main purpose of studying stomach contents of cod and other demersal fish for comparison with data from spring. The stations occupied during these surveys were a subset of the IGFS stations.

In the bottom trawl surveys, stomachs were collected in addition to the primary tasks of length measuring, weighing and sampling the fish for otoliths. The stomach sampling was length stratified, *i.e.* on a given station a maximum of 5 stomachs was collected from each of a number of predefined length groups (for saithe 15-19, 20-24, 25-29, 30-39, ... , 90-99, 100-119 and larger than 120 cm). The sampling length intervals were coded, according to MRI procedures as given in the text table below:

Length group	4	5	6	7	8	9	10	11	12	13	14	15
Interval (cm)	15-19	20-24	25-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-119	>= 120

The codes for the various length groups are used in some of the figures presented later in this study.

There was a limit of two samples from a length group in any one statistical square, but only one sample was taken if more than half of the square fell outside of the study area, *i.e.* on land or outside the 500 m isobath. The dimensions of a statistical square are 0.5° latitude by 1° longitude, or approximately 30 by 25 nautical miles in this area. The limit of two samples per square applied to the collection in the spring of 1992 but the sampling intensity was lower in spring 1990 and 1991. When a new square was entered the personnel usually started to sample predators according to length group as they occurred, *i.e.* sampling was systematic with regard to stations where stomachs were collected. This strategy applied to all the major predator species being collected, their number being variable and greatest in 1992, when the MRI conducted an extensive stomach sampling program in Icelandic waters and virtually all fish caught were candidates for stomach collection. The scattered distribution of saithe in summer and autumn necessitated the collection of stomachs at all stations where saithe were caught.

While the length of the fish from each haul was being measured, they were sorted into length groups for stomach sampling, up to a maximum of 5 fish in each length group, *i.e.* stomach sampling at a station was systematic. The fish sampled for stomach contents were first examined for signs of regurgitation, gutted and their stomachs removed. If empty stomachs occurred their number was recorded and in the case of regurgitation a new individual was selected. Stomachs containing food were emptied into a sieve of 1 mm mesh size and the contents rinsed in seawater. The stomach contents from all fish in the same length group were pooled and safely placed in the same container (bulked sample). Due to the heavy work load during the surveys, it was sometimes not possible to rinse the digestive juices from the stomach contents and the stomachs had to be emptied directly into a container. When safely contained in a suitably sized plastic cup or bucket, the stomach contents were immersed in 7:3 mixture of isopropyl alchohol (2-propyl alchohol) and seawater for fixation and conservation. The working rule was to use a volume of isopropyl alchohol equal to or greater than that of the stomach contents to be fixed.

Table 2.2 gives the number of stations, on which saithe stomachs were collected, the number of samples and the number of saithe sampled by year and season.

Table 2.2. The collection of saithe stomachs

		Number of stations	Number of samples	Total number of stomachs	Percent empty
1990	Spring	75	169	405	24.9
	Summer	20	43	146	37.0
	Autumn	12	21	40	35.0
1991	Spring	66	112	278	23.7
	Summer	14	47	174	22.4
	Autumn	16	34	76	47.4
1992	Spring	148	299	736	23.8
	Summer	44	81	177	11.3
	Autumn	46	183	183	27.9
All years and seasons		441	989	2215	25.1

Figure 2.4 shows the size distribution of saithe sampled for stomach contents by length group for each year and season included in this study.

2.2. Laboratory analysis

In the laboratory, stomach contents were poured into the same type of sieve as used at sea and rinsed under running tap water in order to reduce noxious vapours. After excess water had dripped off, the material was transferred to blotting paper.

The contents were then analysed according to the following guidelines:

i. Fish and shrimp prey were determined to the lowest possible taxon while it was permitted to lump other prey items into higher categories, *e.g.* Euphausiacea, Hyperiidea, Gammaridea, Anthozoa, Porifera, Cephalopoda.

ii. Three stages of digestion were identified:

0 - prey were little affected by the digestive process
1 - prey semi-digested but relatively easily identified
2 - prey almost completely digested, *e. g.* only the vertebral columns of fish or the eyes of euphausiids remaining.

iii. The blotted wet weight of all prey categories in each digestive stage was measured to the nearest decigram on a Mettler microscale.

iv. The number of prey in each category was counted when possible. When in doubt, the lowest number of prey that could have given rise to the observed number body parts, *e.g.* vertebral columns, eyes, mandibles or other appendages, was recorded. To determine the number of abundant small prey it was often necessary to resort to subsampling.

v. Prey were length measured when their condition allowed and if they had been identified to species.

The main references used in the naming of the prey items were Jónsson (1992) for the fish prey, Härkönen (1986) when otoliths were examined, and Enckell (1980) for the crustaceans. In adddition, various compendia and standard textbooks were referred to, as supplementary information, for identifying other prey and in the ordering of the higher invertabrate taxa (*e.g.* Squires 1990, Pethon 1989, Barnes 1980). For definition of prey subsets used in subsequent analyses, see section 2.3.2.

The author took part in the summer survey of 1992 and was responsible for the analysis of the material collected in spring and summer 1992. Other material was analysed by biologists at the MRI.

2.3. Data analysis

2.3.1. Data manipulation

The records of saithe stomach contents in 1992 were entered into a spreadsheet by the author, initally with one record for each digestive state of every food category occuring in a given sample. The 1990 and 1991 data were provided by the MRI in text file format, with one record for the occurrence of each food category. Digestive status was not recorded in these two years and this information was, therefore, omitted from the 1992 data when compiling the common dataset. Information on catch, position, depth, temperature, time and duration of the trawl hauls for all stations where saithe were caught was compiled in a separate file.

The data analyses in this study were carried out in the S+ environment for statistical and graphical analysis and in the Excel spreadsheet. The distribution of stations in each survey and an index of stomach fullness were plotted using plotting utilities developed at the MRI as an integated part of the S+ software.

Information on digestive status was used in an analysis of diel variability and prey size distributions were examined based on data from the 1992 surveys (cf. Sections 3.5 and 3.6). These two datasets were compiled separately. Data on the predation by cod on capelin was extracted from the fish food data base at the MRI (cf. Section 3.7).

2.3.2. Definition of prey subsets

After a first inspection of the feeding data 15 subsets or groups of prey were defined (cf. Tables 3.1 and 3.3). Taxa closely related or occupying similar habitats were pooled. These categories were ordered by their weight in the total stomach content analysed and their contribution to the diet, both in weight and number of prey items, was studied. On occasion these categories were lumped into 4 main groups, *i.e.* capelin, krill, fish other than capelin and invertebrates other than krill. The last of these also includes unidentifiable material, or indeterminatus.

2.3.3. A convention for establishing predator numbers

Because samples consisted of the bulked contents from up to 5 stomachs, the number of predators on a given prey in a sample could not be determined with certainty, an exception being when prey items occured singly or when a sample consisted of only one stomach. Bogstad *et al.* (1994) derive the probability of occurrence on an individual predator basis from the observed frequency of occurrence in bulked samples and applied the results in their study of cannibalism among Atlantic cod.

However, in this study the simpler procedure of showing a range of possible values for the frequency of occurrence by predator size and time of day graphically was followed (cf. Sections 3.4 and 3.5). In the study of feeding levels (cf. Sections 3.3 and 3.6), prey were assumed to be equally diveded among the predators in a bulked sample, since in these analyses abundant prey groups are the most interesting. In other words, it was assumed in the feeding level analysis, that due to intra-haul correlation (Bogstad *et al.* 1995), the alternative of equal distribution of prey among predators was more fitting. The other extreme might be more appropriate in a study of rarely occurring prey.

2.3.4. The partial fullness index

As a descriptor of aspects of the feeding of saithe, the average partial fullness index (PFI) was chosen (Lilly 1991, 1994; Pedersen and Riget 1993, Fahrig *et al.* 1993, Bogstad *et al.* 1994). This index is nothing more than an attempt at standardizing the stomach contents with length. The PFI was calculated on a station basis, *i.e.* for each station where a prey category occurred (cf. Sections 3.2 and 3.3). The PFI was calculated according to the formula:

$$\mathrm{PFI}_i = \frac{1}{n}\sum_{j=1}^{J}\frac{w_{ij}}{L_j^3} * 10^4 \qquad (2.1)$$

where i denotes prey category; n the number of saithe in a cell; J the number of samples in the cell; w_{ij} is the weight of prey category i in sample j; and L_j is the midpoint of the length interval from which sample j derived. The midpoint was chosen to avoid having to calculate mean lengths of the fish in each length category for every sample. For the same reason, standardized stomach contents were not weighted with total numbers in each length category in the catch, the procedure chosen by Lilly (1994).

The PFIs could also be calculated according to the number of predators on a given prey category, either the maximum possible number or the minimum number as determined by the combination of prey and predator numbers in the samples. This was done for the maximum numbers alternative, *i.e.* equal distribution of prey among predators in a sample, when studying diel variations (cf. Section 3.5).

2.3.5. A note on log-transformations and back-transformed confidence limits

The distributions of stomach contents are characterized by large positive skewness (Magnússon 1993, Fahrig *et al.* 1994). This makes it necessary to transform data before applying linear models or making confidence statements about mean contents, when the number of observations is limited. In the present study these characteristics were dealt with as follows:

> The logarithmic transformation was applied to stomach content data prior to investigating capelin contents in spring using the linear model of Section 2.3.6 and also on capelin, krill and other fish contents before calculating confidence intervals by length group. The logarithm of stomach contents is assumed to be normally distributed and confidence intervals were based on the t-distribution. Back-transformed confidence intervals have the advantage over confidence intervals based directly on the t-distribution, which would be appropriate for normally distributed observations, since they will not give unrealistic negative lower limits (Zar 1984, Krebs 1989).

2.3.6. Interannual and seasonal variations in feeding level

To obtain an overview of general trends in the feeding intensity of saithe, average stomach contents of the four main groups of prey were calculated based on the total number of saithe sampled each season.

For comparison, mean PFIs in March 1990-1992 were established for the capelin, but pooled over years on a seasonal basis for krill and fish prey other than capelin. For these means, approximate 90% confidence limits were established. The number of PFI observations for these prey groups were sufficient for assuming mean PFIs to be normally distributed. This assumption was preferred to log-transforming the PFI data since exploraratory transformations did not appear to reduce skewness down to normality.

2.3.7. Diet differences according to predator size

The possible range of frequency of occurrence (FO), *i.e.* the number of stomachs containing a given prey category, was determined for selected prey groups. The number of fish sampled for stomach contents was tallied by length group for the set of stations on which the prey in question occurred. This restriction was applied in order to avoid artifacts arising from different predator length distributions, within and without the distribution area of a prey group. Thus, for prey *i*, three numbers for each length group were calculated: N, the total number sampled; P, the maximum number that could possibly have preyed on *i* ; and p, the lowest possible number of predators on *i*. From these numbers, the range in which the percent frequency of occurrence must have lain, was found, *i.e.:*

$$FO \in \left[100 * \frac{p}{N}, 100 * \frac{P}{N}\right] \qquad (2.2)$$

Log-transformed capelin contents in spring were modelled by length group midpoint and year to investigate whether there was a significant year effect in the saithe's predation on capelin, after predator size had been accounted for. Variants of the following model were compared:

$$y_{ij} = \mu_i + \beta_i x_{ij} + \varepsilon_{ij} \qquad (2.3)$$

where y is log capelin content, x is the midpoint of a sampling interval in cm, i denotes year and j length group. The year effect is denoted by μ and the increase in content with size by β, *i.e.* the intercept and slope in the regression. Errors, denoted by ε, are assumed normally distributed and the same for all years and length groups. By omitting subscripts and/or parameters from (2.3) log capelin contents can be described in various ways, *i.e.* by the trivial model, mean of y; a simple one way ANOVA with year effects; a simple regression by predator size; or by parallel or separate regressions by predator size for each year.

2.3.8. Prey size distributions

The length distributions of capelin and *Meganyctiphanes norvegica* prey were studied. The prey length observations were compiled by predator length group and further pooled into three predator size categories for each prey. These categories consisted of the length groups that were most balanced with respect to numbers of prey length observations and are given in the following text table:

	Small	Medium	Large
Capelin predators	Length groups 6, 7, 8, 9 and 10 (<= 69)	Length groups 11 and 12 (70-89 cm)	Length groups 13, 14 and 15 (>= 90 cm)
M. norvegica predators	Length groups 7, 8 and 9 (<= 59 cm)	Length group 10 (60-69 cm)	Length groups 12, 13 and 14 (>= 80 cm)

2.3.9 . Diel variations

Variations in partial fullness indices for the two main prey categories, *i.e.* krill and capelin, by station and time interval were studied. A station was allotted to the time interval in which the haul was half complete. The 12 time intervals were midnight to 2 AM, 2 AM to 4 AM, ... , 22 PM to 24 PM. In this analysis, only the spring season was considered. Data from the summer and autumn surveys were inadequate since the survey vessel was not operated at night in 1990 and 1991.

The frequency of occurrence (FO) of these two prey groups in the spring period was also studied, in a manner similar to that applied to FO by size. However, instead of summing by length group, numbers were tallied according to time interval as described above.

Observations of the digestive stage of capelin and *M. norvegica* from the 1992 collections were averaged for the time intervals used in the two previous studies and compared to the observations of FO and PFI through the course of the day. For the capelin, only two stages of digestion were recognized, *i.e.* relatively fresh or heavily digested, coded as 1 and 2, while for krill stages 0, 1 and 2 were used. As the contents belonging to these two prey species in a sample were often at different stages of digestion, a weighted average was used.

2.3.10. Comparison of cod and saithe capelin PFIs

For the purpose of comparing the amounts of capelin in saithe and cod stomachs the Wilcoxon rank sum and signed ranks tests were applied to observations of average PFIs and stomach fullness. Non-parametric tests were chosen since the distributions of the PFIs and average contents are poorly known and definitely non-normal.

Prior to the comparison of the two species, the PFI distributions for each, at the stations where the two species co-occurred and where they occurred singly, were put to the Wilcoxon rank sum test.

The null hypothesis of no difference in capelin stomach fullness for the two species was tested by applying the Wilcoxon signed ranks test to two different sets of data:

i. Paired observations of cod and saithe $\text{PFI}_{\text{capelin}}$ were compared for those stations where both species had taken capelin.

ii. The average capelin stomach contents of cod and saithe were compared in samples where both station and length group matched for the two species.

2.3.11 . A model of capelin consumption

A month's consumption of capelin by saithe in an area of overlap between these species in the western part of the Icelandic shelf area in spring 1992 was estimated. The area division is shown in Figure 2.5 and is the same as that defined in the boreal migration and consumption model (BORMICON) for Icelandic waters (Stefánsson and Pálsson 1995). The highest incidence of capelin in the saithe stomachs was recorded in areas 1, 2 and 10. The following model was used:

$$C = 30 * \sum_{a} \sum_{l} p_{al} N_a c_l \tag{2.3}$$

Monthly capelin consumption is denoted by C. The summations represent daily consumption. Age group is denoted by a and l is here used to represent length group as defined in section 2.1. The proportion of an age group belonging to a sampling length group is denoted by $p_{al,}$ numbers in an age group by Na and the daily ration for a saithe in a length group is denoted by c_l.

The model was run with the following datasets and assumptions:

i. Stock-numbers-at-age on March 1 were found by adjusting current estimates of stock numbers on January 1 1992 for the average fishing mortality for age groups 4-9 and a natural mortality of 0.2, *i.e.* the numbers were reduced by 8% (Anon. 1995)

ii. On the basis of numbers of saithe caught in the 1992 IGFS survey, within as well as outside BORMICON areas 1, 2 and 10, it was assumed that 70% of the saithe stock overlapped with the capelin. This simple approach was adopted in preference to weighting length distributions on stations with numbers caught and establishing separate age-length keys for the two areas in order to estimate the proportions of each age group in the overlap area.

Estimates of N_a were derived using data and assumptions listed in i. and ii. above.

iii. The proportion of an age group belonging to the sampling length groups used in this study were estimated by establishing an age-length group key for BORMICON areas 1, 2 and 10.

iii. For simplification, along the lines described for the estimation of capelin consumption by cod in the Barents Sea (Bogstad and Gjøsæter 1994), 100% overlap between saithe and capelin for a period of one month was assumed.

iv. A uniform temperature of 5.6°C was assumed for the area, based on the average bottom temperature reported from the IGFS.

v. The average capelin content in BORMICON areas 1, 2 and 10 were estimated from data collected in the 1992 IGFS survey.

vi. Daily consumption by saithe belonging to length group l, c_l, was estimated using the following formula, which is based on a simple gastric evacuation model (*e.g.* Pennington 1985; Bogstad and Mehl 1990):

$$c_l = 24ES_l \tag{2.4}$$

where S_l are the average capelin contents for length group l and E is rate of evacuation. For a temperature of 5.6°C, a value of 0.05 h^{-1} for for E is reasonable (Bogstad and Mehl 1990), based on digestion experiments on cod (dos Santos and Jobling 1992).

The rationale behind this simple formula is described by Pennington (1985). It is derived by assuming that stomach contents diminish exponentially and it is assumed what is consumed must equal what the stomach evacuates. The concept has been elaborated by later authors (*e.g.* dos Santos and Jobling 1992, 1995; Bogstad and Gjøsæter 1994) by introducing a shape parameter accounting for, on the one hand, initially delayed digestion or, on the other, rapid inital digestion (a power exponential model), and by accounting for the effects of meal size and sequantial feeding. The simpler model used here was chosen mostly because of its conceptual simplicity. It has the further advantage that it does not require correcting average contents for the effects of bulk size (*e.g.* Magnúson and Pálsson 1989, Bogstad and Mehl 1990). Furthermore, digestion experiments on saithe seem to be few and far between (Gislason 1983).

3. Results

3.1. Geographical distribution of PFIs for prey groups

For describing spatial aspects of saithe feeding it seems natural to regard the saithe sampled at a station as a random sample from the saithe population in the area. Consequently, partial fullness indices at a station should reflect feeding levels in that part of the study area. The average partial fullness indices on a station basis for selected prey groups are shown for all observations in Figure 3.1. Figures 3.2-3.10 show how the observations for each of nine prey groups were distributed over years and seasons.

In all of the spring surveys, predation by saithe on **capelin** was concentrated in the waters southwest and west of Iceland (Fig. 3.2). In addition, scattered records were obtained on stations off the east coast. In comparison, the summer and autumn occurrence of capelin was minor.

In spring, **euphausiids** occurred most frequently in the saithe diet west and southwest of Iceland and off the southeast coast (Fig. 3.3). The apparent variability in the occurrence of euphausiids in the saithe stomachs in summer is an artifact caused by insufficient sampling in the area west of Iceland in 1990 and 1991. However, it is clear that the saithe must consume sustantial amounts of euphausiids in the warm water area on and near the shelf break south and southwest of Iceland.

Most of the **gadid prey** derived from samples collected in the southern area (Figs 3.1 and 3.4). In spring, Norway pout were the main gadid prey, occurring mainly in the western part of the area. On the other hand, blue whiting were the dominant gadid in the summer diet and 0-group haddock occurred on a number of stations off the central south coast in 1990.

The **mesopelagic group**, to which the blue whiting should perhaps belong, occurred irregularly in the saithe stomachs and were totally absent in autumn 1990 and spring 1991. In other seasons they were a substatial part of the diet of saithe taken at the shelf break in the warm waters to the south (Fig 3.5). The paralepids and myctophids, to which most of this material belonged, were found in saithe stomach samples of similar geographic distribution, but the myctophids were more widespread and occurred somewhat more frequently.

Sandeels occurred mainly in the stomachs of saithe caught in shallow waters off the eastern south coast and Faxaflói (Figs. 3.1 and 3.6). High concentrations of sandeels are often observed in these areas which were the main site of sandeel fishing experiments, conducted in the 1970s (Friðgeirsson 1983).

Figures 3.7-3.10 show the PFI distribution of prey groups of minor importance by volume (< 1% each). Most of the **squid** occurred in three sampling seasons, *i.e.* spring 1991 and 1992 and summer 1992 (Fig. 3.7). The **Natantia** group, or shrimps, were by far most prominent west of Iceland in spring 1992 (Fig 3.8). Pandalids, constituting more than half of the shrimp prey, occurred most widely, while two other important shrimp species, *Sergestes arcticus* and *Pasiphaea multidentata*, were mainly found in deeper waters. **Hyperiid amphipods** occurred, practically without exception, in samples containing krill. As can be seen by comparing Figures 3.3 and 3.9, the amphipods were, in fact, recorded on a substantial part of the krill stations. **Benthic organisms** were observed sporadically in the saithe stomachs (Fig 3.10). Although benthos may be part of the natural diet of the saithe, it is also possible that these organisms were ingested as "by-catch" in the saithe's foraging for other, more rewarding, prey.

A study of the depth distribution of stations where the two main prey groups occurred confirmed the visual impression from the capelin and euphausiid parts of Figure 3.1. Thus, capelin occurred on stations which were significantly shallower than those where euphausiids were found (t-test, $p<<0.05$). This conforms with the observed winter distribution of capelin and general distribution of krill south and west of Iceland (Vilhjálmsson 1994; Einarsson 1945; Á. Gíslason, MRI, pers.comm.). Saithe at the capelin stations were found to be slightly larger than at stations where krill was found in the saithe stomachs. Furthermore, benthic prey occurred mainly in relatively shallow waters and most of the mesopelagic fish prey at the shelf break in the warm waters south of Iceland.

3.2. Composition of the stomach contents

After a first inspection of the feeding data meaningful sets of prey were defined. Closely related taxa, or those occupying similar habitats, were pooled. The contribution of each of these subsets to the total stomach contents was calculated and the groups ordered accordingly, *i.e.* the total weight of contents from a prey category is taken as a rough indicator of importance in the diet of the saithe. The contribution in numbers of prey individuals was also calculated. The results are given in Table 3.1. The overwhelming contribution of capelin and euphausiids to the saithe diet is clear. Of secondary

Table 3.1. The importance of prey groups as percentage by weight and number of the total stomach contents for 15 groupings ordered by weight both among and within groups

Prey group	W %	N % (rank)	Consists of prey species and higher taxa (in some cases convenience taxa)
Capelin	55.2	6.54 (3)	*Mallotus villosus*
Euphausiids	27.1	68.1 (1)	*Meganyctiphanes norvegica*, *Thysanoessa inermis*, Euphausiacea, *T. raschii* and *T. longicaudata*
Gadid fish	4.12	0.16 (12)	*Micromesistius poutassou*, *Trisopterus esmarki, Melanogrammus aeglefinus, Merlangius merlangus*, Gadidae and *Gadus morhua*
Mesopelgic fish	3.16	1.31 (6)	Paralepididae, Myctophidae, *Maurolicus mülleri*, Argentinidae, *Chauliodus sloani* and Serrivomeridae
Unidentified fish	3.01	3.00 (4)	Pisces
Sandeels	2.67	0.86 (7)	Ammodytidae
Other fish	1.66	0.05 (14)	*Sebastes* sp., *Clupea harengus*, *Hippoglossoides platessoides*, *Helicolenus dactylopterus, Anarhichas lupus,* and *Lophius piscatorius*
Squid	0.92	0.17 (11)	*Gonatus* sp. and Cephalopoda
Shrimps	0.87	0.42 (8)	*Pandalus boralis, Sergestes arcticus, Pasiphaea multidentata*, Natantia, *Pandalus montagui*, Crangonidae and Hippolytidae
Hyperiid amphipods	0.53	17.2 (2)	Hyperiidea
Unidentified crustaceans	0.45	0.28 (10)	Crustacea
Other crustaceans	0.11	1.49 (5)	Mysidacea, Copepoda, Gammaridea, Isopoda, decapod larvae and Pagurus pubescens
Indeterminatus	0.10	0.03 (15)	
Various benthic organisms	0.07	0.30 (9)	Brachiopoda, Porifera, Mollusca, Polychaeta, Echinodermata, Ascidiacea, Pycnogonida, Hydrozoa Anthozoa, Algae, Bryozoa and unspecified benthos
Planktonic organisms	0.01	0.07 (13)	Ctenophora, Chaetognatha and Pteropoda

Table 3.2 Prey groups and taxa ordered by weight. Weights less than 0.5 g indicated with a +. Percentages given are of the total for each of the three main prey categories. Numbers in parantheses for categories which were often not countable, number of individual prey also meaningless for some categories. W: Weight of prey taxon; N: Number of individuals belonging to prey taxon; FO: Frequency of occurrence of prey taxon by sample.

Prey category	W (g)	%W	N	%N	FO
Fish prey					
Mallotus villosus	35 436	79.1	8 655	54.8	311
Unidentified Pisces	1 930	4.3	3 974	25.2	125
Ammodytidae	1 716	3.8	1 143	7.2	41
Micromesistius poutassou	1 554	3.5	46	0.3	19
Paralepididae	1 032	2.3	55	0.3	20
Myctophidae	854	1.9	1 512	9.6	25
Sebastes sp.	712	1.6	19	0.1	17
Trisopterus esmarki	656	1.5	29	0.2	12
Melanogrammus aeglefinus	363	0.8	134	0.8	8
Clupea harengus	316	0.7	36	0.2	5
Maurolicus mülleri	99	0.2	158	1.0	11
Merlangius merlangus	50	0.1	1	+	1
Argentinidae	37	0.1	8	0.1	4
Hippoglossoides platessoides	29	0.1	4	+	4
Unspecified Gadidae	22	0.1	5	+	5
Chauliodus sloani	4	+	1	+	1
Helicolenus dactylopterus	3	+	1	+	1
Serrivomeridae	3	+	1	+	1
Anarhichas lupus	1	+	1	+	1
Gadus morhua	1	+	1	+	1
Lophius piscatorius	+	+	1	+	1
Crustacean prey					
Meganyctiphanes norvegica	16 000	85.8	71 624	61.9	412
Thysanoessa inermis	661	3.5	6 790	5.9	79
Unspecified Euphausiacea	628	3.4	10 743	9.3	158
Hyperiidea	343	1.8	22 708	19.6	202
Unidentified Crustacea	290	1.6	(376)	(0.3)	57
Pandalus borealis	217	1.2	118	0.1	49
Sergestes arcticus	106	0.6	315	0.3	12
Thysanoessa raschii	93	0.5	984	0.8	3
Pasiphaea multidentata	92	0.5	27	+	8
Unspecified Natantia	77	0.4	46	+	17
Pandalus montagui	58	0.3	36	+	30
Mysidacea	34	0.2	362	0.3	28
Copepoda	25	0.1	1 501	1.3	32
Gammaridea	9	0.1	79	0.1	20
Crangon allmani	3	+	2	+	2
Spirontocaris sp.	3	+	3	+	3
Lebbeus polaris	2	+	2	+	2
Sabinea sp.	2	+	5	+	2
Isopoda	1	+	2	+	2
Pontophilus norvegicus	+	+	1	+	1
Decapod larva	+	+	25	+	1
Thysanoessa longicaudata	+	+	7	+	1
Eualus pusiolus	+	+	2	+	2
Pagurus pubescens	+	+	1	+	1
Other invertabrate prey					
Cephalopoda	591	84.4	229	29.7	84
Indeterminatus	61	8.7	(45)	(5.8)	43
Brachiopoda	11	1.6	14	1.8	2
Porifera	8	1.2	(9)	(1.2)	10
Other Mollusca	8	1.2	325	41.8	16
Polychaeta	6	0.8	30	3.9	20
Echinodermata	5	0.7	(18)	(2.3)	15
Ascidiacea	2	0.3	(2)	(0.3)	1
Ctenophora	2	0.3	40	5.2	2
Cnidaria	2	0.3	(8)	(1.0)	9
Chaetognatha	2	0.2	47	6.1	10
Pycnogonida	1	0.2	4	0.5	3
Algae	+	+	(2)	(0.3)	2
Bryozoa	+	+	(1)	(0.1)	2

importance were gadid and mesopelagic fish, followed by unidentified fish, sandeels (Ammodytidae), squid or cephalopods, various shrimps (prey group Natantia) and hyperiid amphipods.

A more detailed list of the prey which occurred in the saithe diet is given, ordered by weight, in Table 3.2. The column containing the frequency of occurrence (FO) of the prey categories gives the number of samples in which the prey occurred. The total number of samples was 989 (cf. Table 2.2). The FO column can therefore be interpreted as an approximate "per mill frequency of occurrence". Since samples consisted of the bulked contents from a variable number of stomachs in most surveys, the figures are higher than the true FO.

Prey classified as fish constitute almost 70% of the total material. As stated above, the capelin dominate the fish prey, while unidentified fish ranked second. Of named taxa, blue whiting, *Micromesistius poutassou*, were second, followed by the families Paralepididae and Myctophidae, *i.e.* barracudinas and lantern fish. By far the most numerous of the lantern fish species was undoubtedly glacier lantern fish, *Benthosema glaciale*. It is common in boreal wates, but was never formally identified in the diet analysis due to the fragility of their photophores, the main character used in the identification of lantern fish. Larger lantern fish species, possibly of the genus *Lampanyctus*, occurred on occasion. No paralepids were identified to species, but *Arctozenus rissoi*, *Magnisudis atlantica* and *Paralepis coregonoides* have been recorded at Iceland. The genus *Sebastes*, or redfish, was represented by the golden redfish *S. marinus* and Norway redfish, *S. viviparus*, also known under the common name of rosefish. Gadids, prominent in the saithe diet, were Norway pout, *Trisopterus esmarki* and haddock, *Melanogrammus aeglefinus*. Finally, a few herring, *Clupea harengus*. were found. These groups of fish all contributed more than 0.5% each to the total fish material. Furthermore, Müller's pearlside, *Maurolicus mülleri,* occurred frequently in the autumn of 1992. The remaining fish taxa occurred rarely.

Crustaceans represented almost 30% by weight of the material analysed. The krill species, *Meganyctiphanes norvegica*, is in a position similar to that of capelin among the fish prey. Two other krill categories follow, *Thysanoessa inermis,* and unspecified euphausiids. Together, these three categories of krill comprise more than 90% of the saithe stomach contents classified as crustacean. Other crustaceans contributing more than 0.5% to the total crustacean contents were hyperiid amphipods; unidentified crustaceans; the commercially utilized northern shrimp, *Pandalus borealis*; the mesopelagic penaeid shrimp, *Sergestes arcticus*; and *Thysanoessa raschii*. Unspecified

Table 3.3. Weight of stomach contents and number of prey items by prey category, year and season. Years and seasons pooled in the margins.

	SPRING 1990				SUMMER 1990			
	W (g)	%W	N	%N	W (g)	%W	N	%N
Capelin	4787	63,4	1514	11,5	209	10,4	104	4,4
Euphausiids	1982	26,2	10207	77,4	637	31,7	1993	84,1
Gadid fish	203	2,7	21	0,2	602	29,9	143	6,0
Mesopelagic fish	123	1,6	26	0,2	256	12,8	11	0,5
Unidentified fish	72	1,0	10	0,1	291	14,5	81	3,4
Sandeels	138	1,8	40	0,3				
Other fish	121	1,6	3	0,0	0	0,0	1	0,0
Squid	30	0,4	12	0,1	6	0,3	4	0,2
Natantia	46	0,6	36	0,3	4	0,2	6	0,3
Hyperiid amphipods	20	0,3	183	1,4	2	0,1	25	1,1
Unidentified crustaceans								
Other crustaceans	14	0,2	1131	8,6	1	0,1	1	0,0
Indeterminatus	14	0,2						
Benthic organisms	1	0,0	4	0,0	1	0,0	2	0,1
Planktonic organisms								
Total contents	7551	100	13187	100	2010	100	2371	100
Number of stomachs	405				146			
Average content	18,6				13,8			

	SPRING 1991				SUMMER 1991			
	W (g)	%W	N	%N	W (g)	%W	N	%N
Capelin	4530	70,2	1172	18,1	2	0,0	1	0,00
Euphausiids	1367	21,2	5152	79,4	6480	78,6	23952	87,31
Gadid fish	45	0,7	3	0,0	337	4,1	12	0,04
Mesopelagic fish					559	6,8	36	0,13
Unidentified fish	28	0,4	8	0,1	833	10,1	3284	11,97
Sandeels								
Other fish	288	4,5	36	0,6				
Squid	159	2,5	31	0,5	28	0,3	28	0,10
Natantia	5	0,1	3	0,0				
Hyperiid amphipods	4	0,1	43	0,7	2	0,0	73	0,27
Unidentified crustaceans	3	0,1	1	0,0				
Other crustaceans	3	0,0	20	0,3	4	0,1	44	0,16
Indeterminatus								
Benthic organisms	14	0,2	20	0,3	1	0,0	1	0,00
Planktonic organisms	2	0,0	2	0,0	0	0,0	1	0,00
Total contents	6449	100	6491	100	8246	100	27432	100
Number of stomachs	278				174			
Average content	23,2				47,4			

	SPRING 1992				SUMMER 1992			
	W (g)	%W	N	%N	W (g)	%W	N	%N
Capelin	24979	80,7	5125	15,6	491	8,8	337	0,9
Euphausiids	3502	11,3	24376	74,4	2947	53,0	18518	48,8
Gadid fish	193	0,6	7	0,0	1124	20,2	23	0,1
Mesopelagic fish	896	2,9	1412	4,3	76	1,4	85	0,2
Unidentified fish	206	0,7	120	0,4	4	0,1	20	0,1
Sandeels					219	3,9	67	0,2
Other fish	600	1,9	14	0,0	36	0,7	4	0,0
Squid	111	0,4	49	0,2	232	4,2	86	0,2
Natantia	316	1,0	418	1,3	15	0,3	11	0,0
Hyperiid amphipods	35	0,1	910	2,8	202	3,6	18641	49,1
Unidentified crustaceans	60	0,2	3	0,0	207	3,7		
Other crustaceans	4	0,0	193	0,6	4	0,1	123	0,3
Indeterminatus	35	0,1	10	0,0	3	0,1		
Benthic organisms	19	0,1	45	0,1	2	0,0	18	0,0
Planktonic organisms	3	0,0	77	0,2	1	0,0	11	0,0
Total contents	30959	100	32759	100	5566	100	37944	100
Number of stomachs	736				177			
Average content	42,1				31,4			

	All SPRING SEASONS				All SUMMER SEASONS			
	W (g)	%W	N	%N	W (g)	%W	N	%N
Capelin	34297	76,3	7811	14,9	702	4,4	442	0,7
Euphausiids	6852	15,2	39735	75,8	10063	63,6	44463	65,6
Gadid fish	441	1,0	31	0,1	2062	13,0	178	0,3
Mesopelagic fish	1019	2,3	1438	2,7	892	5,6	132	0,2
Unidentified fish	306	0,7	138	0,3	1129	7,1	3385	5,0
Sandeels	138	0,3	40	0,1	219	1,4	67	0,1
Other fish	1010	2,2	53	0,1	37	0,2	5	0,0
Squid	300	0,7	92	0,2	267	1,7	118	0,2
Natantia	367	0,8	457	0,9	19	0,1	17	0,0
Hyperiid amphipods	59	0,1	1136	2,2	206	1,3	18739	27,7
Unidentified crustaceans	63	0,1	4	0,0	207	1,3		
Other crustaceans	20	0,0	1344	2,6	10	0,1	168	0,2
Indeterminatus	49	0,1	10	0,0	3	0,0		
Benthic organisms	34	0,1	69	0,1	4	0,0	21	0,0
Planktonic organisms	5	0,0	79	0,2	1	0,0	12	0,0
Total contents	44959	100	52437	100	15821	100	67747	100
Number of stomachs	1419				497			
Average content	31,7				31,8			

Table 3.3. (continued).

	AUTUMN 1990				ALL SEASONS 1990			
	W (g)	%W	N	%N	W (g)	%W	N	%N
Capelin	98	24,3	30	2,1	5094	51,1	1648	9,7
Euphausiids	111	27,6	1065	74,4	2730	27,4	13265	78,1
Gadid fish	52	13,0	2	0,1	857	8,6	166	1,0
Mesopelagic fish					379	3,8	37	0,2
Unidentified fish	3	0,8	2	0,1	367	3,7	93	0,5
Sandeels	79	19,6	94	6,6	217	2,2	134	0,8
Other fish					122	1,2	4	0,0
Squid	19	4,8	8	0,6	56	0,6	24	0,1
Natantia	11	2,6	1	0,1	61	0,6	43	0,3
Hyperiid amphipods	0	0,1	2	0,1	22	0,2	210	1,2
Unidentified crustaceans								
Other crustaceans	29	7,3	227	15,9	45	0,4	1359	8,0
Indeterminatus					14	0,1	0	0,0
Benthic organisms					2	0,0	6	0,0
Planktonic organisms								
Total contents	403	100	1431	100	9963	100	16989	100
Number of stomachs	40				591			
Average content	10,1				16,9			

	AUTUMN 1991				ALL SEASONS 1991			
	W (g)	%W	N	%N	W (g)	%W	N	%N
Capelin	86	31,0	16	1,4	4618	30,8	1189	3,4
Euphausiids	122	43,8	553	48,2	7969	53,2	29657	84,6
Gadid fish					382	2,6	15	0,0
Mesopelagic fish	3	1,1	4	0,3	562	3,8	40	0,1
Unidentified fish	4	1,6	9	0,8	865	5,8	3301	9,4
Sandeels								
Other fish					288	1,9	36	0,1
Squid					187	1,3	59	0,2
Natantia	9	3,3	11	1,0	14	0,1	14	0,0
Hyperiid amphipods	38	13,6	115	10,0	44	0,3	231	0,7
Unidentified crustaceans	5	1,9	5	0,4	9	0,1	6	0,0
Other crustaceans	8	2,9	134	11,7	15	0,1	198	0,6
Indeterminatus	0	0,1	2	0,2	0	0,0	2	0,0
Benthic organisms	2	0,6	299	26,0	17	0,1	320	0,9
Planktonic organisms					2	0,0	3	0,0
Total contents	279	100,001	1148	99,999	14973,1	99,999	35071	100,001
Number of stomachs	76				528			
Average content	3,7				28,4			

	AUTUMN 1992				ALL SEASONS 1992			
	W (g)	%W	N	%N	W (g)	%W	N	%N
Capelin	253	9,4	356	3,7	25724	65,6	5818	7,2
Euphausiids	233	8,6	4332	45,4	6683	17,0	47226	58,8
Gadid fish	90	3,3	5	0,1	1408	3,6	35	0,0
Mesopelagic fish	116	4,3	161	1,7	1087	2,8	1658	2,1
Unidentified fish	487	18,0	439	4,6	698	1,8	579	0,7
Sandeels	1281	47,4	942	9,9	1500	3,8	1009	1,3
Other fish	16	0,6	5	0,1	652	1,7	23	0,0
Squid	4	0,2	11	0,1	348	0,9	146	0,2
Natantia	155	5,7	71	0,7	486	1,2	500	0,6
Hyperiid amphipods	39	1,5	2716	28,4	277	0,7	22267	27,7
Unidentified crustaceans	14	0,5	367	3,8	282	0,7	370	0,5
Other crustaceans	2	0,1	97	1,0	10	0,0	413	0,5
Indeterminatus	9	0,3	33	0,3	47	0,1	43	0,1
Benthic organisms	2	0,1	12	0,1	24	0,1	75	0,1
Planktonic organisms	0	0,0	5	0,1	4	0,0	93	0,1
Total contents	2703	100	9552	100	39228	100	80255	100
Number of stomachs	183				1096			
Average content	14,8				35,8			

	All AUTUMN SEASONS				ALL SEASONS			
	W (g)	%W	N	%N	W (g)	%W	N	%N
Capelin	438	12,9	402	3,3	35436	55,2	8655	6,5
Euphausiids	467	13,8	5950	49,0	17382	27,1	90148	68,1
Gadid fish	143	4,2	7	0,1	2646	4,1	216	0,2
Mesopelagic fish	119	3,5	165	1,4	2029	3,2	1735	1,3
Unidentified fish	495	14,6	450	3,7	1930	3,0	3973	3,0
Sandeels	1360	40,2	1036	8,5	1716	2,7	1143	0,9
Other fish	16	0,5	5	0,0	1062	1,7	63	0,0
Squid	24	0,7	19	0,2	591	0,9	229	0,2
Natantia	174	5,2	83	0,7	560	0,9	557	0,4
Hyperiid amphipods	77	2,3	2833	23,4	343	0,5	22708	17,2
Unidentified crustaceans	20	0,6	372	3,1	290	0,5	376	0,3
Other crustaceans	39	1,2	458	3,8	69	0,1	1970	1,5
Indeterminatus	9	0,3	35	0,3	61	0,1	45	0,0
Benthic organisms	4	0,1	311	2,6	42	0,1	401	0,3
Planktonic organisms	0	0,0	5	0,0	6	0,0	96	0,1
Total contents	3385	100	12131	100	64164	100	132315	100
Number of stomachs	299				2215			
Average content	11,3				29,0			

Natantia, *P. montagui*, mysids, calanoid copepods and gammarid amphipods are noteworthy because of their frequency of occurrence. The presence of the remaining crustaceans seemed only incidental.

The remaining 1% of the total contents was invertebrate prey other than crustaceans. Among these, there was one dominant group, the Cephalopoda, which constituted about 85% by weight of this category. Squid of the genus *Gonatus* are the most commonly occurring cephalopods in Icelandic waters (E. Jónsson, MRI, pers. comm.) and half of the weight of this group was attributed to *Gonatus*. Indeterminatus is included in this part of the table since it is likely that this material was of origin other than piscine or crustacean.

The contribution of the 15 previously defined sets of prey was summed for each year and season. The results are given in Table 3.3, which also includes marginal tables for each season across years and each year across seasons.

A visual representation of the volume of data collected is shown in Figure 3.11. Obviously, the amounts collected in spring, summer and autumn differ considerably. Thus, spring collections amounted to 70% of the total volume, while 25% and 5% derive from the summer and autumn seasons respectively. Figure 3.11 is analogous to the bottom section of Table 3.3, with the exception that prey categories have been combined.

The **spring season** was characterized by the importance of capelin, seemingly stable in all three years, while the remainder of the diet was mostly krill. This pattern was consistent through the three years studied. The spring season was relatively balanced with regard to sampling, approximately two thirds of the material were collected in spring 1992, the remaining one third almost equally divided among the two previous spring seasons.

In comparison to the spring period, the capelin had almost vanished from the diet of the saithe in **summer**. Euphausiids ranked first by weight in all three years, followed by fish prey, mostly of the gadid and mesopelagic categories. Of the summer data, one third was collected in 1992, one half in 1991 and the remaining one sixth in 1990. Due to the limited number of observations, it is difficult to draw definite conclusions about inter-annual variations. However, sampling effort in terms of numbers of saithe examined was much more stable than the amounts of food recorded in their stomachs. Therefore, it seems likely that feeding level was unusually low in 1990.

The most variable diet was observed during the **autumn season**. Sandeels were the largest prey group by weight when all three autumn seasons are combined (40%). Gadids, mesopelagics and unidentified fish contributed approximately 20% and krill and capelin some 14% each. The stomach contents collected in autumn 1990 and 1991 only yielded approximately 10% each of the autumn total. This will inevitably lend dominance to the 1992 data when pooling results for this season. The volume of data from the first two years was such that they can not form the basis of any comparison.

3.3. Inter-annual and seasonal variation of feeding level

3.3.1. Average contents

For obtaining a general overview of the saithe's feeding, average stomach contents for four main prey categories were calculated for all years and sampling seasons and are shown in Figure 3.12. The average stomach contents observed showed an increase over time. On an annual basis, the increase in 1991 was due to a much higher krill content, while in 1992 the increase was due to capelin.

In spring, the capelin stomach content showed a moderate increase from 1990 to 1991 followed by a large increase in spring 1992. Changes in the importance of other prey groups were much less pronounced. The most probable reason for the increase in capelin contents during this season is variation in capelin stock biomass (Fig. 3.12a).

In summer, the capelin had almost vanished from the saithe diet. Except in 1990, krill were the most important prey group, with a complete dominance in 1991. Fish prey other than capelin were obviously an important diet item in the summer season (Fig. 3.12b).

As compared to the other two seasons, the autumn was characterized by much lower average stomach contents (Fig. 3.12b). Noteworthy is the contribution of the other fish category in 1992, one half of which consisted of sandeels. As the sampling in the autumns of 1990 and 1991 yielded by far the fewest saithe, these results must be interpreted with caution.

3.3.2. Capelin

It is clear from Figures 3.2, 3.11 and 3.12 and Table 3.3 that capelin dominate the saithe diet in spring, but were of minor importance in summer and autumn. This general trend is due to annual variations in the distribution of capelin in Icelandic waters. These natural variations result in the greatest overlap between saithe and capelin in spring, inacessibility of adult capelin in the summer months and renewed availability of maturing capelin in the shelf waters north and east of Iceland in late autumn. Immatures can be available in a wide area all the year round and did indeed show up on occasion in saithe stomachs sampled north and east of Iceland in summer and autumn. The observations of capelin in the saithe diet off the central west coast in autumn 1992 are striking since these stations lie outside the general distribution area of capelin in autumn. That this was a misclassification of sandeels, which were observed in the area, is a possibility. However this is unlikely since capelin were recorded in a number of samples by two different observers. An alternative explanation could be migration of the predadors in these samples from nearby capelin areas off the Vestfirðir peninsula.

A slightly different picture of the saithe's feeding on capelin emerged when PFIs were studied. Interannual variation in mean $\mathrm{PFI}_{\mathrm{capelin}}$ in spring is shown in Figure 3.13. Clearly, the spring season of 1990 differs from the other two. The most probable reason for this is a very low capelin abundance during the spawning season of 1990. The large standard error for the average capelin PFI in spring 1991 is due to an outlier from one station to the west of the Vestfirðir peninsula. This observation was verified. However, when omitting this observation, the standard error of the 1990 spring data was much reduced and the general trend in mean PFI over the years showed an increase similar to that observed for overall average capelin contents in March (Figs. 3.12 and 3.13).

3.3.3. Krill and fish prey other than capelin

Euphausiids occurred in considerable amounts in the diet of the saithe in all years and seasons (Fig. 3.11 and 3.12). The mean PFIs for krill and other fish were highest in summer (Fig 3.13) . However, it was clear that in autumn the smaller saithe continued to prey heavily on the krill, while larger saithe found other suitable prey, mainly fish (cf. Fig. 3.14). There was an increasing proportion of other fish in the total material, from 6% in spring to 62% in autumn. Different groups of fish dominate the other fish index, from year to year and season to season. The most striking variable is the dominance of sandeels in the autumn of 1992.

3.4. Variations in the diet according to predator size

3.4.1. Weight percentage by length group

Figure 3.14 shows the percentage contribution by weight of four main food categories by saithe length group in the three sampling seasons.

In spring , only small variations were apparent in prey preference with respect to predator size. Capelin dominated the diet of all size categories of saithe in this season, to the extent that possible changes in size-related preference for other prey may be masked. However, a closer look at the spring data revealed that, apart from the capelin, the proportion of fish prey increased while that of krill decreased with saithe size.

The summer diet consisted predominantly of euphausiids, with the exception of the largest sized saithe, whose stomach contents consisted of up to 50% fish.

In autumn, there was a clear switch in prey preference with predator size similar to that described by Bergstad (1991). Krill and other invertebrates, *i.e.* relatively small prey items, were mainly taken by the smaller saithe, while the larger saithe preyed mainly on fish.

3.4.2. Frequency of occurrence by length group

Figure 3.15 shows how the frequency of occurrence (FO) of fish prey changes with the size of the saithe, while Figure 3.16 shows this for invertebrate prey categories. As explained in section 2.3.3 the FO for a prey group in a certain predator length group could have ranged over a set of possible values, as indicated by the intermediate shading in Figures 3.15 and 3.16. This analysis was based on numbers sampled on the stations were the prey in question occurred, and two different assumptions about the distribution of prey items among saithe in a sample. It is therefore difficult to draw firm conclusions from the figures but some general observations can be made.

Among the fish prey, capelin appeared to occur evenly for all length groups of saithe, while sandeel occurrence was too variable to draw any conclusions. On the other hand, and not surprisingly, both gadid and mesopelagic fish occurrence seemed to increase with predator size. In addition, the length distributions of saithe on the stations, where gadids and mesopelagics were observed in the stomachs, are different from saithe length distributions on capelin and sandeel stations.

The invertabrate data were more difficult to interpret (Fig. 3.16). Euphausiid occurrence was fairly evenly distributed on saithe size classes. For squid, the expected increase in FO with saithe length (Pálsson 1983; Bergstad 1991) was not observed. Somewhat surprisingly, shrimp occurrence showed an increasing trend. Benthic organisms may occur incidentally in the stomach contents. However, the expected decrease in their occurrence with length (Sæmundsson 1926) was not apparent in the data.

3.4.3. Average stomach content by length group

Figure 3.17 shows how the average capelin content by sample increased with saithe length in the spring season. The apparent variability in the data is largly due to small sample sizes near the two extremes of the predator length range. The data on capelin contents in spring are analysed in section 3.4.4.

The seasonal changes in the amounts of euphausiids and fish other than capelin observed in the saithe stomach samples are shown by predator size in Figure 3.18. There were considerable variations in krill contents by season. A steady increase with saithe size was observed in the spring, but especially, in the summer data. Only small amounts of krill were taken in autumn. However, it seems that krill were the main part of the diet of saithe smaller than 60 cm in the autumn season (cf. Figure 3.14).

Although there is much variability in the other fish contents, a general increase in average content of these fish with saithe size is fairly obvious (Fig 3.18). The relative importance of fish prey other than capelin increases from spring to autumn (cf. Fig. 3.12). However, when the actual amounts of other fish, observed in the stomachs, are studied, no seasonal difference in stomach content is apparent.

3.4.4. A linear model of capelin contents

Capelin are by far the largest component of the diet of saithe in spring and deserve special attention. The proportion by weight of capelin in the stomach contents was stable with respect to predator size (cf. Figure 3.14). The mean capelin content in spring shows, however, a regular increase by predator length group. This is most readily apparent in 1992 (cf. Figure 3.17).

The results from linear modelling showed that, of the models considered, 3 parallel regressions gave the best description of the data. On their own, both year and predator size showed significant effects ($p<<0.01$ in both instances). Together, year and predator size were an improvement on both the ANOVA and a simple regression by size ($p<<0.01$). The full model (2.3) was not a significant improvement on the model

$$y_{ij} = \mu_i + \beta x_{ij} + \varepsilon_{ij} \tag{3.1}$$

i.e. three parallel regressions ($p=0.529$). These regressions are shown in Figure 3.19, but explain only 20% of the variation in log capelin contents. While the intercepts for the 1991 and 1992 regression lines did not differ significantly, the 1990 intercept was found to be significantly lower than the other two.

The previous observations of a positive relationship between capelin contents and capelin biomass on the feeding grounds were supported by this simple modelling experiment. The available material on the saithe's predation on capelin at other times of the year are insufficient for further establishing the importance of this predator-prey relationship.

3.4.5. Prey size distributions for the two main prey species

Overall mean individual weights of 8 prey categories were plotted against predator length groups and are shown in Figure 3.20. For a number of categories a remarkably clear trend of increasing prey weight with the size of saithe appeared. This applied in particular to krill, shrimps and gadids. However, for shrimps and gadids the picture is occasionally disturbed by numerous small prey in some length groups.

The 1992 length distributions of capelin and *Meganyctiphanes norvegica* from the saithe stomachs were examined. The capelin measurements derived from spring only, while measurements of krill carapace length were from both spring and summer. All measurements in a length group were pooled by season, without taking account of prey abundance in the samples or predator numbers on the station. The resulting prey length distributions were compared visually.

For the capelin prey, three modes appeared in the length distribution, corresponding to the 1, 2 and 3+ age groups of capelin, as shown in Figure 3.21a. Figure 3.21b shows capelin length distributions with respect to predator length group. When the saithe are grouped into three size categories, defined in Section 2.3.7, it appears that small saithe preyed on capelin of all size groups, medium sized saithe on capelin age groups 2 and 3-4, while the largest saithe only took age groups 3-4.

However, the length distributions observed (Fig. 3.21c) cannot serve to support a hypothesis of a shift in size preference by the saithe. This simply demonstrates the differences in overlap between the various size groups of saithe and capelin. Thus, the smallest saithe had preyed on 1 group capelin north of the Vestfirðir peninsula, while capelin belonging to age group 2 were found in saithe stomachs taken mainly on outer part of the shelf west of Iceland. Pálsson *et al.* (1989) found smaller saithe to have a more northerly distribution than the mature fish in the first two IGFS surveys.

To further check whether size differences in capelin prey between the different sizes of predator had been lost through pooling of data, two short analyses were made. First, the station with the highest number of capelin measurements (202, prey length range 11.5-17.5 cm, predator length range 50-100 cm) was singled out. The data from this station did not indicate that capelin mean lengths increased with predator size. Second, capelin size at a set of stations to the west of the Reykjanes peninsula (SW-Iceland), where capelin had been observed in the stomach contents, was examined. As in the first case, most of the capelin were from age groups 3 and 4 (>= 10.5 cm) and the analysis was restricted to this size group (367 fish). This data set also showed no correlation between capelin and saithe length.

The measurements of *Meganyctiphanes norvegica* derived, for the most part, from spring and summer stomach collections (70% and 30% respectively) and are shown in Figure 3.22. In general, no clear differences in the length distributions of *M. norvegica* were apparent for the three size classes of saithe. However, it appears that the krill length distributions in summer are shifted upwards for each saithe size class (Fig. 3.22b). A small mode appears in summer for the juvenile generation from spring. Like in the case of capelin, the juveniles were observed in the stomachs of the smallest saithe. Another conclusion, which can be drawn from Figure 3.22 is that the *M. norvegica* taken by saithe in summer 1992 was significantly larger than in spring of the same year (t-test, $p<0.01$).

3.5. Diel variations in the feeding on capelin and krill

Boxplots of the capelin and krill PFI distributions by time of day are shown in Figure 3.23. In spite of some irregularities, it seems that there generally is a low in the PFI indices during the daytime for both of these prey categories, with higher values being more frequent in twilight and during the night.

The frequency of occurrence of capelin and krill in spring, shown by time of day in Figure 3.24, does not indicate any diel variation in the feeding pattern. However, indices of digestion, averaged for the same time intervals, also shown in Figure 3.24, conform better with the observed diel variations in PFIs.

3.6. Comparison of predation on capelin by cod and saithe

Both saithe and cod had capelin in their stomachs on 59 stations in the spring surveys in 1990-1992, while capelin was preyed on by one of the two species, on 97 and 413 stations, for saithe and cod respectively. Prior to the testing of the null hypothesis of no difference in capelin contents for the two species, the PFI distributions in the overlap area and non-overlap area were compared for each species. Average PFIs were lower outside of the area of overlap for both species. For cod, the difference was insignificant while saithe outside the area of overlap had significantly lower PFIs (Wilcoxon rank sum test, p=0.13 and p<0.01, respectively).

The capelin PFI distributions for saithe and cod on the overlap stations are shown in Figure 3.25 which also shows the length distributions of saithe and cod sampled for stomach contents at those stations. The null hypothesis of no difference in capelin feeding level between saithe and cod could not be rejected. When the distributions of capelin partial fullness indices of saithe and cod were compared, no difference was detected (Wilcoxon signed ranks test, p=0.21). Observations were also paired with regard to length group and sampling station. This yielded 48 observation pairs of capelin contents for saithe and cod in the same length group and at the same station. Again, no evidence of different amounts of capelin in the stomachs of these two predators was observed (Wilcoxon signed ranks test, p=0.68).

3.7. Consumption model results

Stock numbers at age from the Northwestern Working Group of ICES adjusted for fishing and natural mortality for a period of 2 months (Anon. 1995) and thereafter reduced by 30% to account for non-overlapping saithe are given below:

Age group	3	4	5	6	7	8	9	10+
Numbers (*10^{-3})	13 500	16 800	10 400	8 800	8 600	12 100	3 000	2 300

The estimated average capelin contents in BORMICON areas 1, 2 and 10 are given in the following text table:

Length group	7	8	9	10	11	12	13	14
Average contents (g)	3.4	10.6	21.1	26.7	38.8	64.0	103.8	123.0

The age groups in the western shelf area were divided on length groups according to the following table:

	Age group							
Length group	3	4	5	6	7	8	9	10+
7 (<=39 cm)	0.03							
8 (40-49 cm)	0.91	0.18	0.01					
9 (50-59 cm)	0.06	0.79	0.24		0.01			
10 (60-69 cm)		0.03	0.69	0.28	0.04	0.03		
11 (70-79 cm)			0.05	0.69	0.49	0.18		
12 (80-89 cm)				0.03	0.44	0.50	0.22	
13 (90-99 cm)					0.02	0.27	0.67	0.55
14 (>=100 cm)					0.01	0.02	0.11	0.45

Based on these data and model 2.3, daily capelin consumption by saithe on the southwestern and western parts of the Icelandic shelf could have been approximately 3 500 tonnes or a monthly consumption of around 100 000 tonnes in the period February-March 1992.

4. Discussion

4.1. Consumption and feeding level

It is clear from the results in sections 3.1-3.4 and 3.7 that saithe at Iceland must consume large amounts of capelin in February-April, just prior to and during the capelin spawning season. Because of the commercial importance of capelin and the size of the saithe stock at Iceland consumption by the saithe in winter and spring is of direct interest for fisheries management. Furthermore, the quantities of euphausiids consumed by the saithe might be needed in a future model for a krill stock.

Consumption models based on the assumption that the amounts of food fish populations consume can be estimated from gastric evacuation rates (GER) have been dealt with at length in the literature, mainly based on experiments whith cod, haddock and whiting (*e.g.* Jones 1974; Bromley 1991; dos Santos and Jobling 1992). Two schools of thought seem to exist, one advocating a constant rate of evacuation and the other that gastric evacuation is linearly related to stomach contents. Fish prey are often considered to have the first mode of evacuation, while it is frequently stated that invertebrate prey is evacuated linearly and an example of the opposite situation has been recorded for capelin (*e.g.* a review by Bromley 1994). To the knowledge of this author, the only experiment on gastric evacuation by saithe is that of Gislason (1983). However, that study must be regarded as exploratory, since it was conducted with only 30 saithe.

Bioenergetics models for estimating food consumption of a population of fish are an appealing alternative to GER models. Such models are based on relating the energy requirements of fish (*e.g.* for growth, migration and spawning) to the energetic content of their prey (Jones 1976; Magnússon and Pálsson 1989; Jobling 1993).

Elaborate estimation of consumption of a predator species may not even be necessary. If GER is linearly related to stomach contents, the average stomach contents or feeding level will be approximately proportional to consumption (Lilly 1991). The average stomach contents or a derived index such as the PFI can then be viewed as a meaningful varible on its own.

The values for average capelin contents by length group used as input for Model 2.3 are higher than the values for the geometric mean of capelin contents shown in Figure 3.17. This should not be taken too seriously in this exercise, since the underlying datasets are not quite the same although BORMICON areas 1, 2 and 10 naturally yielded the largest part of the observations of capelin contents. Furthermore, this is a demonstration of the relation between arithmetic and geometric means. Figure 3.17 indicates how the resulting consumption estimate should be regarded, *i.e.* a 90% confidence limit could well have a lower limit of 50% and an upper limit of 200% of the result, due to the variability in stomach contents alone.

Only under doubt was a consumption estimate included in this study. There are numerous reasons for this, a few of which are listed below:

i. Lack of digestion experiments for saithe.
ii. Sampling difficulties related to the schooling nature of the predator. Bottom trawl is perhaps not the ideal sampling gear for saithe (Gislason 1983; Ajiad 1990, on differences in stomach contents of pelagic and demersally occurring cod).
iii. Oversimplification, *i.e* not taking account of meal size and fish size, poorly described overlap between predator and prey and the value for *E* in Model 2.4 may be inappropriate for saithe.
iv. More samples of saithe and a longer time series would be needed for establishing confidence in feeding model results.

However, although the available data may not be appropriate for such estimation, they are the only data from Icelandic waters and were therefore used to obtain a preliminary estimate of capelin consumption by saithe.

4.2. Diet composition

Capelin

Capelin emerges as by far the most important fish prey. They are mainly taken in winter and spring when they may constitute up to 80% of the saithe's diet as descibed earlier. Since capelin is a cold-water species which neverthless spawns in the warm waters to the south and west of Iceland the winter feeding of saithe on capelin is a reflection of the overlap of these two species at that time of year. However, the practical absence of capelin from saithe stomachs collected in summer and autumn need not reflect the true situation. Observations have been made of schools of large and medium sized saithe in the areas north and east of Iceland in spring. The distribution of saithe is likely to shift to the north in summer to area where capelin may be available. The fast-swimming saithe could well have avoided the gear towed by the survey vessels in summer.

Herring

The scarcity of herring in saithe stomachs at Iceland is notable because it is an important component of the diet of Northeast arctic saithe off the coasts of northern Norway (K. Nedreaas, IMR, Bergen, pers. comm.). Herring were recorded only a few times in March data from 1991 and 1992. Thus, from 2 to 8 individual saithe in the length range 50-69 cm had divided 33 herring, with a mean weight of 7 g, among them at a station to the west of Iceland in 1991. A 14 cm herring was recorded on a station to the west of Vestmannaeyjar and herring of 18 and 20 cm length at two stations to the southeast of Iceland in 1992. These occurrences coincide with the main distribution areas of the Icelandic summer spawning herring at the time. The three predators that had eaten herring in 1992 were in the length range of 70-89 cm. This does not preclude the possiblity of heavy feeding on herring by saithe being missed by these surveys, or taking place at other times of the year.

Gadids

No evidence of cannibalism was observed, which can be explained by different distributions of adults and juveniles. However, Bergstad (1991) observed a conspecific in the stomach of a saithe in the length range 50-59 cm from the Norwegian Deep, and cannibalism has been recorded among saithe in the inshore nursery areas (Bertelsen 1942; Mironova 1961, in Reinsch 1976). At Iceland, little is known about the times and places of recruitment, when juvenile saithe would be most at risk of predation by their elders. Furthermore, sampling effort, in particular during summer and autumn, may have been inadequate and, consequently, cannibalism by adult saithe at Iceland can not be ruled out.

At Iceland, 46 occurrences of predation on gadids were recorded, in 41 of which the prey were determined to the species level. Saithe in 19 samples had preyed on blue whiting, taking a total of 46 individuals. A total of 29 Norway pout was identified in 12 samples, 134 haddock were found in 8 samples, one whiting and a cod otolith were observed.

An analysis of the length distributions of the saithe that had food in their stomachs at the stations were gadids were observed in some samples showed, not surprisingly, that the saithe that prey on other gadids are generally of a larger size than those that had other prey in their stomachs, or were not feeding.

Crustaceans

Meganyctiphanes norvegica was the most numerous category, occurring 412 times. The genus *Thysanoessa* occurred less frequently, *T. inermis* was identified in 79 samples, *T.*

raschi 3 times and *T. longicaudata* in 1 sample. Krill recorded only as Euphauciacea occurred in 159 samples. These numbers have to be interpreted with caution, since it is entirely possible that some thysanoessans were missed in samples dominated by *M. norvegica*, the largest krill species at Iceland. It can also be hypothesised that, among the unidentified krill, the genus *Thysanoessa* had a disproportionately low share. Because of their smaller size they are not as easily identifed, and when in doubt, there might have been a tendency to place them in the higher taxon.

Predation on shrimp of the genus *Pandalus* in the North Sea by main fish predators, including saithe, has been estimated (Daan 1991). Based on shrimp observations amounting to some 2-3% of the diet, Daan calculated an annual consumption ranging from 10-20 thousand tonnes. This estimate is based on the average shrimp weight percentage and the spatial distibution of saithe is accounted for. At Iceland, shrimp were present in most season but particularly in autumn, when they accounted for up to 5% of the diet by weight. In view of similar saithe abundance in the two areas, this implies that Icelandic saithe may consume a few thousand tonnes of *Pandalus* species annually.

Hyperiids occurred in some 319 samples in all at 121 stations. Some 297 of these samples also contained euphausiids, *i.e.* hyperiids were present in only 22 samples where krill were not observed. This agrees well with submarine observations of species assemblages of euphausiids, hyperiids and myctophids on the shelves of Georges Bank (Auster *et al.* 1992)

Comparison of feeding studies on saithe

Pálsson's (1983) study of saithe at Iceland in 1980-1981, based on samples from the same sampling periods shows similar results to those presented here with respect to main prey groups and average contents. Pálsson was able to demonstrate a shift in the diet from euphausiids to capelin with increasing predator size. This is not readily apparent in the present study except in the autumn period (cf. 3.14). The difference is most probably due to the generally smaller sized saithe in Pálsson's study. In addition, the largest saithe in 1980-1981 had preyed heavily on squid, but the numbers sampled in the largest size categories were low. In the present study, squid contributed almost 1% to the total diet but were not taken exclusively by the largest saithe.

Bergstad (1991) reports on the diet of saithe in the Norwegian Deep and the Skagerak. The results of his study agreed well with those of Pálsson in that there was a gradual shift in diet with predator size from crustacean to fish prey. The crustaceans were mainly krill, but most important fish species were Norway pout and Müller's pearlside.

The annual consumption of commercially utilized fish by North Sea saithe was estimated by Gislason (1983). Two estimates are given. Age groups 1 and older was estimated to devour 1.3 million tonnes, consisting of half a million tonnes each of Norway pout and sandeels and the rest mainly haddock. Since sampling of the youngest saithe was poor another estimate, considered more realistic, was made for ages 4 and older. The reduced total figure was 434 tonnes annual consumption, three quarters of which were estimated to be Norway pout.

Du Buit (1991) estimated annual consumption by age groups 3-9 of saithe in the Northern North Sea and age groups 4-9 to the west of Scotland. Her estimates amount to a total of 3.8 million tonnes consumed annually by North Sea saithe, or considerably more than Gislason's estimate. Krill was estimated to account for one third of this biomass, the rest mainly Norway pout and blue whiting. Saithe west of Scotland are far less numerous and their total annual consumption is given as 0.5 million tonnes, mostly fish.

Faroe saithe are estimated to consume a total of 1.15 million tonnes annually, mainly Norway pout and crustaceans. The crustaceans were mostly krill, consumed in greatest amounts in autumn (Nicolajsen 1993).

It is clear that euphausiids are the common denominator of the diet of saithe in the NE-Atlantic. It is equally obvious that fish are a highly important constituent, but the species consumed differ between the various areas. This must be a simple reflection of availability. Thus, Norway pout and blue whiting are more common in the North Sea, Norwegian Deep and around the Faroes than at Iceland and off Northern Norway, where these species are substituted by capelin and herring respectively. It is likely that the importance of herring and capelin in the saithe diet in these areas fluctuates with the dynamics of the herring and capelin populations.

4.3. Size variations

In order to show the change in proportion of saithe that had taken fish and invertebrate prey categories (cf. Fig. 3.16) it was necessary to select a method of comparison. For this purpose only the data from stations on which the prey in question occurred were selected, thus avoiding area differences in predator size distributions. It is likely that such analysis can give clearer answers regarding prey selectivity by different size groups of saithe than the analysis of pooled data sets. However, in the present study, bulking was a confounding factor.

4.4. Diel variations

In the material presented here, there are some indications of diel differences in feeding behaviour of saithe when preying on capelin and euphausiids, *i.e.* a crepuscular peak in feeding activity. The diel varibility observed in the trawl catches by the commercial fleet, where the highest catch rates are obtained at night (cf. Synthesis 3.8), could be explained by the saithe avoiding the fishing gear more effectively during the daytime. On the other hand, diel differences in vertical distribution coupled with feeding could also be part of the explaination. This phenomenon merits more attention, preferably with the incorporation of acoustic studies. Knowledge of diel variations in stomach fullness could be of value in fish stock assessment by acoustic methods (Ona 1990).

4.5. Sources of error and methodological weaknesses

The fate of the stomach content analyst has been, still is and will probably continue to be that of dealing with inadequate or limited sets of problematic data, difficult methodology, and many variables to consider. The problems are numerous and a few error sources and inadequecies of methodology will be mentioned here.

Bulked samples

Bulking of stomachs in the samples leads to problems in finding the number of predators on a given prey in a length group at a station. This will inevitably cloud analyses of frequency of occurrence and will have different consequences for different prey. Common prey types will obviously be more evenly distributed among predators in a sample than less common prey, for which the alternative of only one predator might be more correct.

The main drawback with bulking of samples is that information on individual variation in stomach contents is lost. Individual observations of biological variables such as length, age and maturity of the fish sampled for stomach contents allow *i.a.* improved analysis of frequency of occurrence and average contents to that presented here and further make it possible to compare the stomach contents of saithe before and after spawning.

Stefánsson and Pálsson (1993) showed that bulked samples make it difficult to model emptiness separately for individual prey groups, since only completely empty stomachs are recorded during collection. It can also be pointed out that bulking has the additional drawback of confounding the actual analysis of the stomach contents *e.g.* when the same prey group occurs in two or more stomachs but in different stages of digestion, often making enumeration difficult, or at least non-trivial, or when similar prey in advanced stages of digestion become mixed in the bulked contents, making identification and weighing much less reliable than if the prey had occurred singly.

The practice of bulking stomachs into samples of 5 has been abandoned at the MRI in favour of sampling individual stomachs and analysing the contents at sea in most cases.

Regurgitation

Regurgitation is a potential source of bias in feeding studies. In a study conducted on the Southern New England shelf on many fish species, Bowman (1986) found it plausible that gadiform piscivores regurgitate more frequently than *e.g.* clupeid planktivores. Bowman further suggests that it is possible that regurgitation can either go undetected or be partial and therefore bias feeding estimates downward. He compares samples from two different depth intervals and shows how regurgitation is more frequent at stations in deeper water due to the higher pressure drop which fish from the depths experience when ascending to the surface. In the present work, regurgitation was only noted in a few saithe and no analysis was therefore possible. Whether regurgitation went unnoticed by the stomach samplers or, alternatively, was not duly recorded, remains unanswered. It would be possible to investigate depth effects on the stomach fullness by correlating TFI with depth but it must keep in mind that food availability can change with depth (Fahrig *et al.* 1993).

Feeding in the trawl has been named as a possible confounding factor in feeding studies (Bergstad 1991; Main and Sangster 1981, in Gislason 1983), these authors taking pains to remove prey apparently just recently ingested, assuming that netfeeding has occurred. This seems to be a dangerous practice because one has no means of determining how recently a fresh looking prey item was actually ingested. In this study, food in the stomach was counted as prey. In the dataset, the prey most likely to have been taken in this manner were the redfish, but they are also a part of the natural diet of the saithe, as evidenced by specimens in advanced stages of digestion. Furthermore, *Sebastes* did not contribute large amounts to the diet.

Several laboratory workers

The saithe stomach contents were analysed by several workers at the MRI. Differences in routine can have affected the results of this study. As the level of systematic precision in the analysis was not rigoursly set, some differences can be seen. Among krill, the Euphausiacea group occurred more frequently in some seasons and, unfortunately, a fairly high proportion of the fish was only classified as Pisces in others. These differences were neither analysed systematically nor otherwise accounted for. The procedures for blotting and sorting of contents as well as weighing and counting prey must inevitably have differed.

4.6. Conclusions

Hopefully, it is possible to learn some lessons concerning the feeding behaviour of saithe from the results of the present study. Although the data were collected primarily with the intent of estimating consumption for the purposes of fish stock management, and will thus be used as input for the BORMICON model, the Icelandic multispecies project had additional biological objectives. With respect to the present study, these objectives should perhaps have been more clearly defined in advance. However, it is felt that this study has been worthwhile.

The ICES study group on the analysis of feeding data (Anon. 1992) listed a number of questions that might be adressed by feeding studies. A few of these seem to have been clarified to some extent by the present results.

i. Are there significant year effects on mean stomach weight, proportion of empty stomachs, *etc.*?

> Capelin contents varied approximately in proportion to capelin abundance in the area as tested by a linear model of the logarithm of contents and krill data showed signs of a similar trend.

ii. Are there significant differences in digestion stage and stomach fullness with respect to time of day?

> The indications of crepuscular peaks in stomach fullness for both main prey types, capelin and euphausiids, can on no account be regarded as significant. The recording of digestion stage would have benefitted from finer gradation, more samples and further emphasis in the contents analysis work. However, taken with other observations of diel differences in saithe behaviour, these data could both be helpful in future work and become meaningful in the light of new results.

iii. Are there significant year or quarter effects in the percentage of fish or other aggregated prey categories (capelin, crustacea, mollusk, polychaete, echinoderm, other food, unidentified fish) in the diet?

From the results plot of weight percentage of food categories by length group (Fig. 3.14), it is clear that a seasonal effect is present. This is obvious in the case of capelin because of its varying availability and a difference in the proportions between krill and other fish is clear.

iv. Is there a significant effect of prey abundance on mean stomach weight, proportion of empty stomachs or mean weight of the specific prey in the stomach?

See answer to question i. above. Of the important preygroups, the only reliable estimate available is that of capelin abundance. The lack of abundance data on krill is of course most regrettable. Furthermore, the time series is very short, 3 years of mean stomach weights to compare with the capelin estimates.

The saithe-capelin interaction documented here must be of both ecological and commercial importance. It can quite possibly have profound effects on the capelin stock, although probably not to the same extent as the much studied interaction between cod and capelin. The dual nature of the saithe's interaction with the capelin is also interesting. In addition to their predator-prey relationship, the saithe also feed on krill to a much greater extent than cod, the krill in their turn being of great importance in the diet of the Icelandic capelin (Sigurðsson and Ástþórsson 1994).

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6. Figures

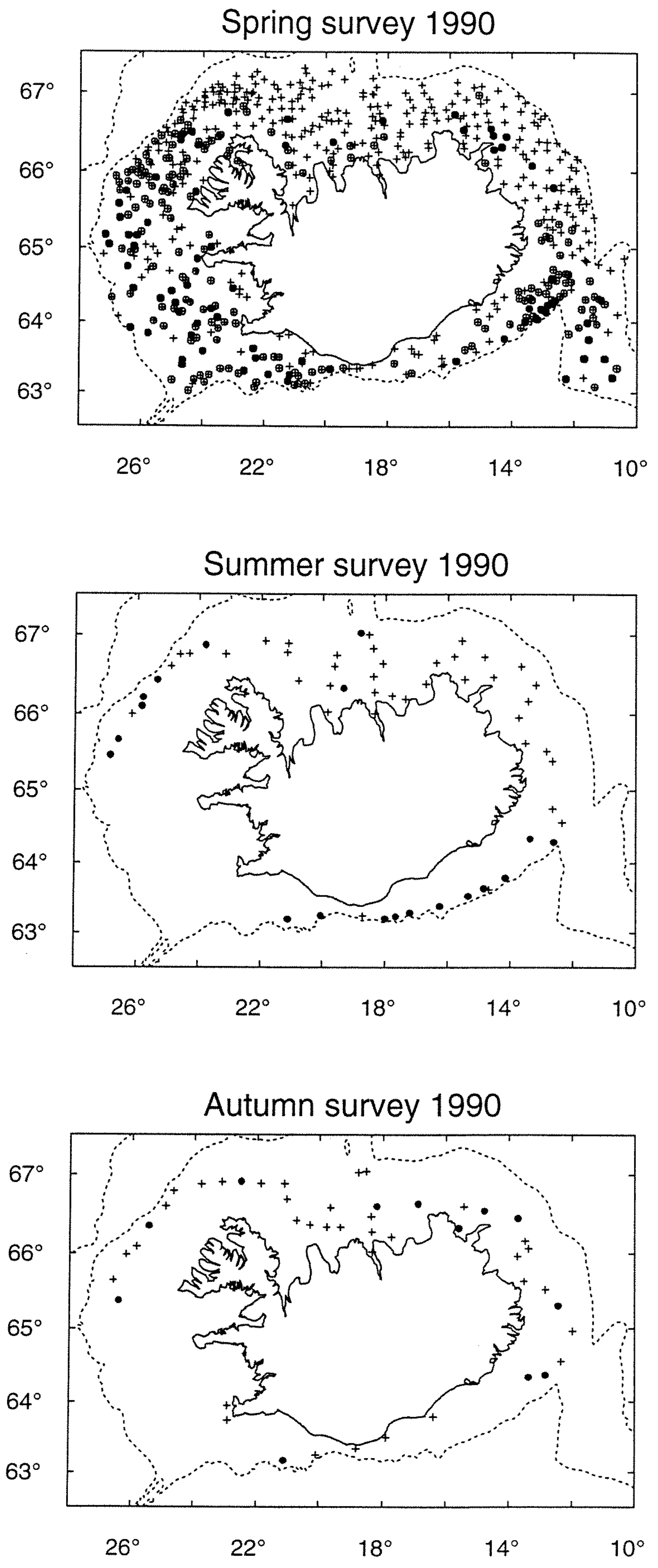
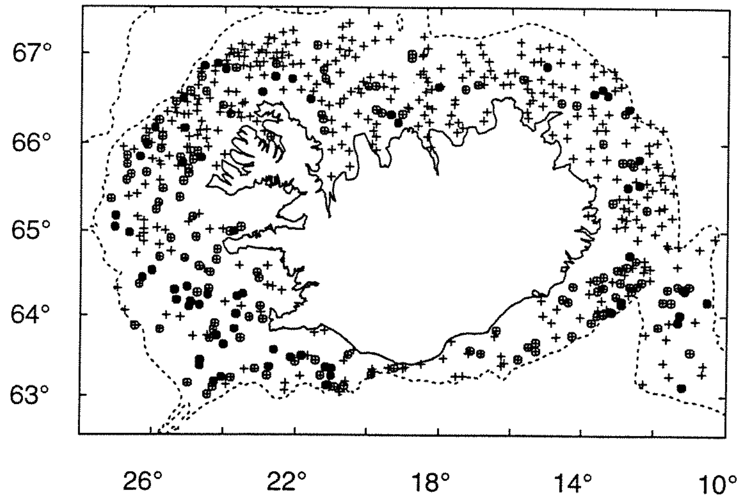
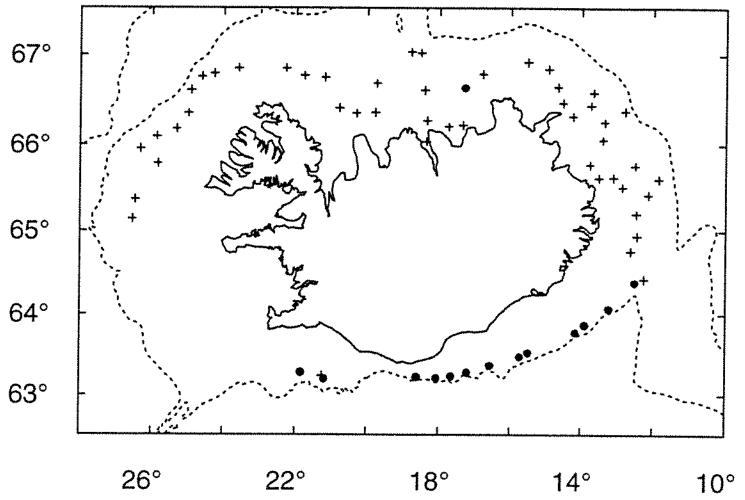


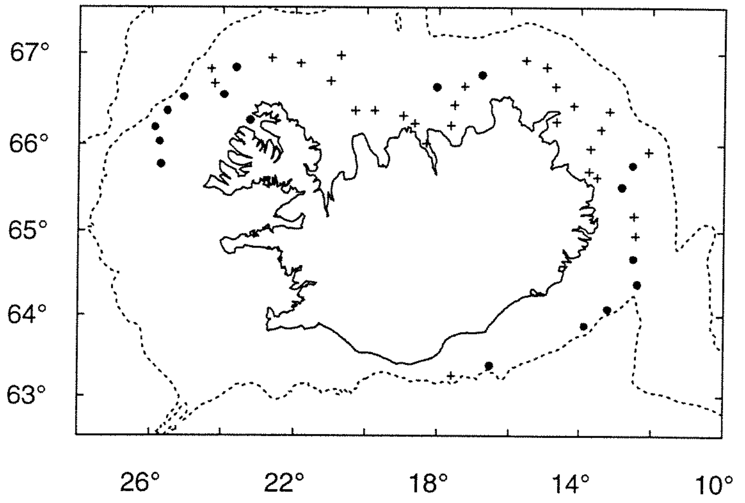
Figure 2.1. The station grid in 1990. Trawl stations are denoted by +, open circles denote stations where saithe ocurred and filled circles stations where stomachs were sampled. Stomachs were taken whenever saithe occurred in summer and autumn.



Spring survey 1991



Summer survey 1991



Autumn survey 1991

Figure 2.2. The station grid in 1991. Trawl stations are denoted by +, open circles denote stations where saithe ocurred and filled circles stations where stomachs were sampled. Stomachs were taken whenever saithe occurred in summer and autumn.

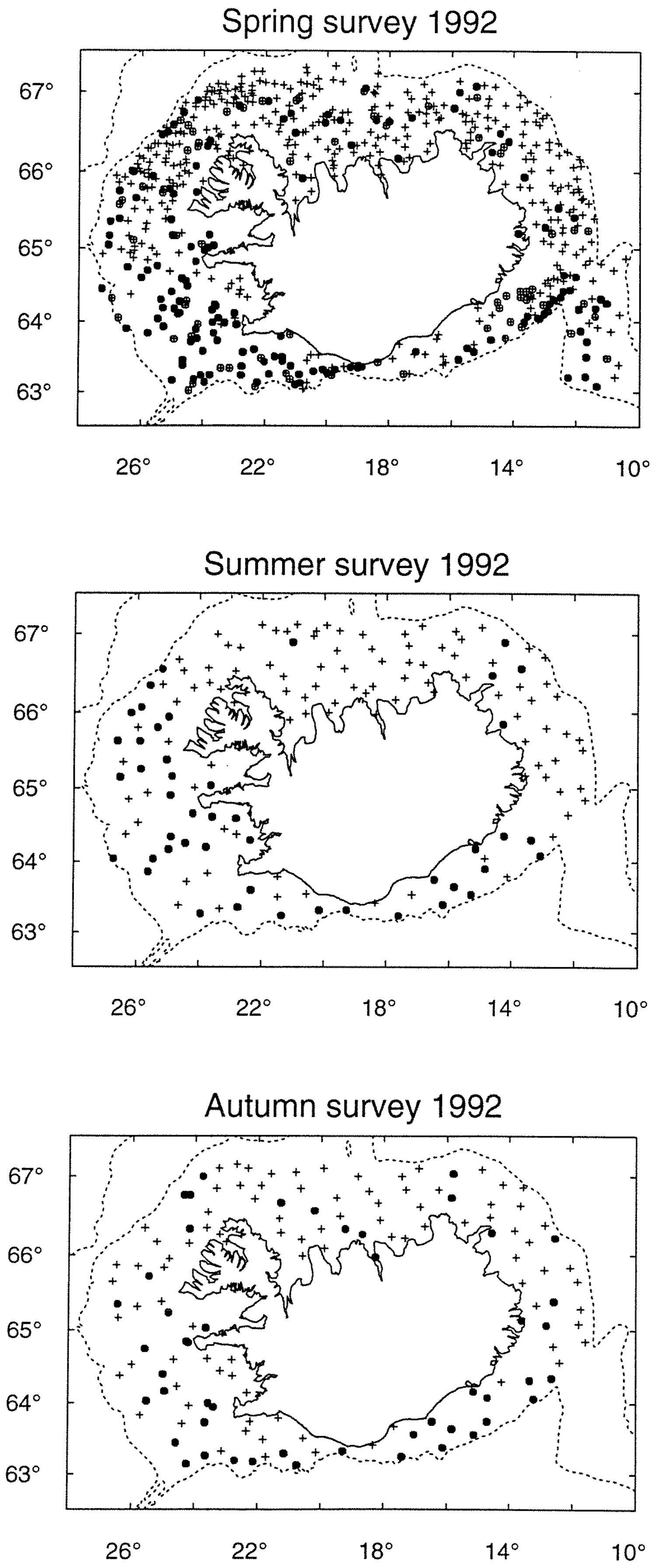


Figure 2.3. The station grid in 1992. Trawl stations are denoted by +, open circles denote stations where saithe ocurred and filled circles stations where stomachs were sampled. Stomachs were taken whenever saithe occurred in summer and autumn.

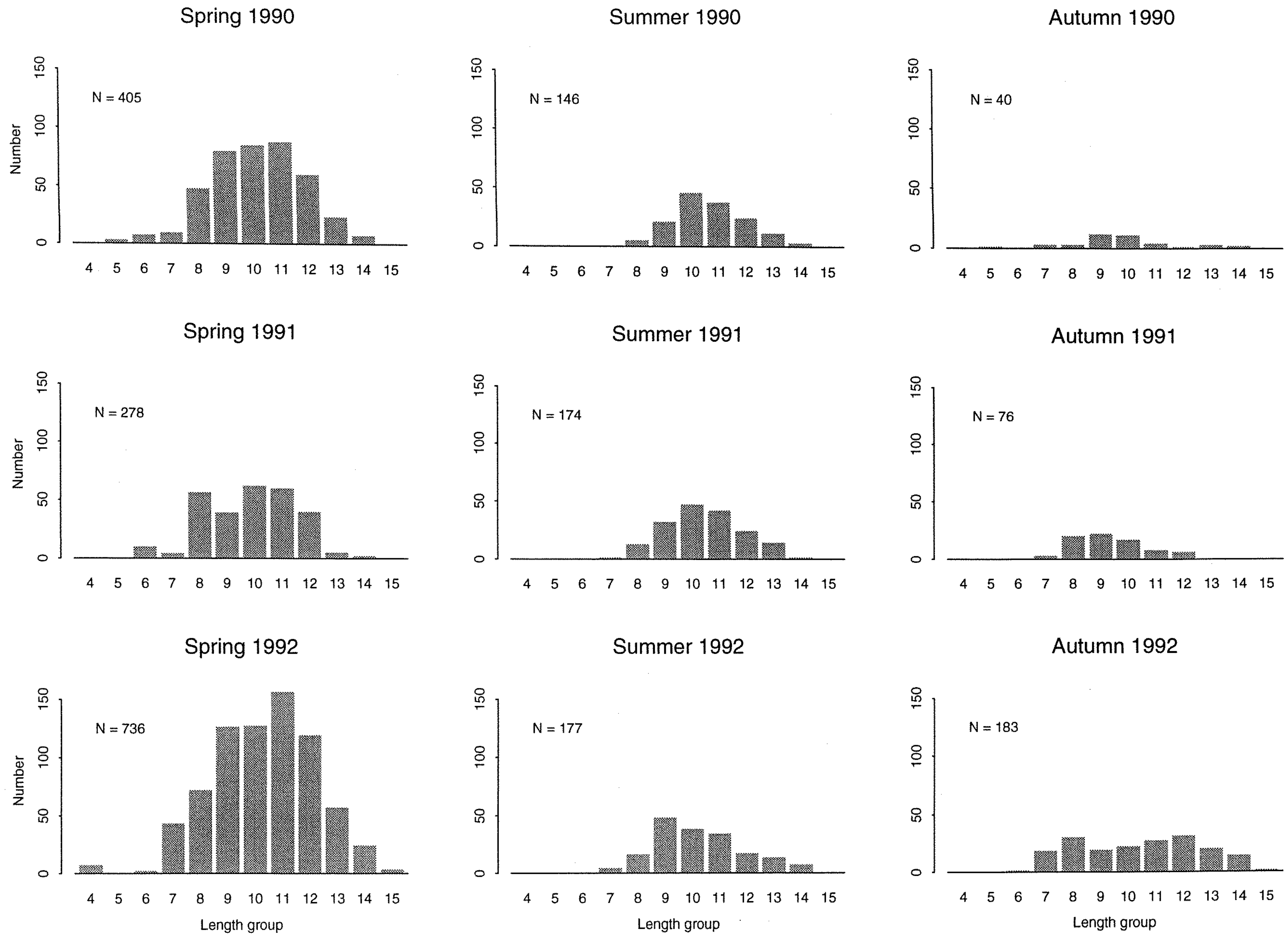


Figure 2.4. Size distribution of saithe (by length group) sampled for stomach contents by year and season.

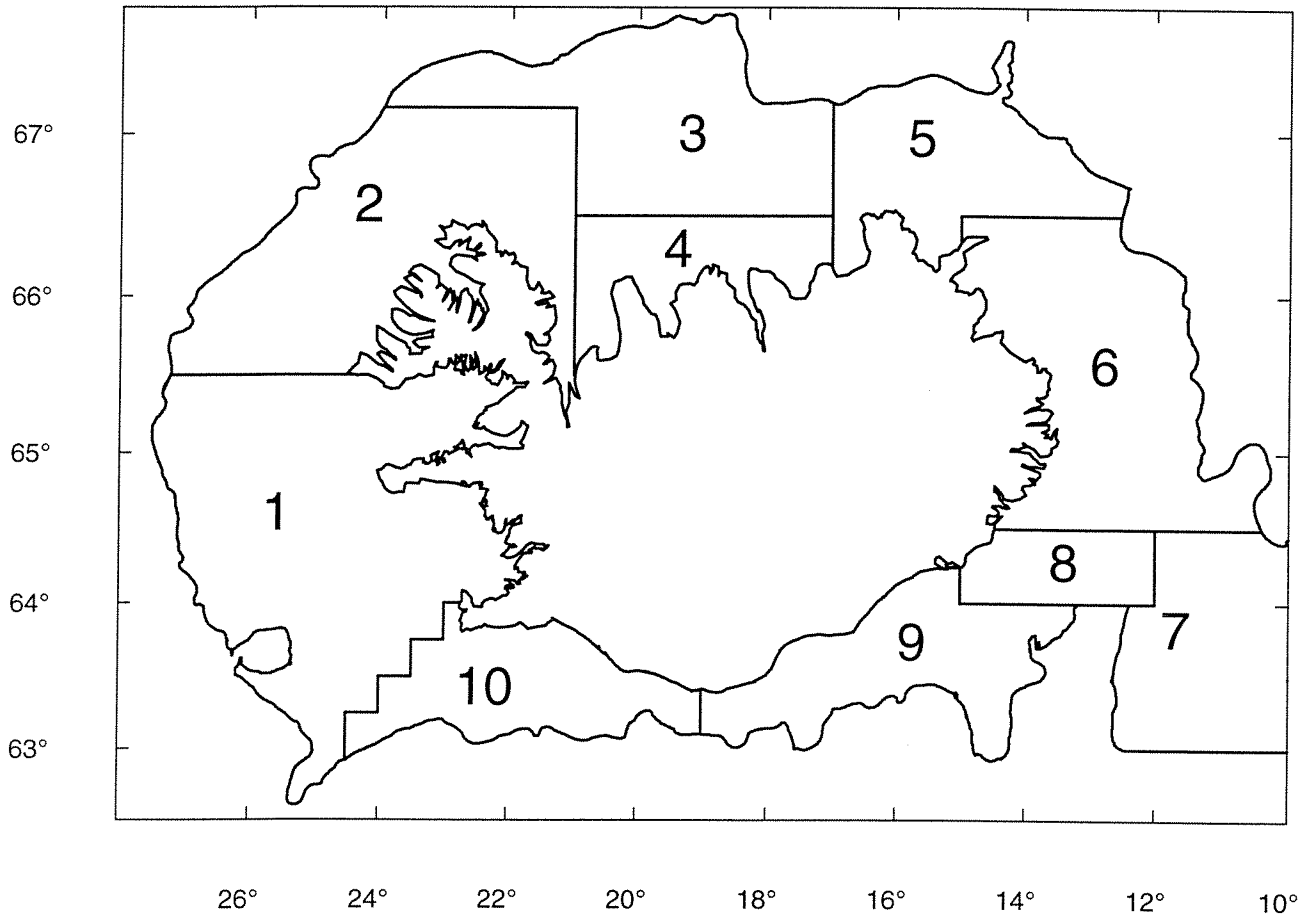


Figure 2.5. BORMICON area division of the Icelandic shelf,

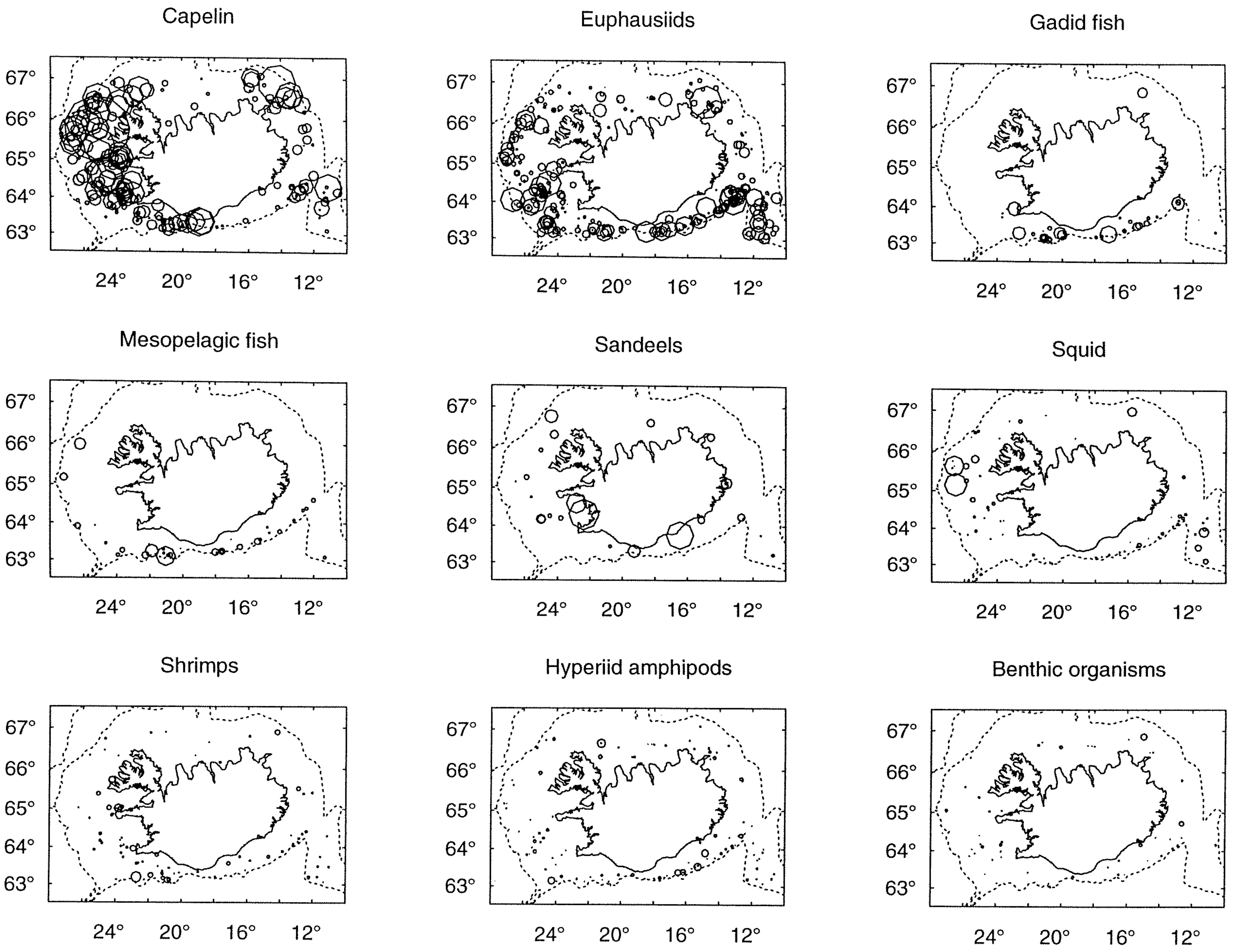
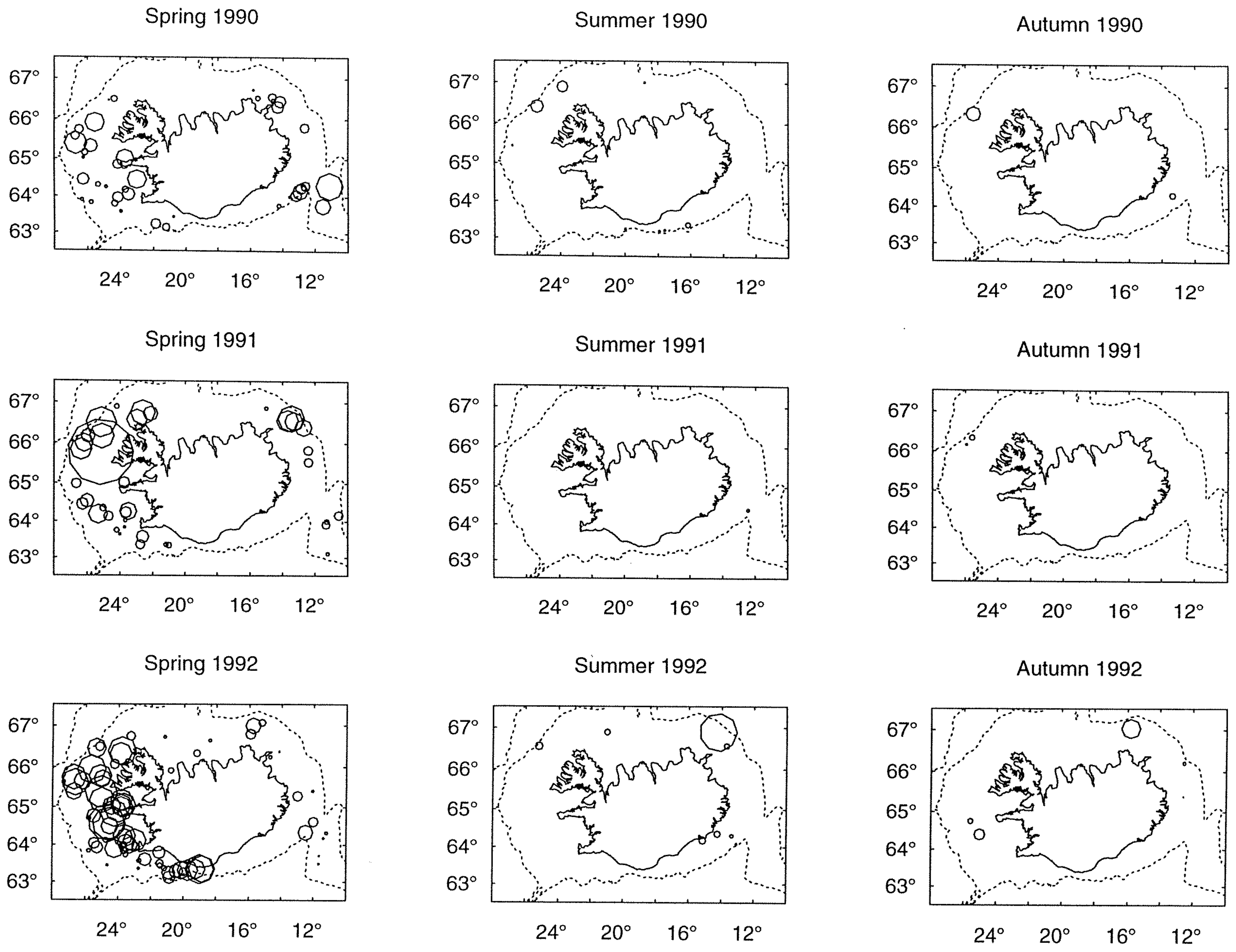


Figure 3.1. PFIs of selected prey groups. Circles are proportional to the square root of observed PFI and scaled by the maximum PFI observed for capelin.



Spring 1990

Summer 1990

Autumn 1990

Spring 1991

Summer 1991

Autumn 1991

Spring 1992

Summer 1992

Autumn 1992

Figure 3.2. PFIs for capelin. Circles are proportional to the square root of observed PFI and scaled by the maximum observed for capelin.

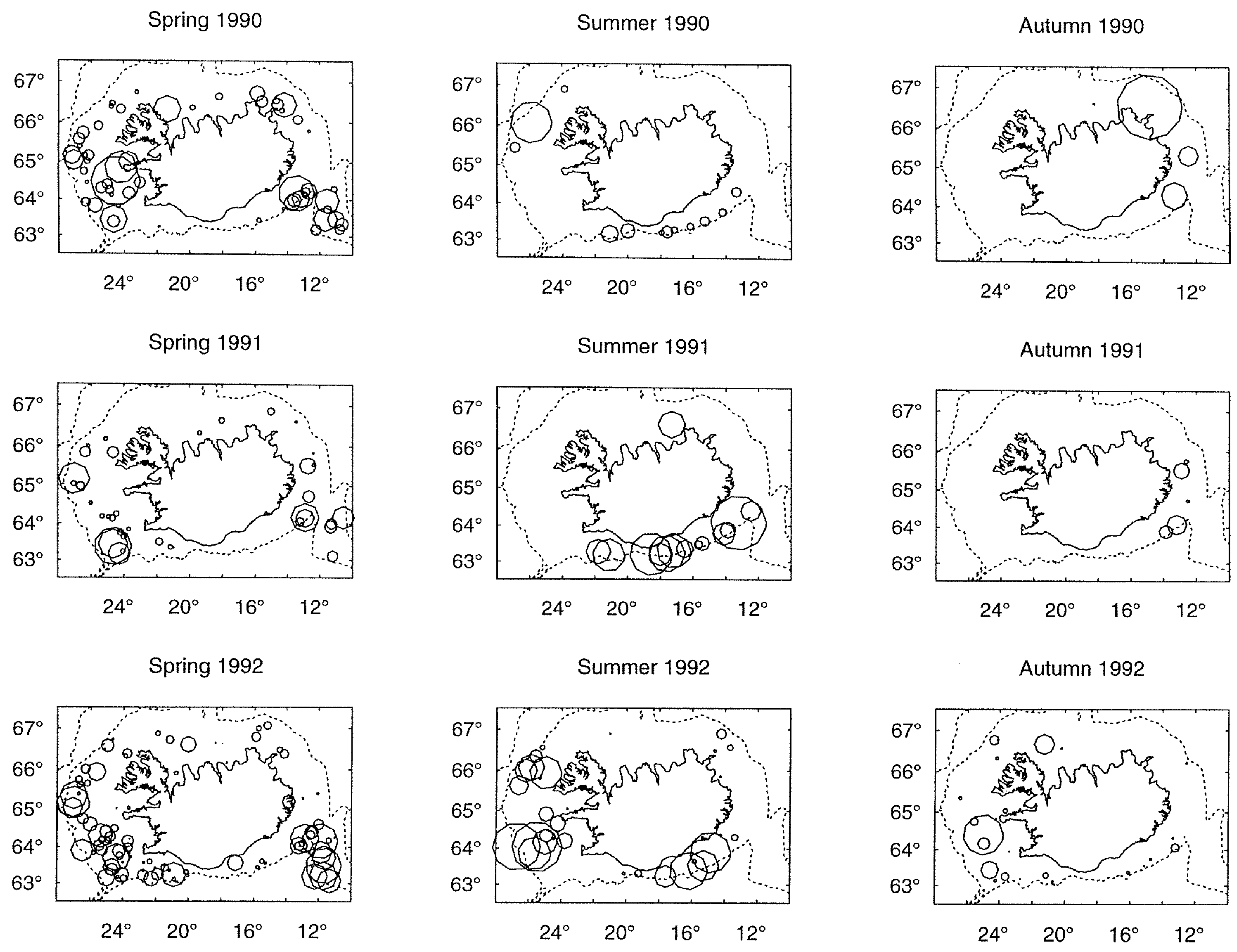


Figure 3.3. PFIs for euphausiids. Circles are proportional to the square root of observed PFI and scaled by the maximum observed for euphausiids.

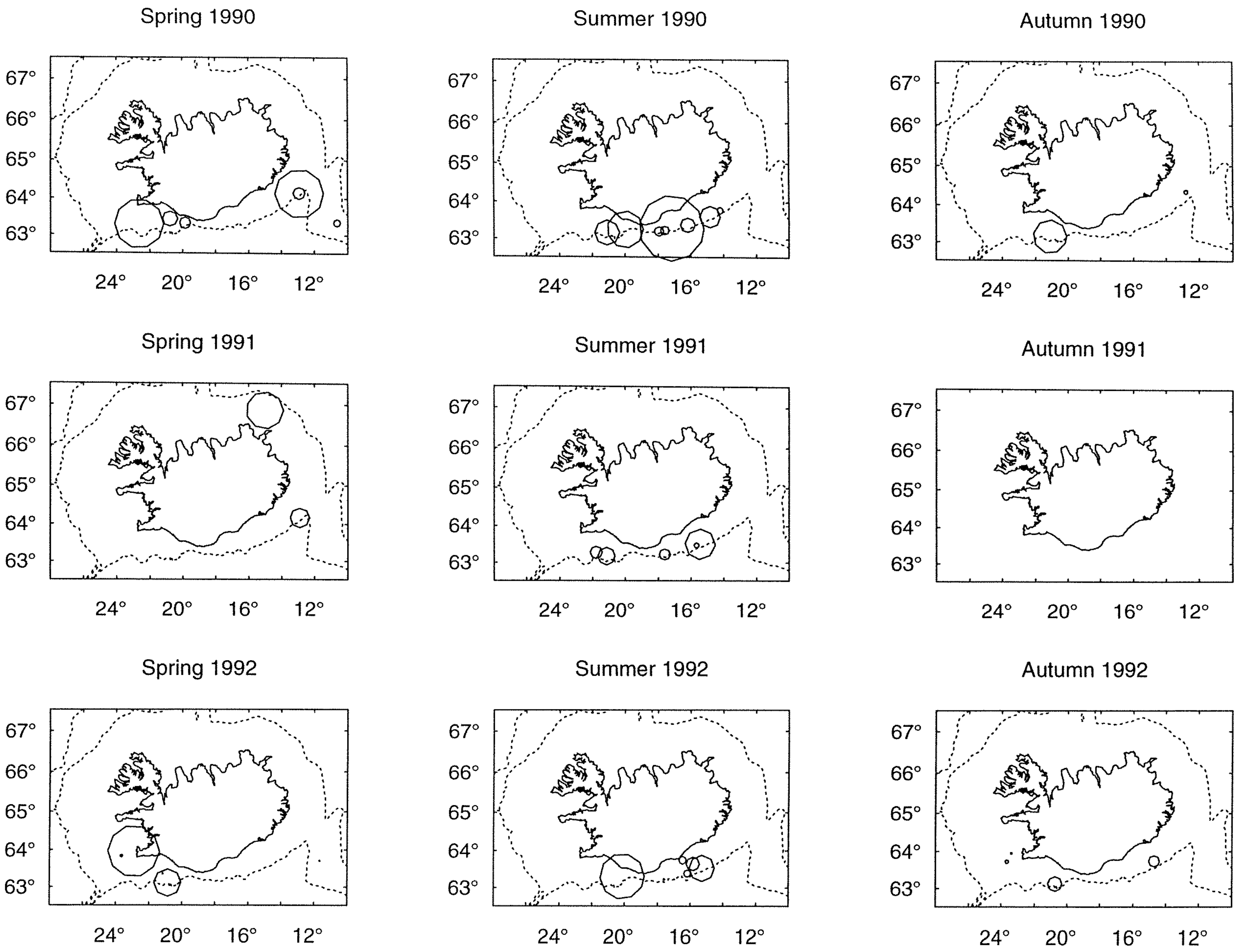


Figure 3.4. PFIs for gadid fish. Circles are proportional to the square root of observed PFI and scaled by the maximum observed for gadids.

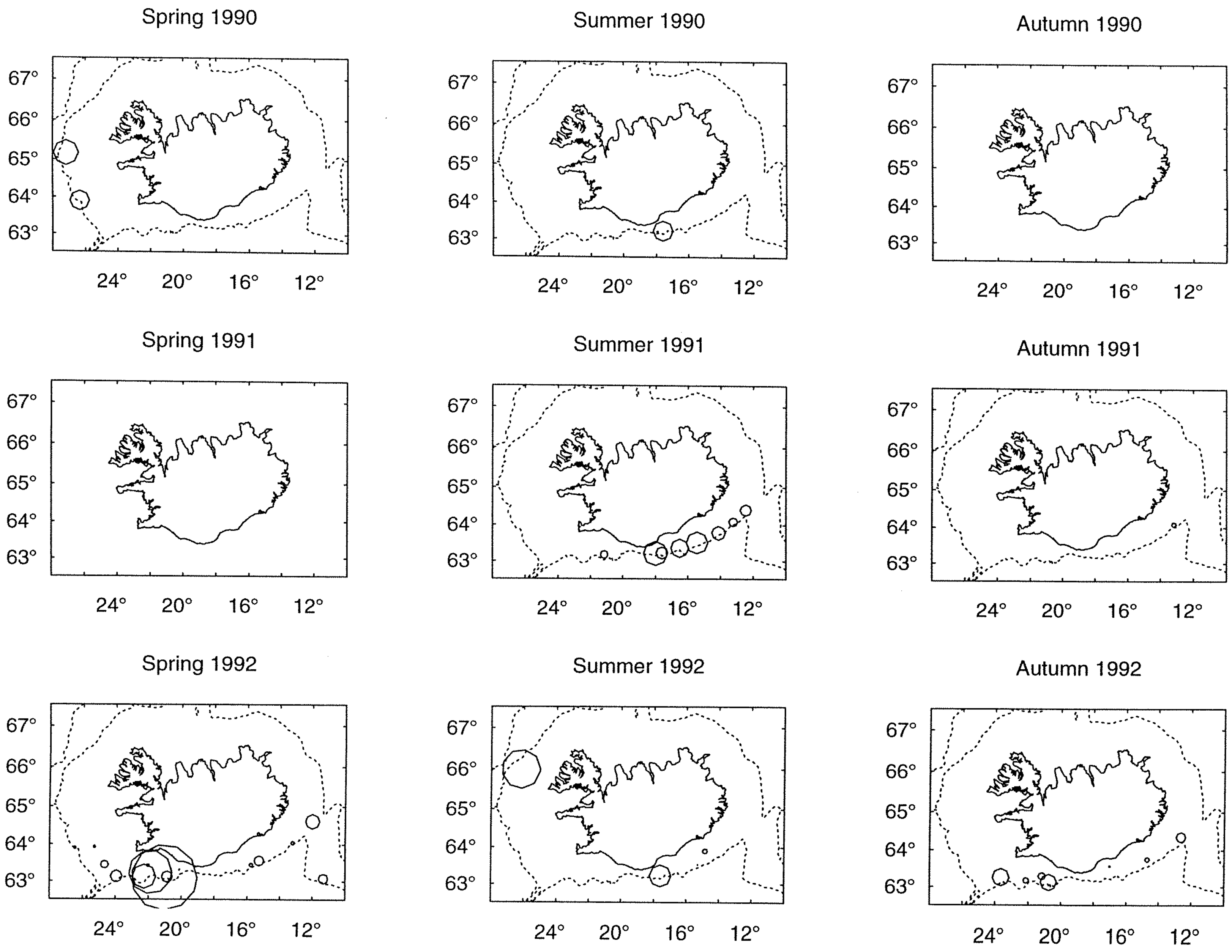


Figure 3.5. PFIs for mesopelagic fish. Circles are proportional to the square root of observed PFI and scaled by the maximum observed for mesopelagic fish.

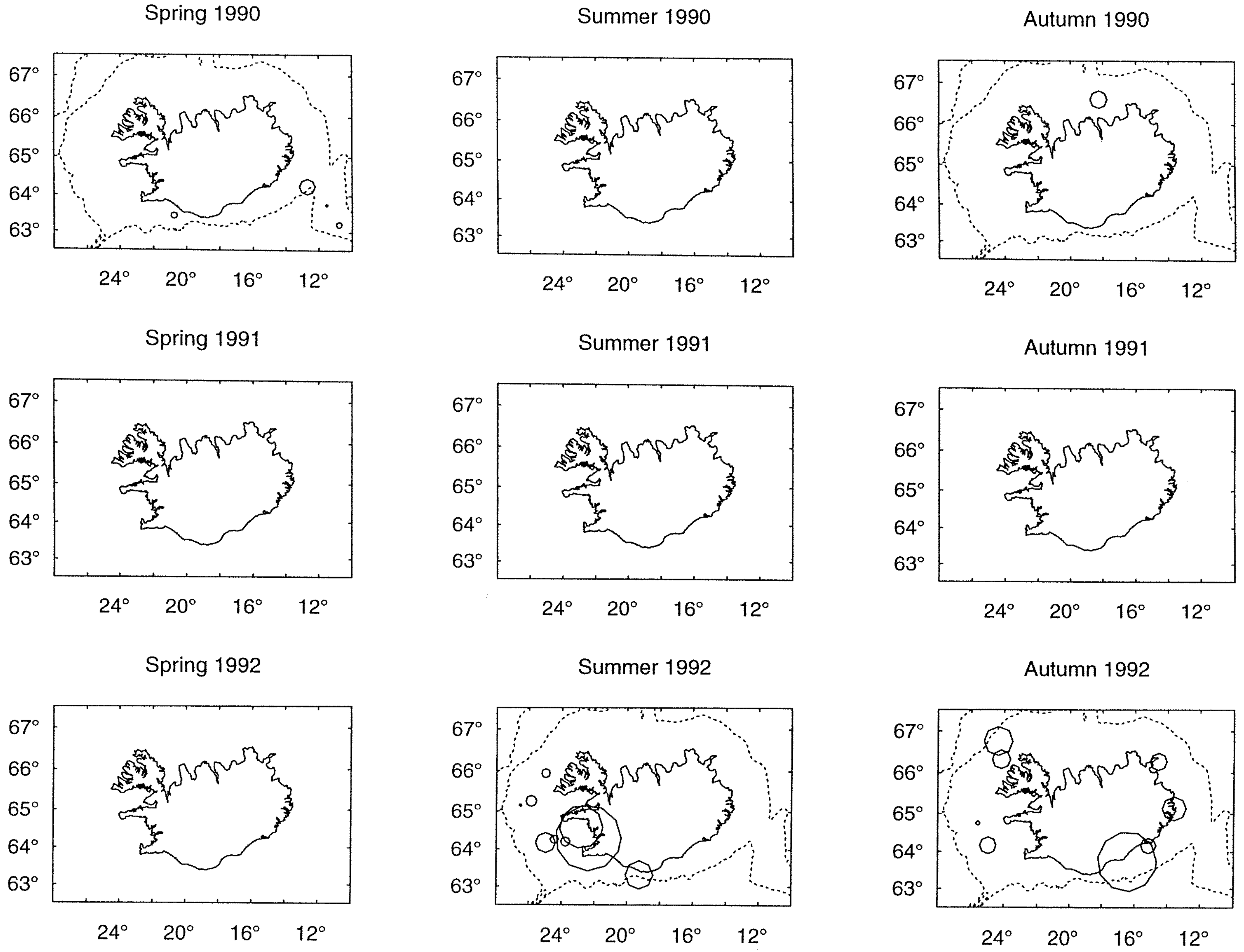


Figure 3.6. PFIs for sandeels. Circles are proportional to the square root of observed PFI and scaled by the maximum observed for sandeels.

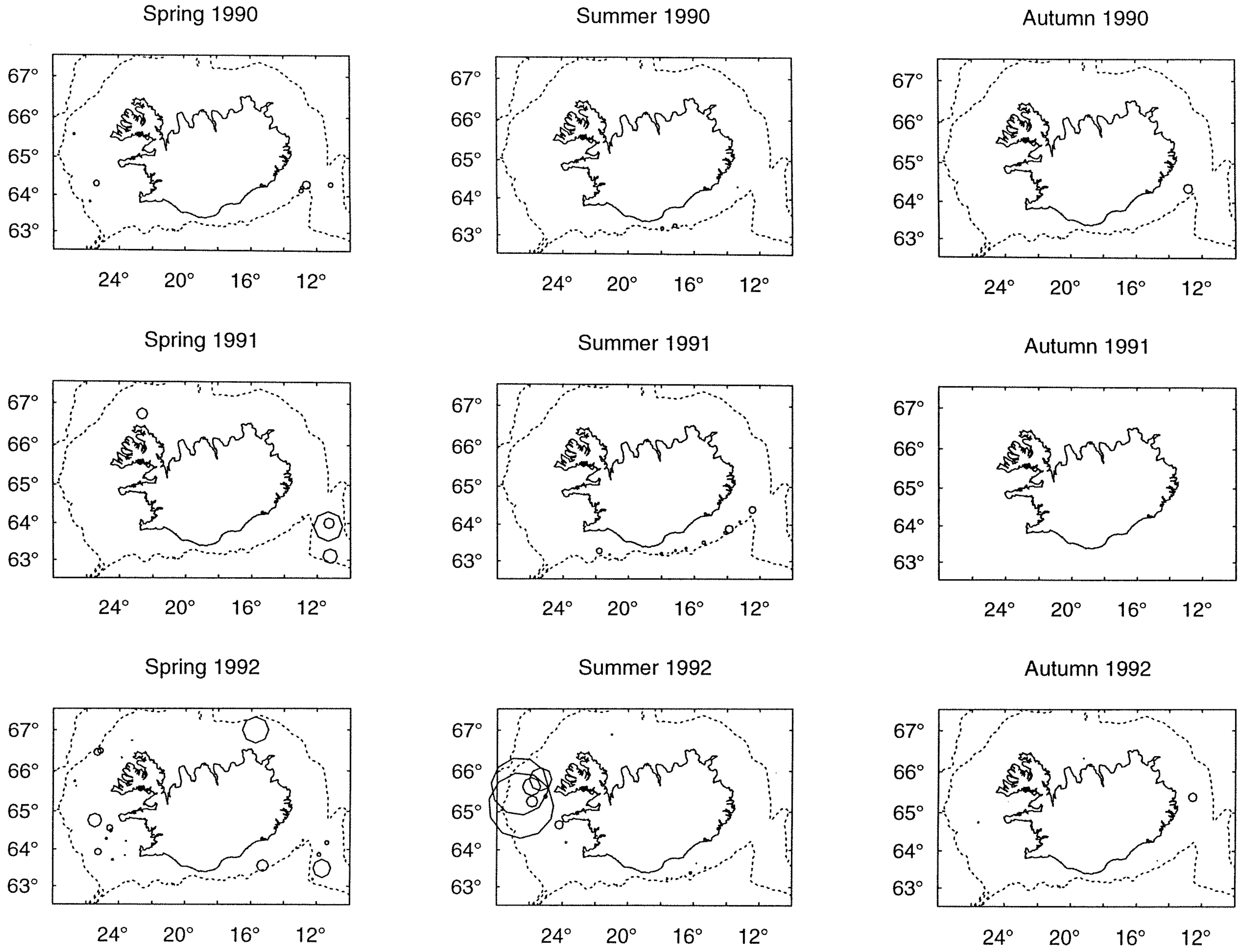


Figure 3.7. PFIs for squid. Circles are proportional to the square root of observed PFI and scaled by the maximum observed for squid.

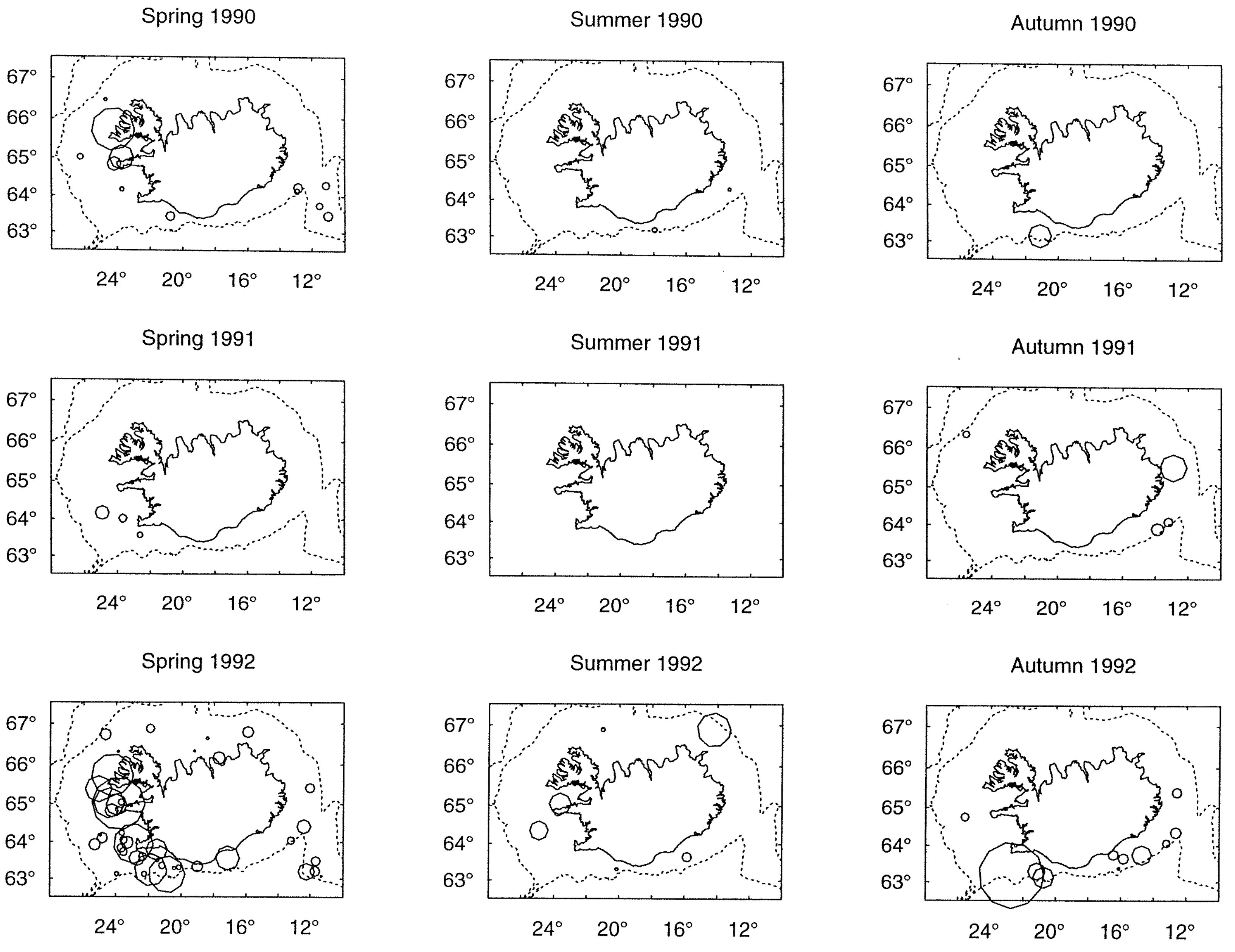


Figure 3.8. PFIs for shrimps. Circles are proportional to the square root of observed PFI and scaled by the maximum observed for shrimps.

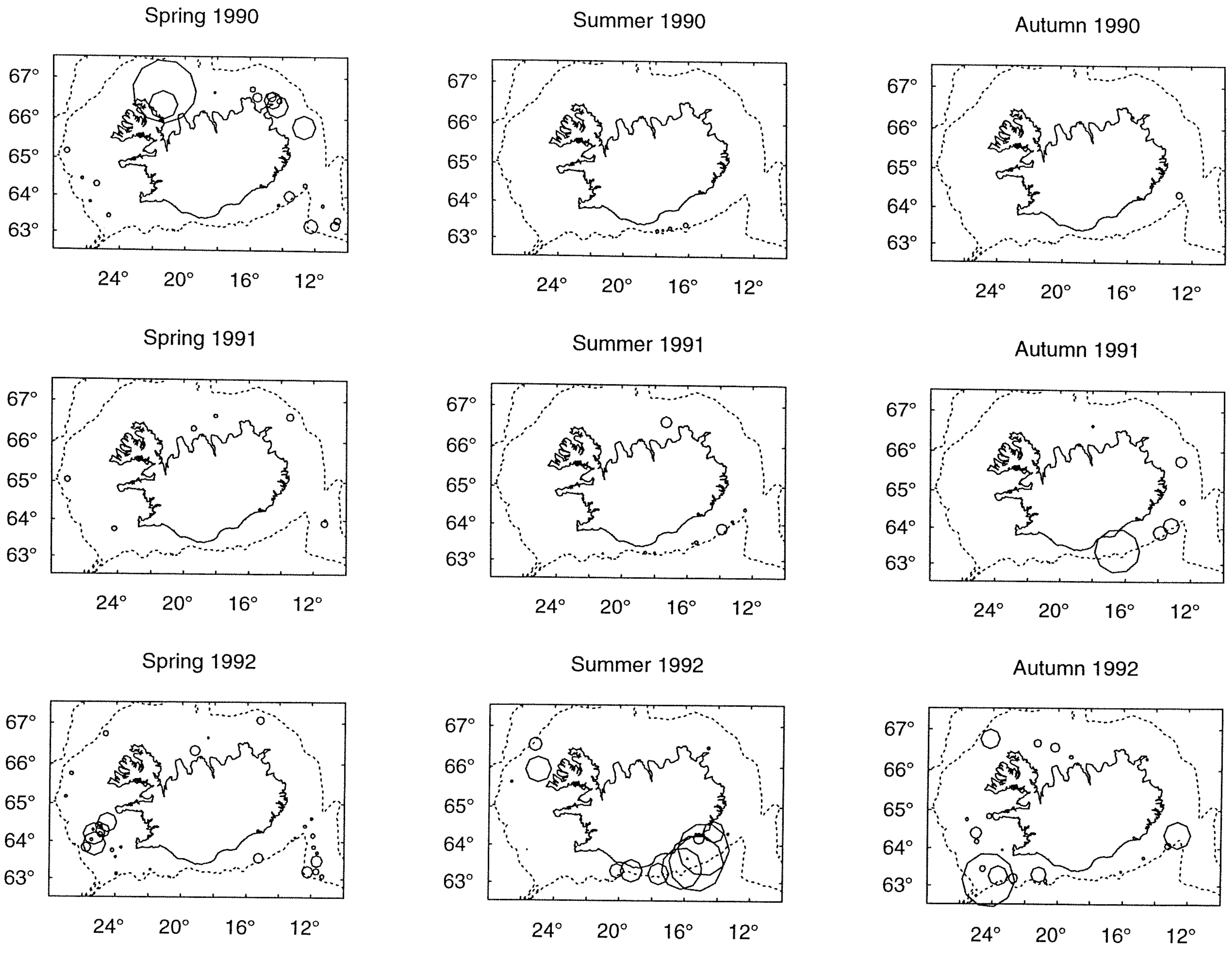


Figure 3.9. PFIs for hyperiid amphipods. Circles are proportional to the square root of observed PFI and scaled by the maximum observed for hyperiid amphipods

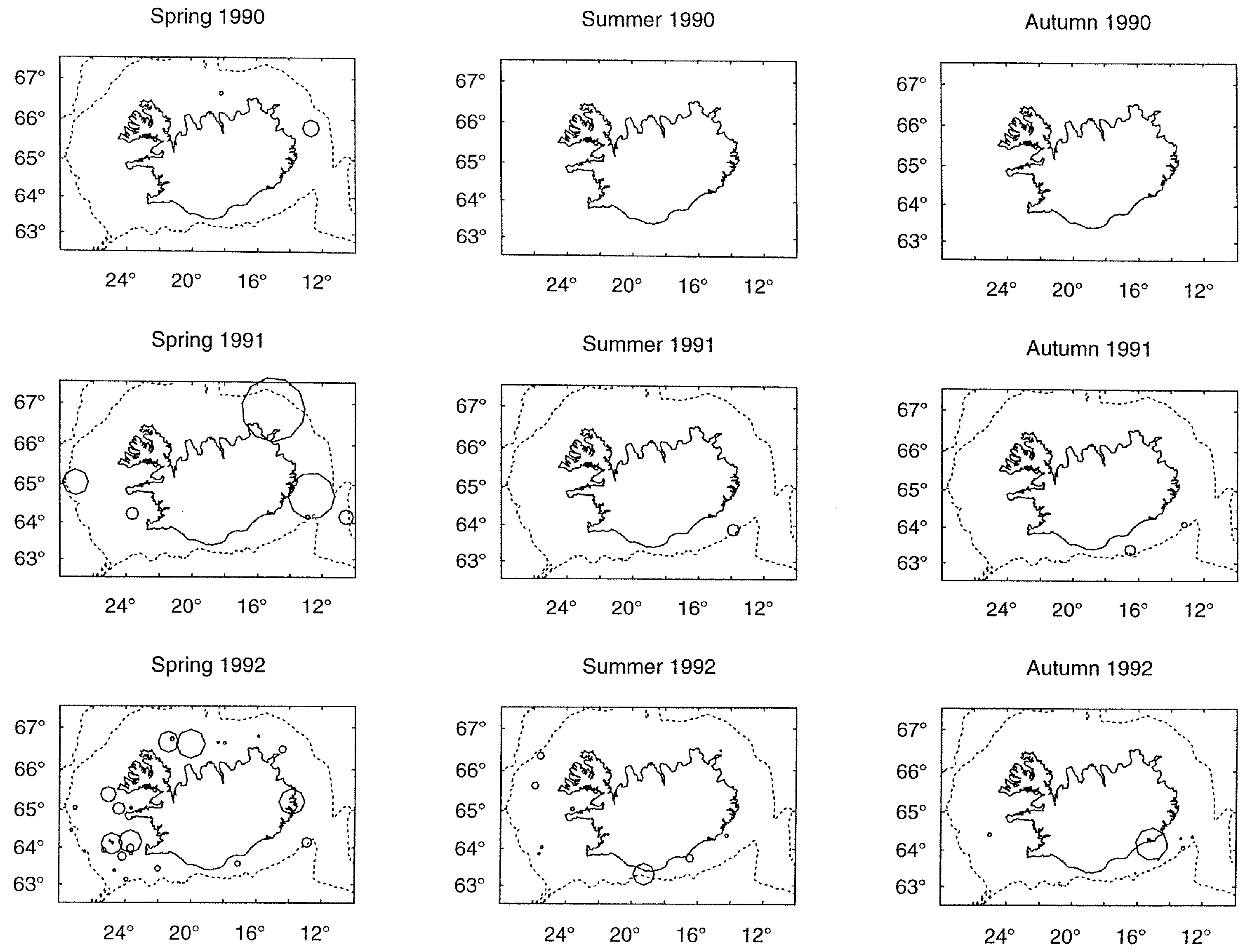


Figure 3.10. PFIs for benthic organisms. Circles are proportional to the square root of observed PFI and scaled by the maximum observed for benthic organisms.

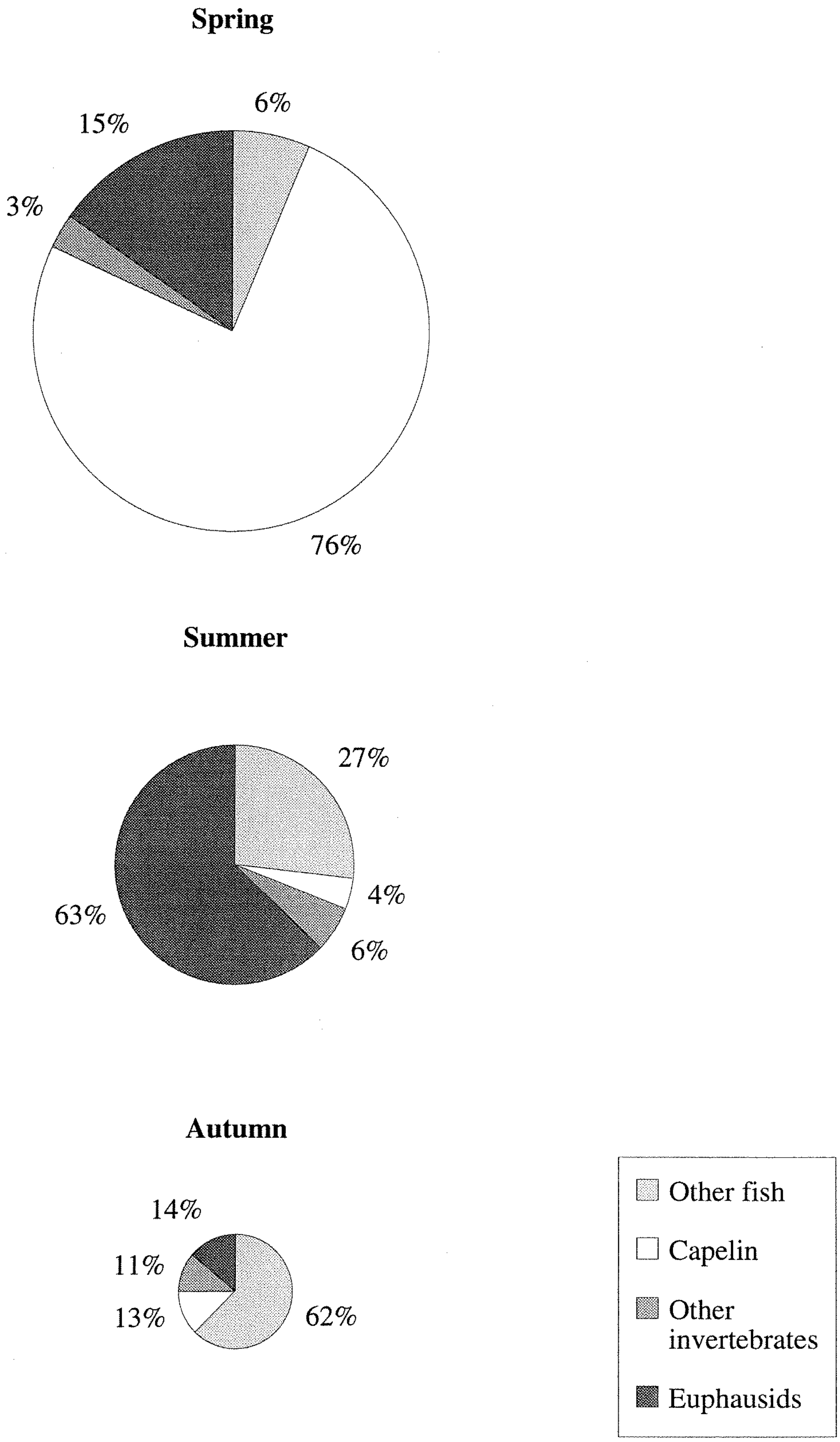


Figure 3.11. Weight percentage of main prey categories by season. Pie sizes are approximately proportional to the amounts analysed in each season.

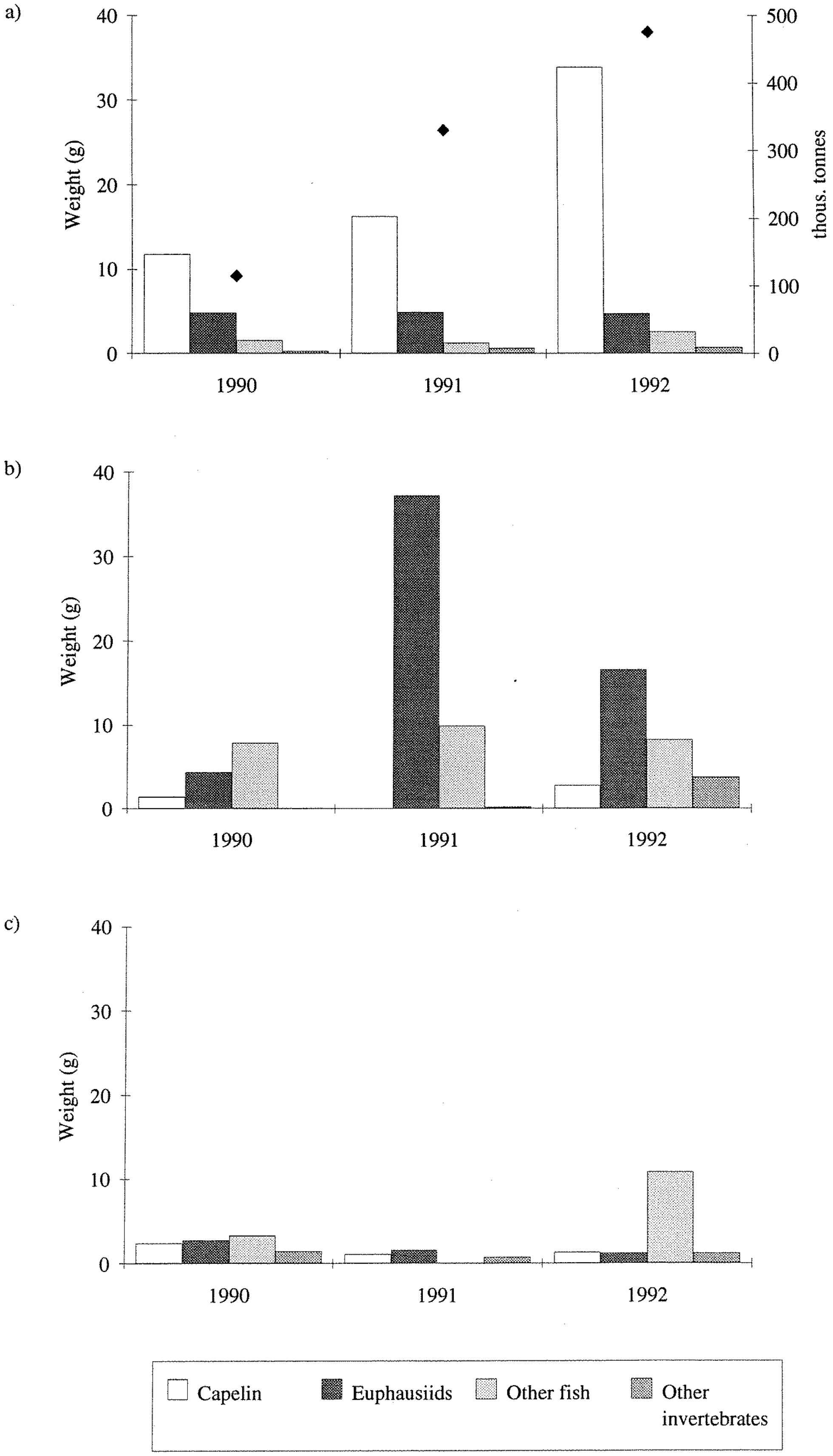


Figure 3.12. Average contents of main prey categories in a) spring, b) summer and c) autumn 1990-1992. Capelin biomass in March (from Vilhjálmsson 1994) is denoted by black diamonds in a).

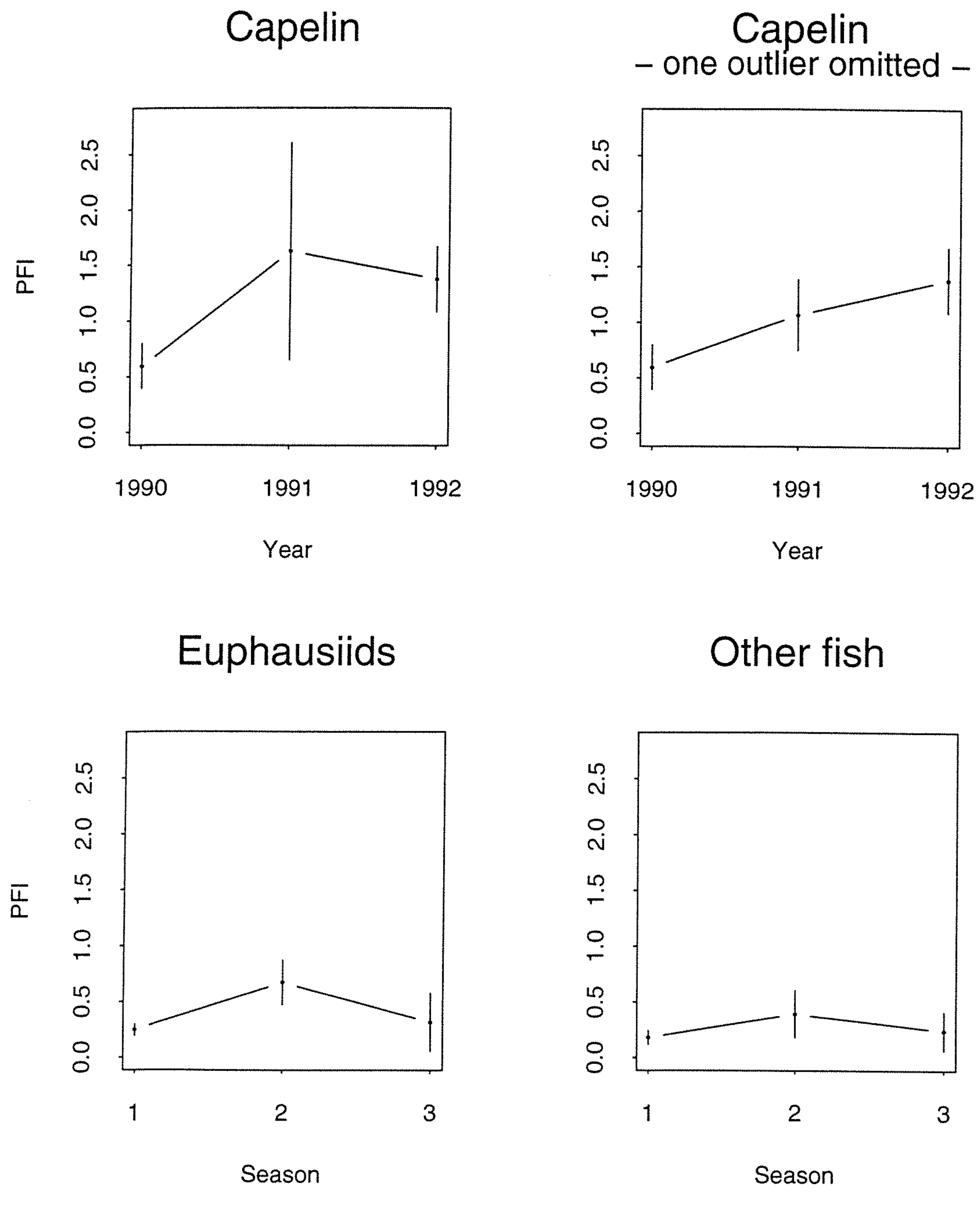


Figure 3.13. Mean PFI of main prey groups with approximate 90% confidence intervals. Spring data only for capelin. Data for euphausiids and other fish pooled for each season. 1 = Spring, 2 = summer, and 3 = autumn.

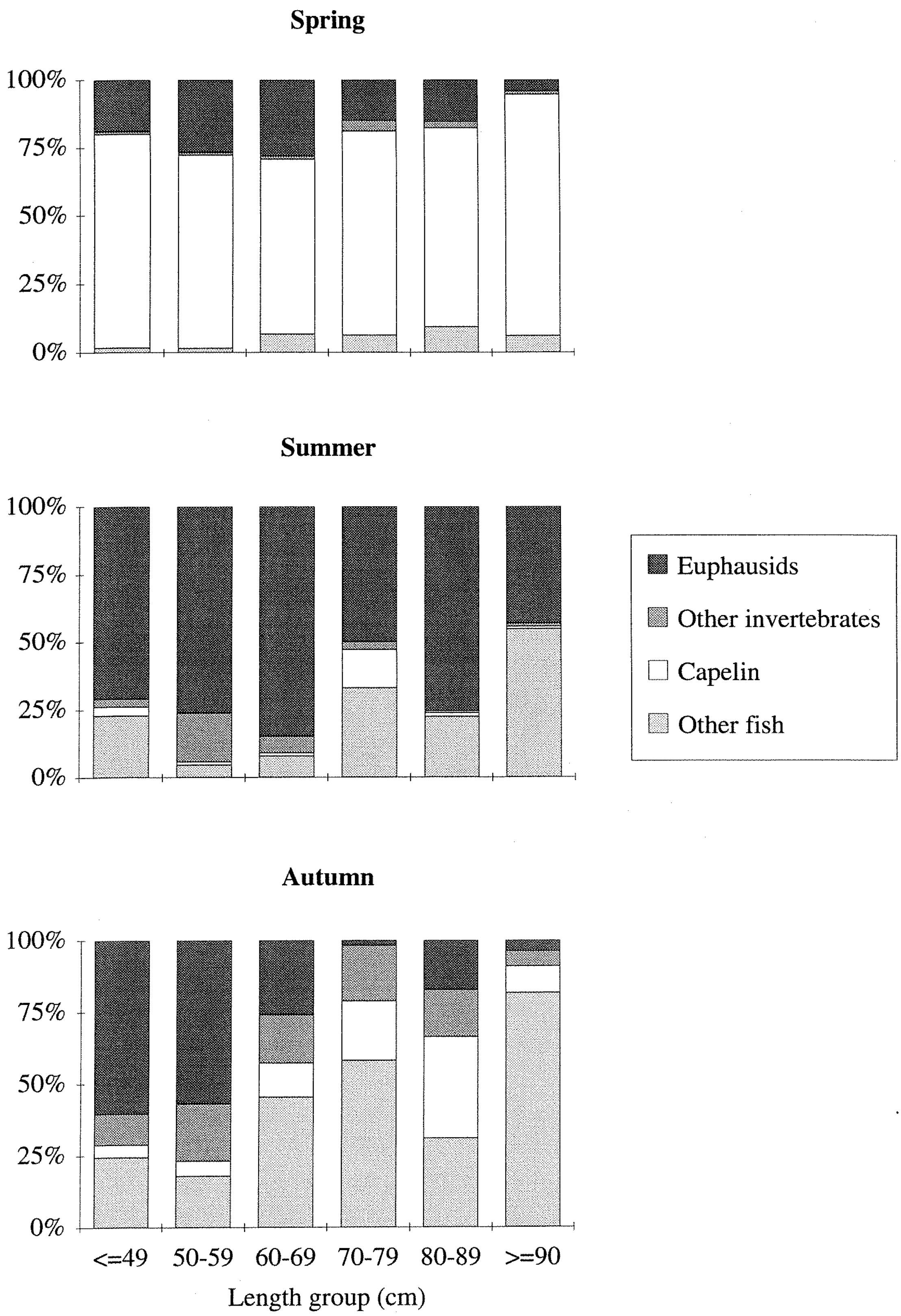


Figure 3.14. Overall weight percentage of main prey categories by saithe length group and season.

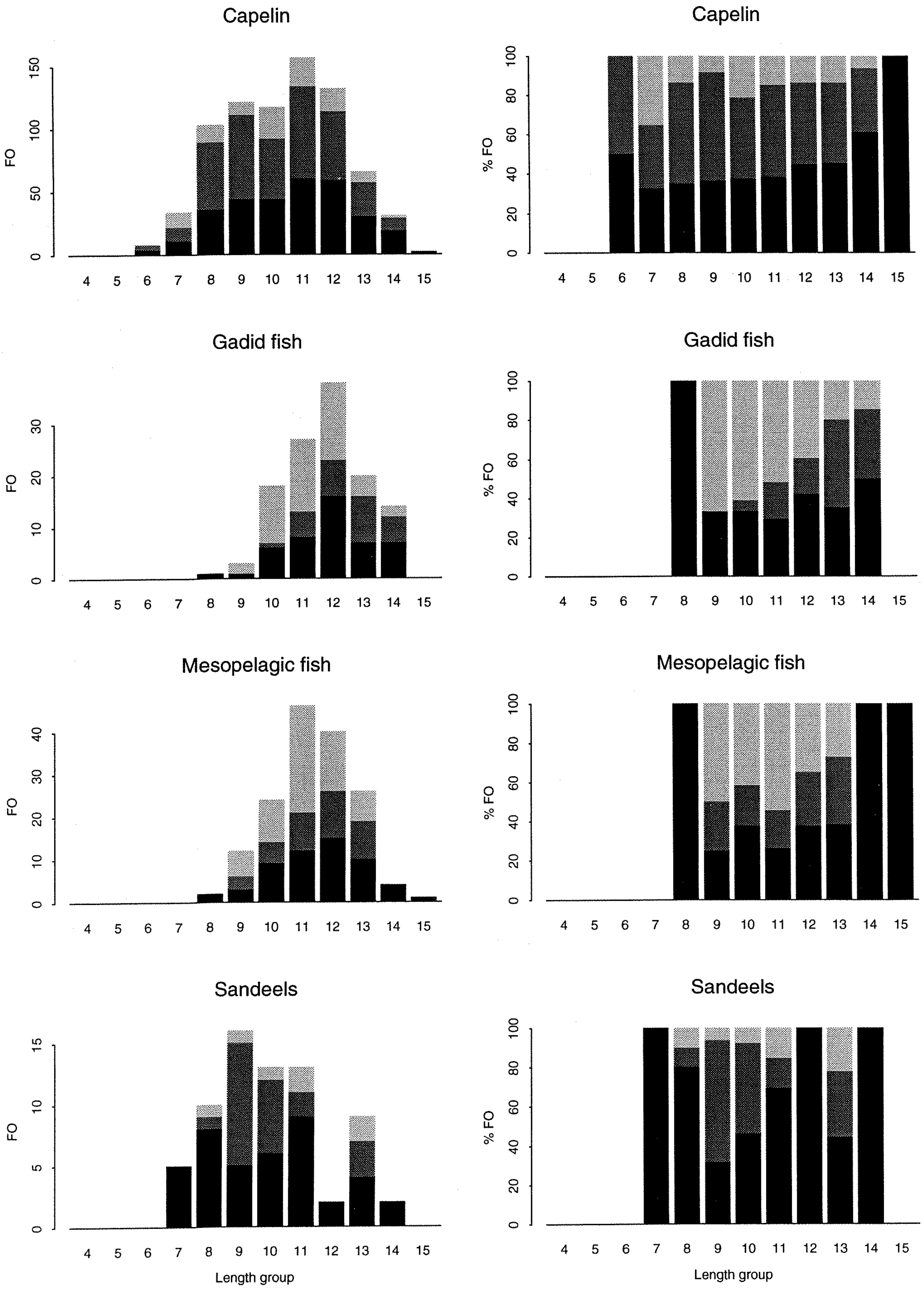


Figure 3.15. Frequency of occurrence of fish prey by saithe length group.
Dark shading represents feeding saithe, light shading non–feeding.
Gray shading indicates the possible range of FO and %FO.

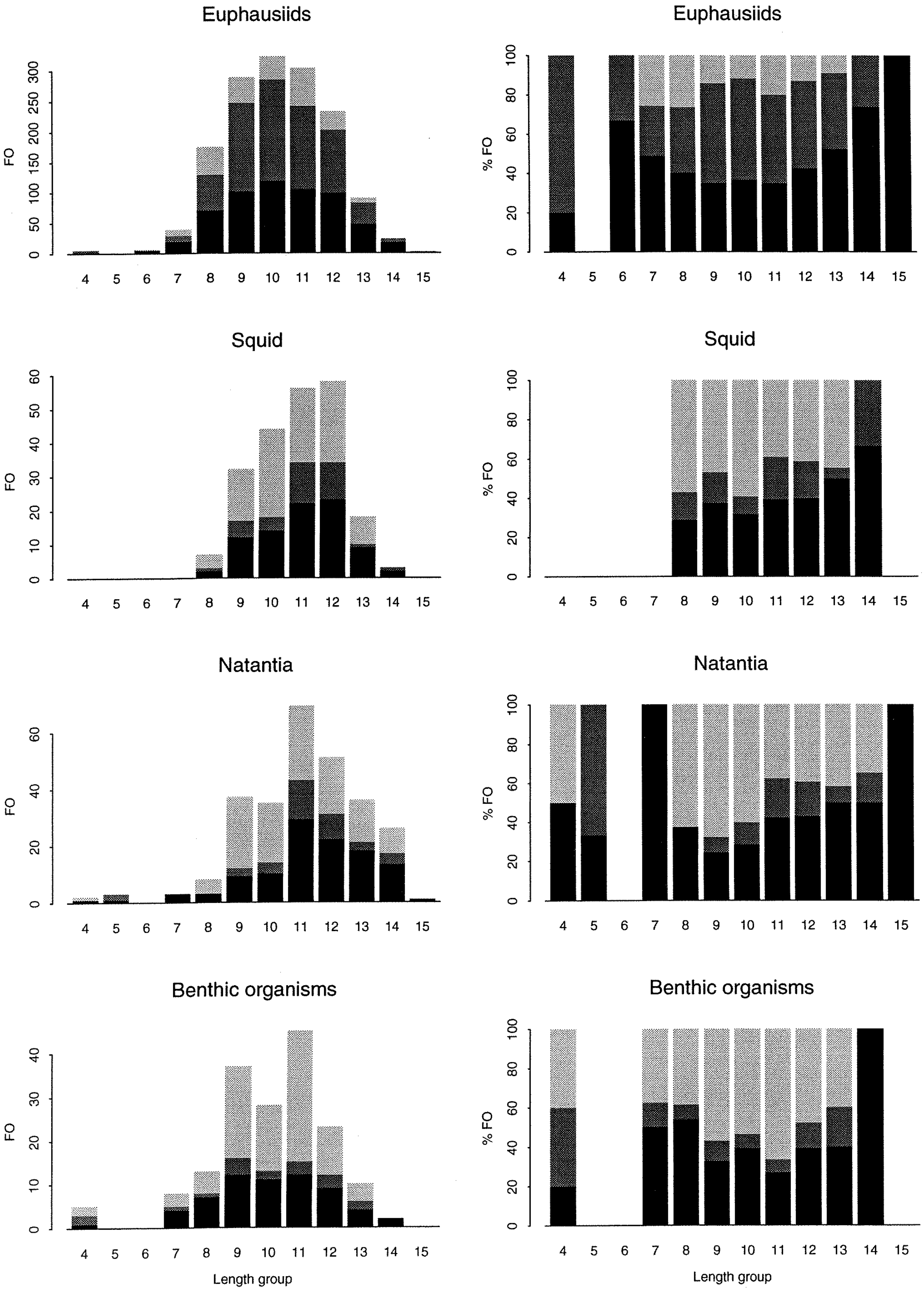


Figure 3.16. Frequency of occurrence of invertebrate prey by saithe length group.
Dark shading represents feeding saithe, light shading non–feeding.
Gray shading indicates the possible range of FO and %FO.

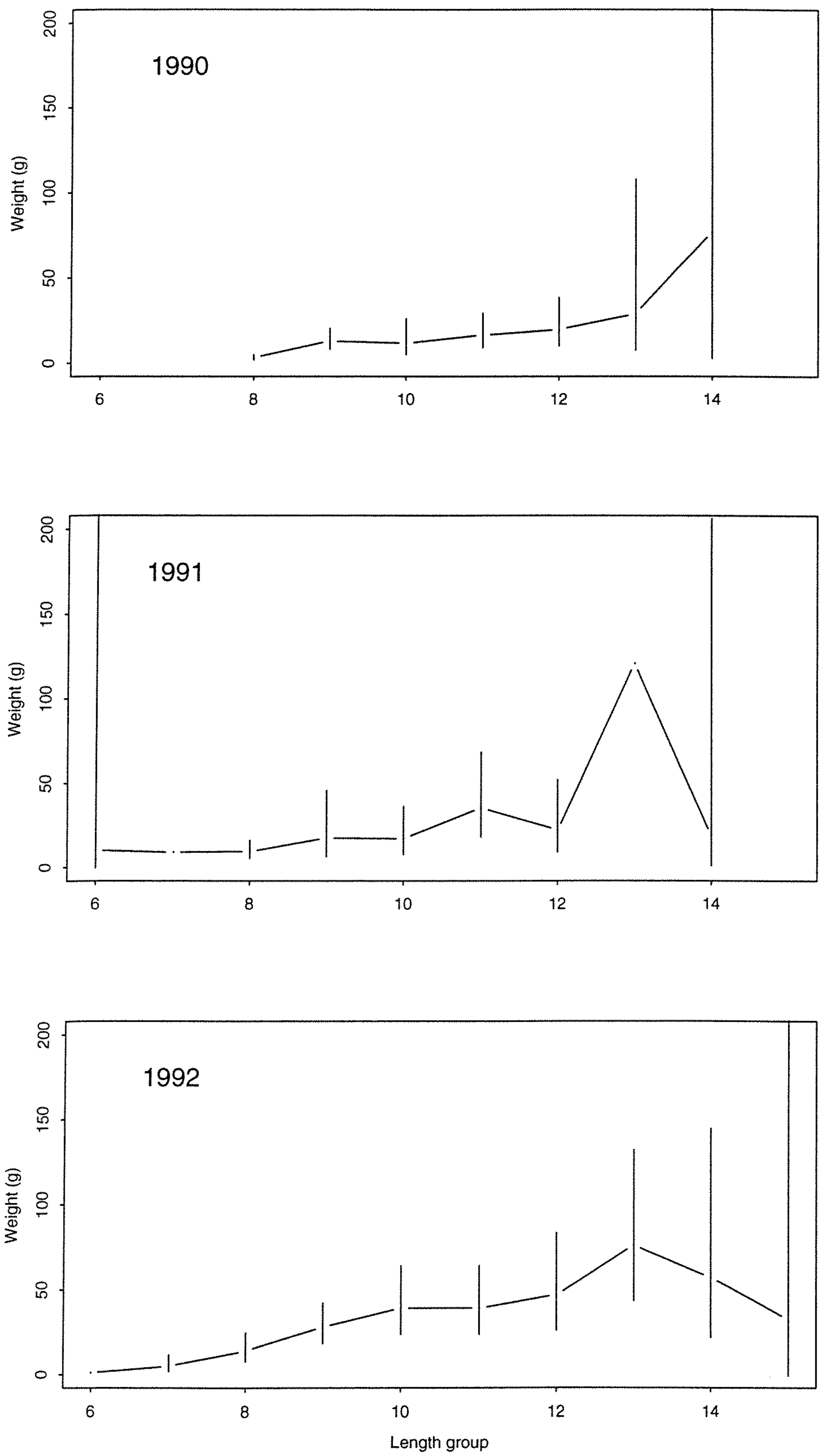

Capelin contents in spring

Figure 3.17. Geometric mean of capelin contents in all samples for each saithe length group along with approximate 90% confidence intervals based on the t-distribution. Means and confidence limits are back-transformed from the logarithmic transformation.

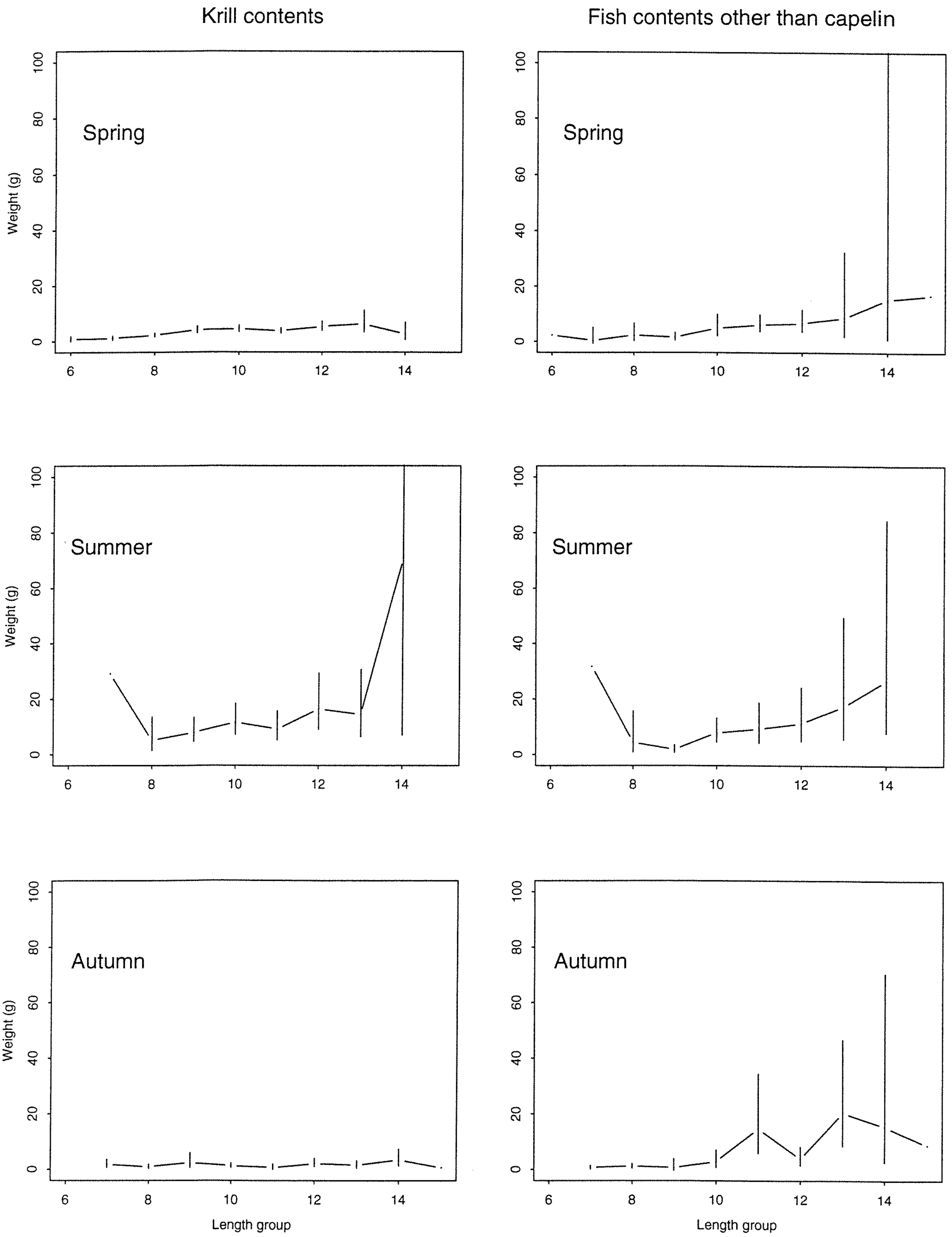


Figure 3.18. Geometric mean of krill and other fish contents in all samples for each saithe length group along with approximate 90% confidence intervals based on the t–distribution. Means and confidence limits are back–transformed from the logarititthmic transformation.

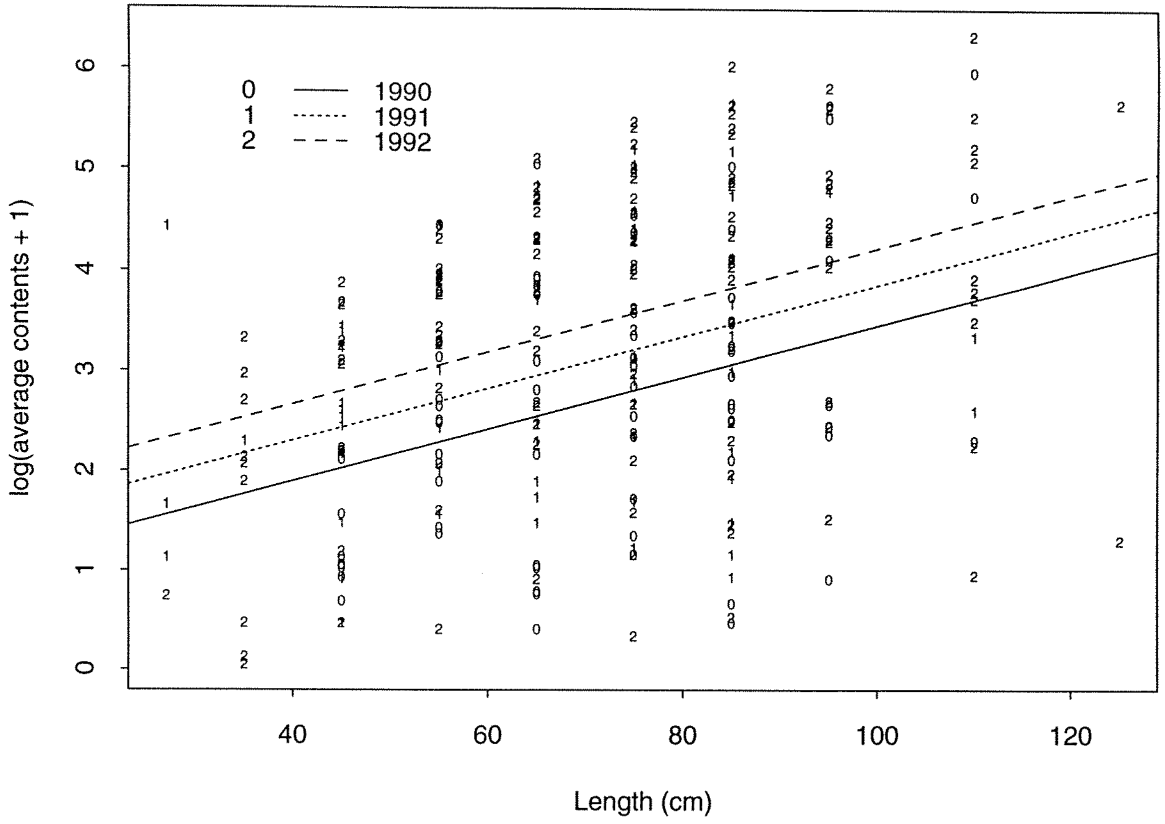


Figure 3.19. Log capelin content in spring by saithe size. Regression lines for each year have the same slope but different intercepts.

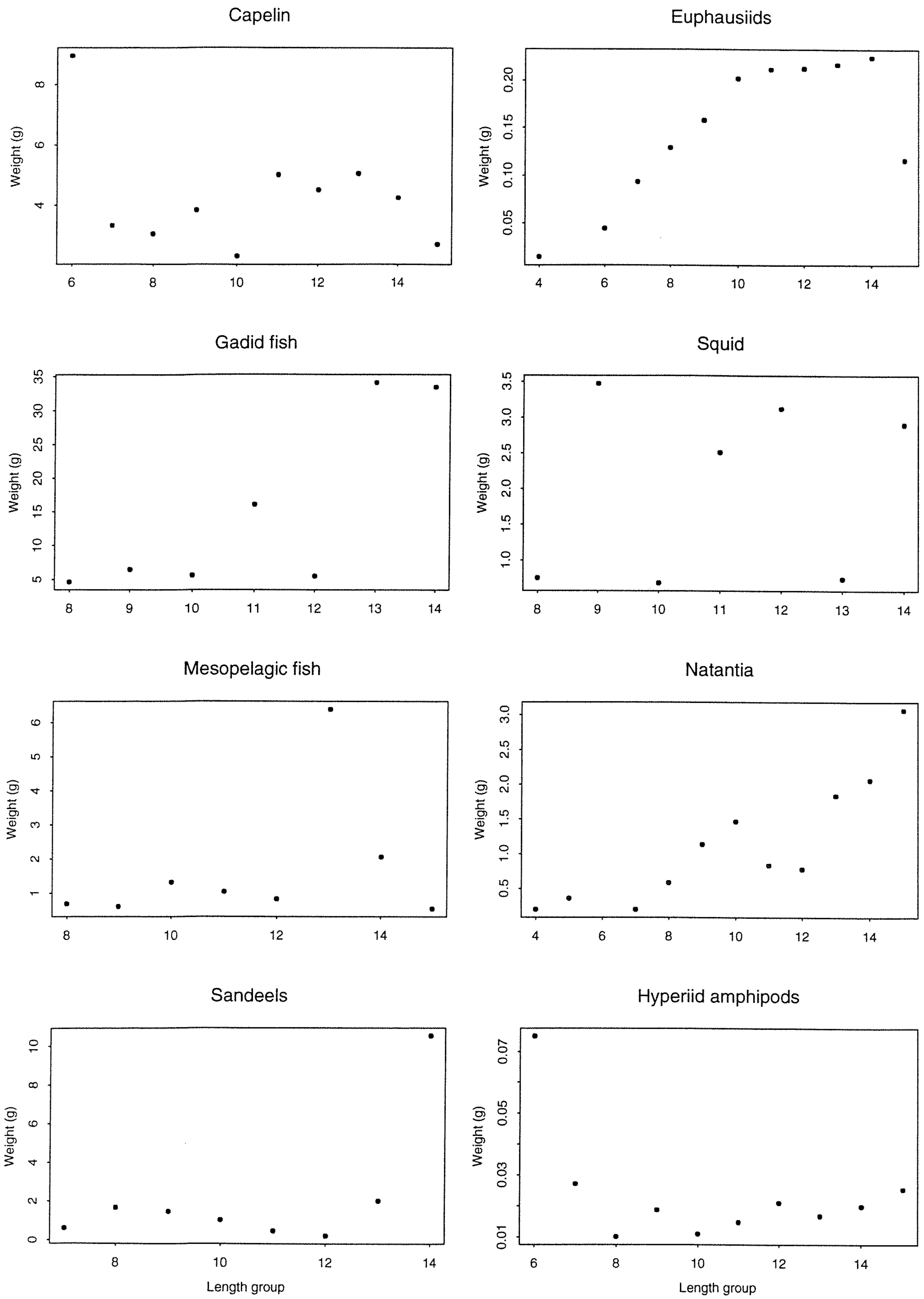


Figure 3.20. Average individual weight of selected prey categories by predator length group.

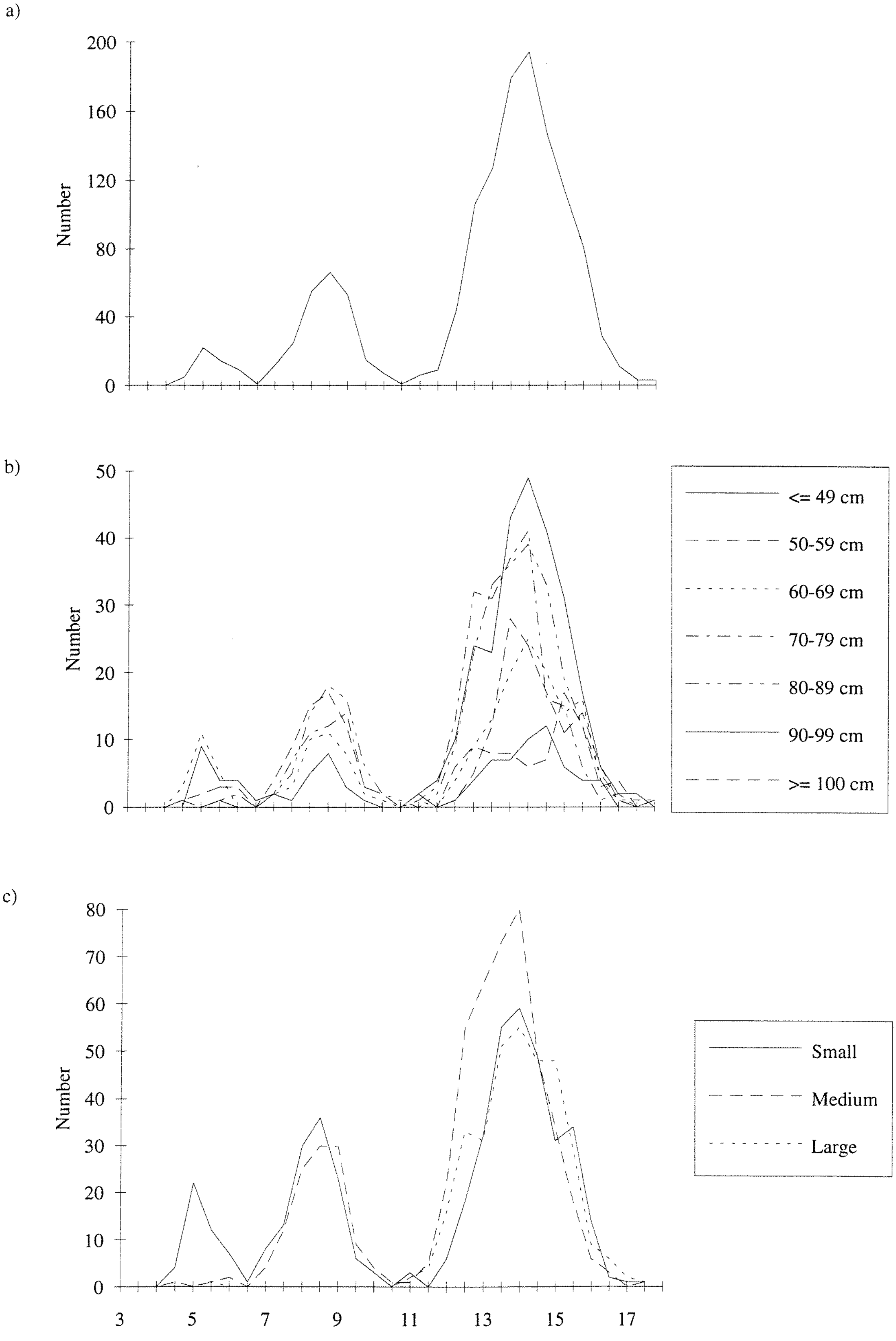


Figure 3.21. Length distribution of capelin prey in 1992 spring samples.
a) All measurements pooled, b) by length group of saithe and c) by size class of saithe.

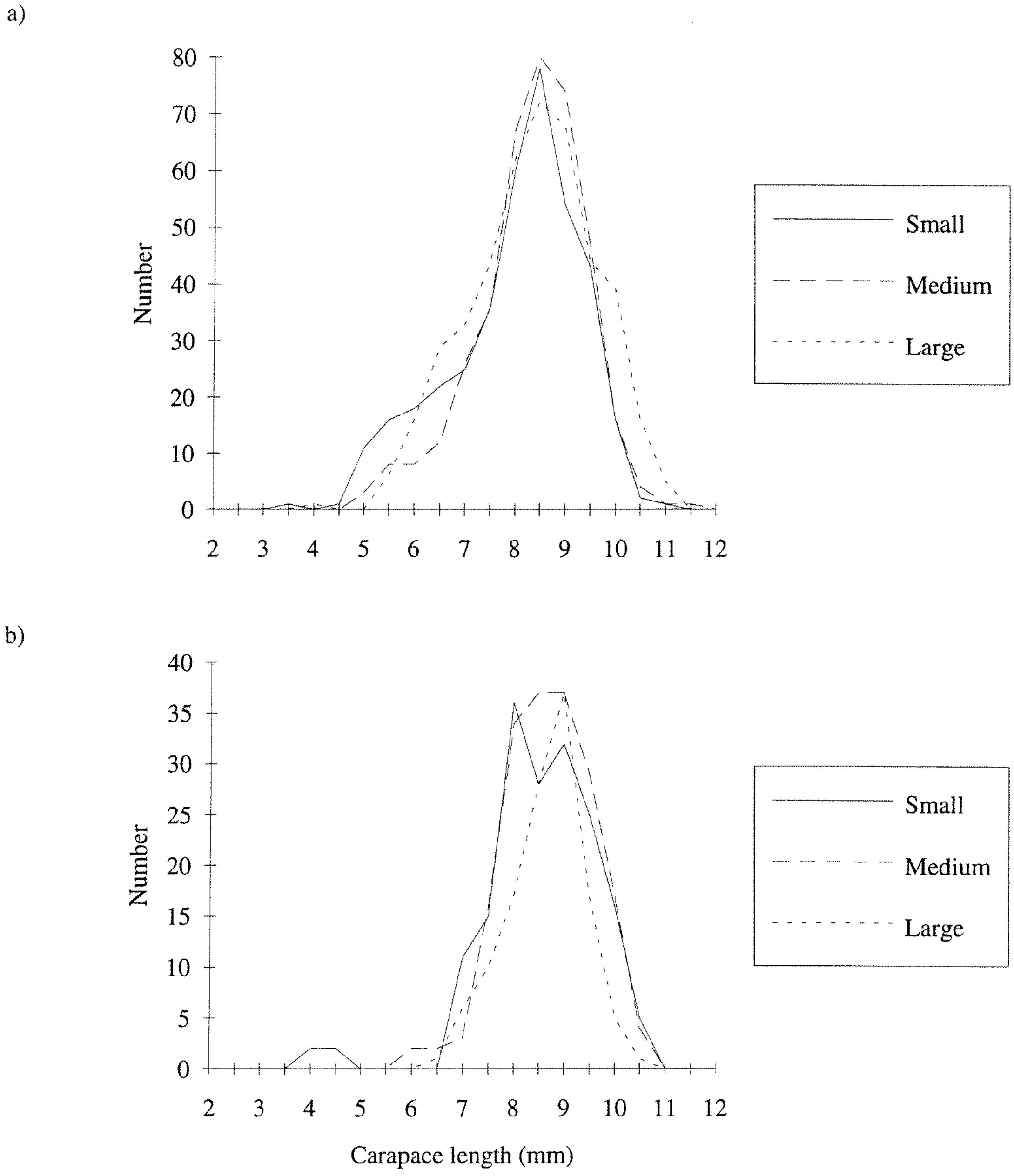


Figure 3.22. Length distribution of *Meganyctiphanes norvegica* in a) spring and b) summer samples 1992 by size class of saithe.

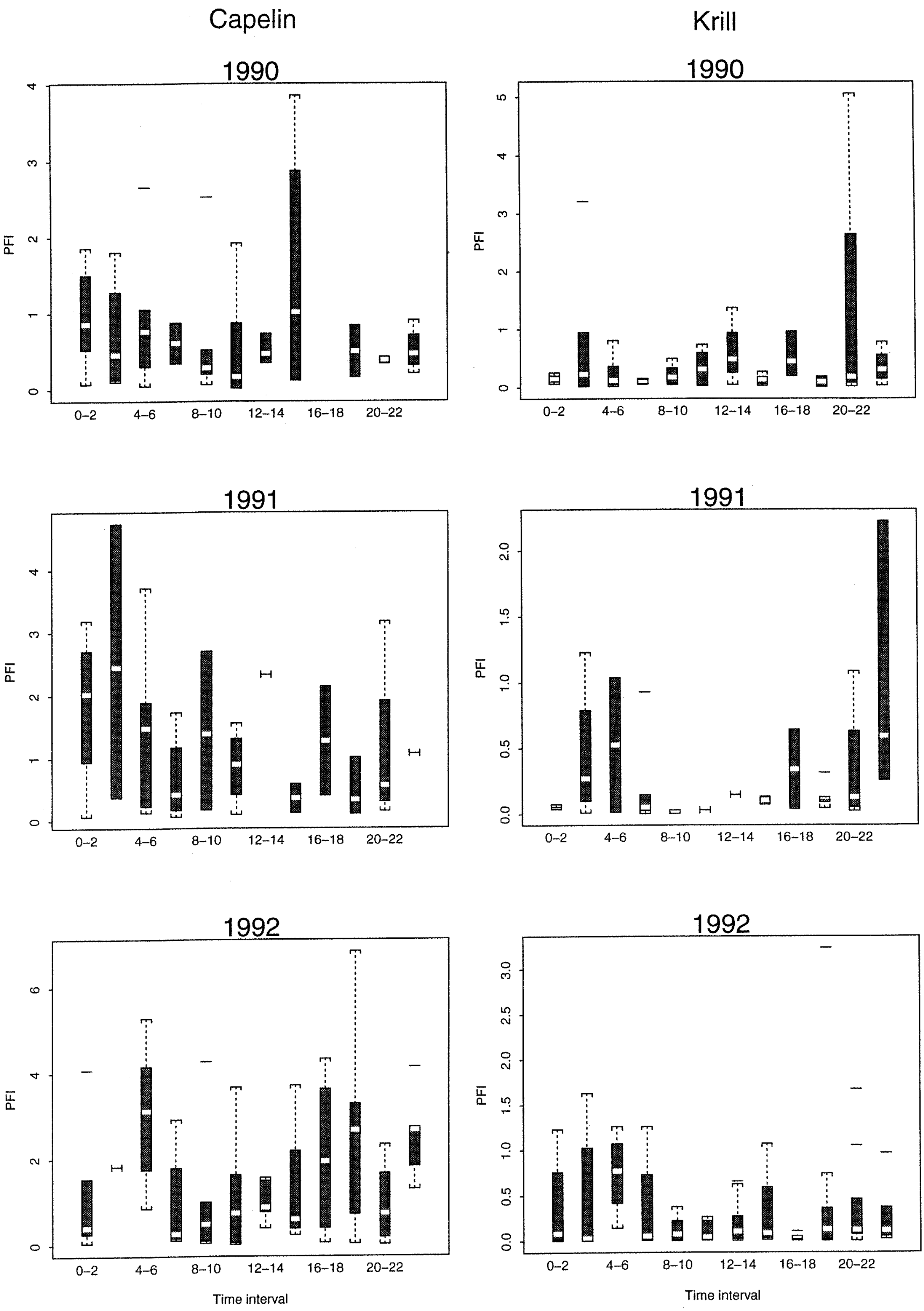


Figure 3.23. Diel variability in average partial fullness indices (PFI) for capelin and krill in spring 1990–1992. White bars denote the median, boxes the inter–quartile range (IQR) and whiskers 1.5*IQR. Isolated lines are outliers, one outlier inomitted.

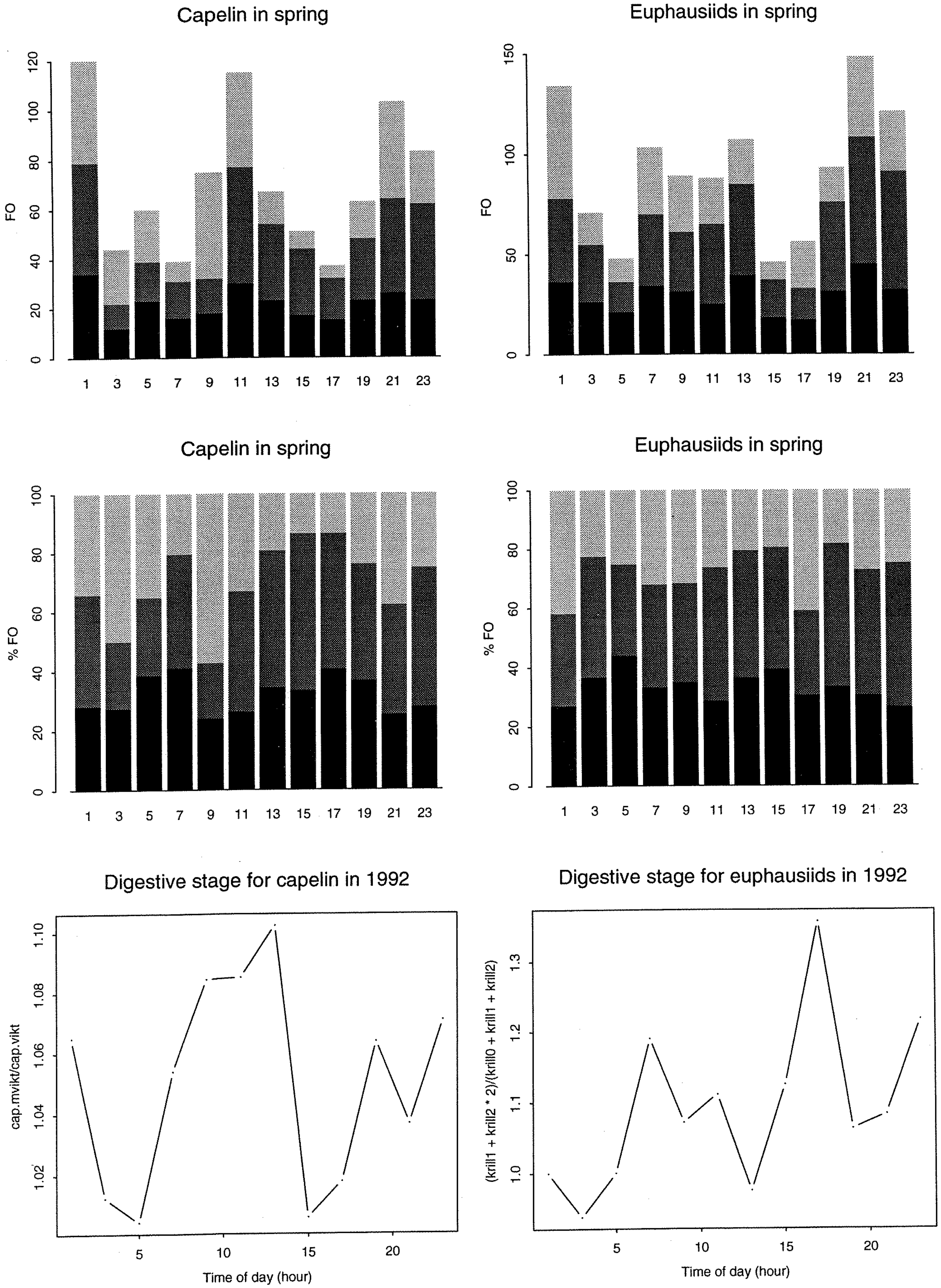


Figure 3.24. Frequency of occurrence and average digestive stage of capelin and krill by time of day in spring. Dark shading indicates feeding, light non-feeding, FO and %FO lay in gray shaded area. Average digestive stage for capelin weighted witith contents, plain average for euphausiids

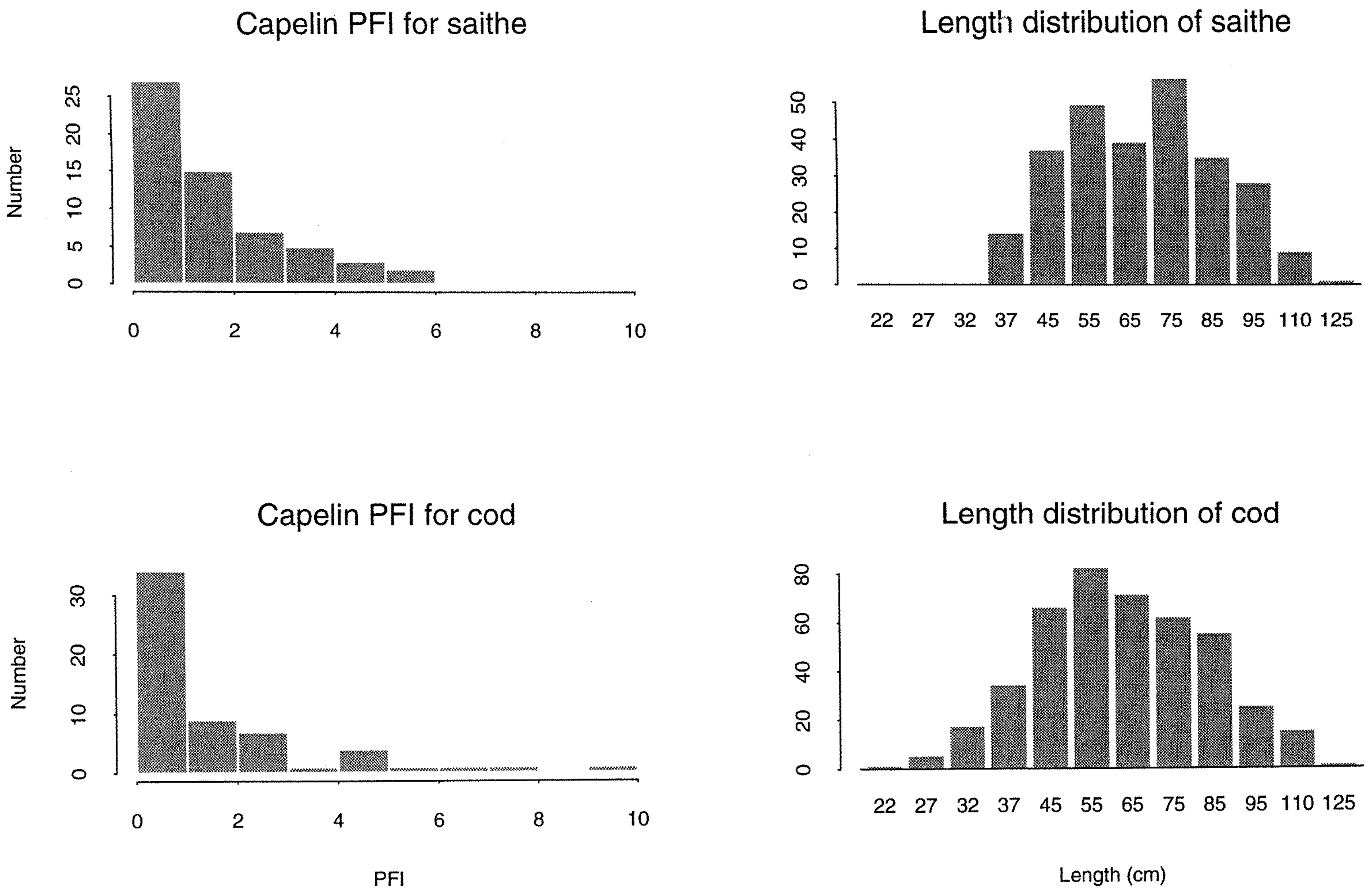


Figure 3.25. PFIs and length distributions of cod and saithe sampled for stomach contents on stations where both species had preyed on capelin

PAPER II

ON SAITHE (*Pollachius virens*) MIGRATIONS TO ICELAND

ABSTRACT

Past and present evidence of saithe migrations in the NE-Atlantic, with emphasis on those between Norway, the Faroe Islands and Iceland, is reviewed. A re-analysis of the only tagging experiment conducted at Iceland indicates that migration from Iceland to Norway is just as likely as migration in the opposite direction. Catch at age curves for a number of year classes of saithe at Iceland peak at a later age than normal, coincident with increased frequency of recaptures of Norwegian tags at Iceland and abnormally low mean lengths at age for the same year classes. Based on deviations in mean lengths at age and an application of the mixture model, the immigration of 7 year olds from the 1984 year class of the Northeast arctic saithe to the Icelandic stock is tenatively estimated at 3.5-7 million saithe or approximately 12-25 thousand tonnes.

1. Introduction

Although the Icelandic shelf waters can generally be regarded as an independent and well defined ecosystem with self-sustained stocks for many of the major commercial fish species, fisheries biologists working there have to take into consideration the possibility of interactions with other ecosystems.

The migrations of the Norwegian spring spawning herring, the main part of the Atlanto-Scandian herring complex, are a case in point and of special current interest. The presence of Norwegian herring at Iceland was first suggested in the 1930s (Friðriksson 1944) and later verified by tagging experiments (Friðriksson and Aasen 1952). In the 1950s and 1960s, the adult part of this potentially largest herring stock in the world migrated annually, after spawning off the west coast of Norway in February-March, across the Norwegian Sea to feed in the shelf waters off East- and North-Iceland and in the area between Jan Mayen and Iceland. At the end of the feeding season these herring assembled in an area some 40-80 nautical miles east of Iceland, where they remained until the onset of the return migration to their spawning grounds off Norway. Due to environmental adversities, this migration pattern was disrupted in the late 1960s, which, coupled with overfishing, led to the collapse of the stock (Dragesund *et al.* 1980). At present this herring stock is recovering and the adult biomass is estimated to be in the range of 3-4 million tonnes. Concurrent with this, the stock has again begun to migrate west across the Norwegian Sea in search of food in spring and summer. In 1994 and 1995 the feeding migration reached the eastern border of the East Icelandic Current, but continued north and northeast along the Polar Front. A further increase of the adult stock biomass is expected in the coming years with the recruitment of the 1991 and 1992 year classes (Anon. 1995a). When that happens, the earlier migration pattern might be re-established, with overwintering east of Iceland instead of in the Lofoten area, where the herring have spent the winter since the 1970s. The direct impact of several million tonnes of herring on the Icelandic marine ecosystem in the future is not clear but must be considerable.

Among the gadids, both export of fish larvae from the Icelandic area and immigration of older fish returning later to spawn are known occurrences. For cod, the drift of larvae to Greenland (Jensen 1926; Sæmundsson 1934; Vilhjálmsson and Magnússon 1984) and a migration returning to spawn at Iceland have been documented (Táning 1937; Jensen 1939; Jónsson 1996) and to some extent quantified (Schopka 1993; Anon. 1992;

Stefánsson 1992; Shepherd and Pope 1993). The Greenland migration has at times given a considerable boost to the Icelandic cod stock, the record being the case of the migration of the 1945 year class, which is estimated to have added more than half a million tonnes to the Icelandic stock as 8 year old cod in 1953. Presently, however, there is no hope of even a small migration, due to record low abundance of cod at Greenland. (Anon. 1995b).

It has been established from recaptures of tagged fish, that the saithe, *Pollachius virens* L., are highly migratory and abundant evidence exists of a connection between the various stock units inhabiting the NE-Atlantic. This has been demonstrated for the Icelandic and Northeast arctic saithe stocks (Schmidt 1958; Olsen 1961; Jones and Jónsson 1971; Reinsch 1976; Jakobsen and Olsen 1987; Anon 1992; Bjørke and Sætre 1994; Anon. 1995c; Nedreaas and Smedstad 1995) with years when there have been signs of a significant migration of mature or maturing fish from Norway to Iceland (Schmidt 1958; Olsen 1961; Jakobsen and Olsen 1987). Furthermore, Olsen (1959) has suggested that these migrations are linked to the migrations of the Norwegian spring spawning herring, *i.e.* that the saithe cross the Atlantic while hunting herring. Indeed, the question of whether saithe travel from Norway to the saithe spawning grounds at the Faroes and at Iceland was part of the motivation for the first saithe tagging experiment, carried out in northern Norway in 1921 (Sund 1925).

To further investigate the topic of interactions between the saithe stocks in the NE-Atlantic, the literature on tagging and migrations of saithe and the drift of saithe larvae in this area was reviewed.

In the following, it will be established that the mean lengths at age of the Northeast arctic and the Icelandic saithe populations are different. It should therefore, in theory, be possible to detect an immigration of saithe from Norway, if one has sufficient knowlegde of its time and place of arrival. For the sake of simplicity, the main emphasis was put on the Icelandic and Northeast arctic saithe stocks, although it is clear that the Faroe saithe also enter these relations (cf. Section 2.1 on tagging experiments).

The age-length database and virtual population analysis (VPA) tables for saithe at Iceland were examined for signs of immigration. In order to identify potential migration events, differences in size at age between areas, variations in mean length at age (MLA) from spring survey data and on a quarterly basis from samples of the commercial catch, as well as variations in the mean weight at age used in VPA assessments, were studied (Anon. 1995b).

Furthermore, an analysis of published data from VPA of the Icelandic saithe dating back to the 1960s (Anon. 1993) revealed indications of a migration, in addition to those noted in a report by the North Western Working Group (NWWG) of the International Council for the Exploration of the Seas (ICES) (Anon 1992).

Finally, we go one step further and assume, for the sake of argument, that saithe from Norway or from other areas outside Icelandic waters are in part responsible for the, at times, considerably reduced MLA of the saithe at Iceland. The mixture model (*e.g.* James 1978; Shepherd and Pope 1993) was applied to the 1984 year class, the proportion of immigrants in the Icelandic area in 1991 was estimated along with the variance of that estimate.

2. Review of evidence of saithe migrations

2.1. Tagging experiments

A summary of the tagging experiments on saithe in the NE-Atlantic that have been reported is given in Table 2.1.

Table 2.1. Summary of saithe tagging experiments in the NE-Atlantic

Conducted by	Reported in	Tagging locality	Period of tagging	Number of tags	Tag returns
Norway	Reviewed by Jakobsen 1995	Norway	1921 and 1954-1982	87 000	≈15% overall recapture rate
Norway	Bjordal and Skar 1992	West coast of Norway	Nov. 1990 - Nov 1991	2 607	334 or 12.8% by June 1992
Faroes	Nicolajsen 1995	Faroes	1960-1965, 1976 and 1991	12 597	1 098 with known position or 8.7%
Iceland and England	Jones and Jónssson 1971	Iceland	In July of 1964 and 1965	6 000	3 175 or 52.9%
Scotland	Newton 1984	N. North Sea and W. of Scotland	1973-1988	4 658	310 or 6.7%
England	Jones and Jónsson 1971	Various localities	prior to 1964	unknown	393 with known position
France	Fontaine *et al.* 1985	N. North Sea and W. of Scotland	1980 and 1983	1 752	326 or 18.6%
				More than 115 000 saithe tagged	More than 18 500 tags recovered

Recapture rates in these tagging experiments vary a great deal. The tag releases north of Iceland in 1964 and 1965 had the singularly highest return rate, over 50%, while returns from the other experiments were more similar, ranging from 5-20%.

Table 2.2 summarizes recaptures from a part of the experiments above. The overview is incomplete, since the results of the experiments are given in varying detail and can not be directly compared. Furthermore, the Scottish and French experiments, conducted in the northern North Sea and west of Scotland, yielded no returns outside of the general area of tagging, other than from across the North Sea off the west coast of Norway and from the Norwegian Deep.

Table 2.2. Summary of recaptures of tagged saithe according to release and recapture locality.

Tagging locality	Recapture locality					Tagging period	Notes	Source
	Iceland	Faroes	North Sea	Mid-Norway	Norway north of 67°N			
Iceland	3 155	8	3	6	?	1964-1965	a	2)
Faroes	116	1 080	48	13	?	1960-65, 1976, 1991	a	2), 9)
North Sea	4	11	879	86	11	Prior to 1964, 1972-74		2), 3)
Mid-Norway	2	14	207	685	42	1971-74		4), 6)
Mid-Norway	0	4	59	236	9	1975-77		7)
Norway north of 69°30'N	106	50	?	388	?	1954-80	b	8)
Norway north of 69°30'N	20	6	?	?	?	1955-58	c, d	1)
Norway north of 67°N	6	5	35	20	1 055	1970-74	e	5)
Norway north of 67°N	2	5	29	90	1 161	1975-77	e	8)

a No distinction between Mid- and northern Norway.
b Reference 8) gives an analysis of the Norwegian taggings from 1954-1980 with respect to rates of migration to the Faroes and Iceland, recaptures from the North Sea and northern Norway not given.
c Included in the total recaptures from taggings in northern Norway in 1954-80 given above.
d Only the number of recaptures from Iceland and the Faroe Islands given.
e Part of the recaptures from these experiments included in total recaptures for 1954-80.

Sources: 1) Olsen 1959, 2) Jones and Jónsson 1971, 3) Jakobsen 1978, 4) Jakobsen 1978a, 5) Jakobsen 1978b , 6) Jakobsen 1978c, 7) Jakobsen 1981, 8) Jakobsen and Olsen 1987, 9) Nicolajsen 1995

For the sake of curiosity it is noted that 3 saithe, tagged north of Iceland in 1964 and 1965, were caught off W-Greenland.

The results of the tagging experiments conducted by Norway, concerning migration to Iceland and the Faroes, are dealt with most thoroughly by Jakobsen and Olsen (1987). These authors give recapture rates in Norwegian statistical areas 06 and 07, which encompass the Northeast arctic saithe's main spawning grounds off the central west coast of Norway and compare them to recaptures at the Faroes and at SE- and NW-Iceland, but only from taggings in northern Norway. The return rates are given relative to returns per 1 000 tons fished by German vessels, scaled to represent 1 000 fish tagged each year. Such scaling makes numbers from different periods comparable, although the tagging effort might have varied. Furthermore, the analysis was restricted to returns from the northernmost releases only, *i.e.* some 40 000 out of a total of 87 000 tags (Jakobsen 1995). Since numbers have been scaled we can neither study single tagging experiments with respect to returns by area, nor are there data for all areas. However, recaptures have been made at Iceland from taggings in other areas off Norway (Jakobsen 1978, 1978a, 1978c, 1981, 1995; Bjordal and Skar 1992).

From the Norwegian tagging experiments, which still continue, 106 tags out of 40 000 saithe tagged north of 68°30'N were returned from Iceland, 55 from the Faroes and 388 from Norwegian statistical areas 06 and 07. This, together with the fact that in some years in the period 1954-1980, return rates from one or both of two Icelandic subareas were actually higher than from areas 06 and 07 off the central west coast of Norway, is given as evidence of an ongoing and sometimes large-scale migration to Iceland and the Faroes (Jakobsen and Olsen 1987). That the westward migration may in some years take the form of mass movements has also been suggested previously (Schmidt 1958; Olsen 1959, 1961; Reinsch 1976). The English/Icelandic taggings in 1964 and 1965 and their returns are often cited as indicating that an emigration from the Icelandic area is less likely, *i.e.* that the traffic is one-way (Jones and Jónsson 1971; Jakobsen and Olsen 1987).

It is interesting to apply the same analysis as Jakobsen and Olsen (1987) to the results of Jones and Jónsson (1971), *i.e.* returns from spawning grounds *vs.* returns of emigrant tags, the underlying assumption being that the migrations are spawning migrations. From maps showing the distribution of tag returns around Iceland, the returns from an area encompassing the spawning grounds of the Icelandic saithe were counted. This area was defined as the shelf area south of Iceland, with boundaries along latitude 65°30'N in the west and 64°30'N in the east. This area division is based on the distribution of the two main water masses in the Icelandic shelf area, and is much used when analysing the results of the Icelandic groundfish survey. The counting is given in Table 2.3 and the results of the two analyses are compared:

Table 2.3. Comparable figures from the Norwegian experiments of 1954-1980 and from the English/Icelandic experiment of 1964 and 1965

	Recapture locality		
Tagging locality	Home spawning grounds	Faroes	Other side of the Norwegian Sea
North of Iceland	55 (80%)	8 (11%)	6 (9%)
Northern Norway	388 (71%)	50 (10%)	106 (19%)

Sources: Jones and Jónsson 1971, Jakobsen and Olsen 1987

Obviously, these experiments indicate a similar pattern of recaptures at the home spawning grounds and away from home for both stocks, *i.e.* about equal probabilities for a saithe from Iceland migrating to Norway as for the opposite case. This statement is independent of any considerations about fishing mortality, tag density, age at maturity, recapture rate and so on, if emigrant spawners and home spawners are identical until the onset of maturity and the choice of spawning ground is made.

At least two authors (Jakobsen 1995; Nicolajsen 1995) mention return rates having dropped over the years. This leads to speculations on whether return rates may differ according to area, the Icelanders, then, being the most diligent tag returners. Another point, worth attention, is the difference in relative returns taken west of Scotland and from the North Sea from Faroese and English taggings at the Faroes. It seems reasonable to assume that the rate of returns from the area closest to the laboratory that "owned" the tags is highest, since the fishermen close to the release areas are likely to be better aware of the taggings and the importance of returning tags than their collegues in other countries or farther away.

2.2. Deviations in mean length at age

Reinsch (1976) discusses the mobility of the saithe in his monograph on this Atlantic species. He quotes Schmidt (1958) as having described deviations from a 5 year average MLA in data from German landings of Icelandic saithe. Schmidt's findings show a deviation becoming apparent in catches taken at NW-Iceland in July and August 1957 from the 1949-1951 year classes. Reinsch then demonstrates the same phenomenon for the 1958-1961 year classes in 1965 and for the year classes from 1961-1963 in 1969. As supporting evidence an extraordinary drop in strength of the 1960 year class in Norwegian waters in 1965 is given. Reinsch concludes that migrants from Norway had reached SE-Iceland in April-May and then spread to other fishing localities later in the year. These findings indicate an immigration of saithe to Iceland.

The possibility of an emigration of saithe from Iceland has also been pointed out by previous authors (Schmidt 1957; Reinsch 1976). Apart from referring to Jones and Jónsson (1971), Reinsch (1976) states that the proportions of some year classes in German saithe landings from Iceland and the Faroe Islands show reciprocal variations, namely, that on at least two occasions a strong year class at Iceland has been reduced disproportionately from one year to the next, while it has increased in strength at the Faroes beyond the normal prognosis. The hypothesized emigration from Iceland is taken to occur at a later age than in the case of the immigration of saithe from Norway. In this case, the evidence of numbers in catches from the year classes is the basis for the emigration theory since the growth rates of saithe at Iceland and the Faroes, estimated from samples of German catches, were similar (Reinsch 1976).

2.3. Indications in VPA data

In a report of the North-Western Working Group (NWWG) of ICES three points are made which could support the hypothesis of an immigration of saithe to Icelandic waters in 1991 (Anon. 1992). First, large discrepancies were found between predicted and actual catch at age 7 in 1991 (*i.e.* the 1984 year class) and, second, the observed mean weight for this age group in the catch was lower than that predicted by the model used by the NWWG. In addition, a comparison of the length distributions of age group 7 in 1990 and 1991 shows that the upper halves of these distributions coincide, while the length distribution for age group 7 in 1991 contains markedly higher numbers of small fish, as shown in Figure 2.1. The total number of seven year olds, sampled for age determination in 1991, was more than 50% higher than average, while no such increase was observed for other age groups. However, the abundant 1984 year class was also represented in numbers higher than average already as 5 and 6 year olds in the two previous years, and shows a negative deviation in both mean length and weight for these age groups.

2.4. Larval drift

During a research programme on the distribution of fish eggs and larvae (HELP), conducted by the Institute of Marine Research (IMR), Bergen, off the Norwegian coast in April - May 1985-1992, saithe postlarvae were in some years observed drifting in from spawning areas outside of Norwegian waters (Bjørke and Sætre 1994; Nedreaas and Smedstad 1995). This was probably the case in 1985, when these surveys started, although a clearer picture might have been achieved by beginning the survey earlier in the year as was done in the following years. A westerly distribution was observed in 1986, 1987 and, to some extent, in 1988. An example of this type of distribution is shown in

Figure 2.2, where it is evident that concentrations of postlarvae entered the survey area at approximately 63°N, near the zero meridian. During the remaining years of the programme a more coastal distribution was observed.

The sources of the imported larvae remain an open question, which will be difficult to answer with present state of knowledge. A hypothesis has been put forth stating that the immature saithe in the area off the coast of Norway between 62°N and 66°N originate mainly from spawning grounds other than the known grounds in that area. These spawning grounds are, ranked in order of importance, the North Sea, Iceland and the Faroes (Bjørke and Sætre 1994).

3. Methods used for estimating a migration

Long distance migrations of fish are mainly connected with spawning or feeding. The means by which the fish find their way across the oceans remain something of a mystery, especially in the case of homing. A whole suite of signals has been mentioned as possible explanations for the orienting capabilities of fish. Some combination of these, along with an element of randomness, must be regarded as the most likely mechanism (Harden-Jones 1968; Legget 1977). This fascinating topic will not be dealt with here but some of the methods used to account for migration in virtual population analyses by assuming that migration takes place, either continously or as isolated events, will be described.

The Northeast arctic and North Sea saithe stocks have been assessed by VPA with the inclusion of a migration from an area north of 62°N south to the North Sea. Jakobsen (1981a) effectively redefines the boundaries between these two stock units. All juveniles (age groups 1-4) in an area off the coast of Norway between 62°N and 64°N are assumed to end up in the North Sea, while the older fish in this area belong to the Northeast arctic saithe. The landings from this area were then divided accordingly in separate VPAs for the two stocks.

The ICES Coalfish Working Group (Anon. 1983) tried a different approach. Juvenile Northeast arctic saithe found in an area between 62°N and 66°N were considered potential migrants to the North Sea and the proportion migrating annually was estimated from tag returns. An estimated rate of emigration was then included in a VPA for the Northeast arctic saithe, and furthermore an equal rate of immigration to the North Sea saithe was assumed. These methods have some obvious drawbacks. The Coalfish Working Group concluded that Jakobsen's procedure overestimated the migration. The use of tag returns to estimate migration rates is questionable due to the non-random distribution of tags in the saithe population (*e.g.* Olsen 1959). A joint VPA for the NE-Atlantic saithe stocks has also been tried and a VPA for saithe in the North Sea and west of Scotland (Anon. 1974; Hastie *et al.* 1995). The conclusion from the joint VPAs has been that the largest stock units tend to dominate the results.

Several alternative models have been proposed for the assesment of immigration of cod from Greenland to the Icelandic cod stock. A summary of four different methods is given below.

1. Shifts in the maxima of catch at age for a year class to ages greater than "normal", coupled with low fishing mortalities (F) at age for the younger age groups from an ordinary VPA, are used to identify migrating year classes (cf. Section 5.4). The Fs for these age groups are then raised subjectively to a level similar to that for the adjoining year classes, or, in the case of consecutive year classes showing evidence of migration, to fit a likely fishing pattern. The migrating quantities are estimated by running the VPA again, but now with the manually adjusted Fs. The estimate of the number of migrants is the numbers of cod one needs to add to the VPA to solve the equations. This method has been applied to the Icelandic cod data for hindcasting immigration from Greenland back to 1941 (Schopka 1993).

2. In the assessment of the Icelandic cod stock, an ADAPT type of tuned cohort analysis (Gavaris 1988; Stefánsson 1988), which incorporates an estimate of migration, is used. For years and ages, at which migrations are known to have occured, a parameter representing migration is added to the model. The results of the cohort analysis for a given set of terminal Fs and, in our case, of numbers of migrants, are tuned to catch per unit effort (CPUE) data from a number of fleets, *i.e.* CPUE from different gear types, areas and seasons, including both commercial and survey data. Tuning consists of the minimization of the weighted sum of the squared difference between observed and predicted CPUE, with the prediction based on a simple linear model relating log-CPUE to log-abundance. In the minimization process, the fleets are weighted subjectivly in a manner preventing any single fleet or age group from becoming overly important in the estimation. Migrations are assumed to occur as fixed numbers, estimated by the minimization procedure, as additions to the population at the beginning of a year. The method has been decribed as not very stable statistically and the choice of weights is crucial (Stefánsson 1992; Shepherd and Pope 1993).

3. To overcome the subjectivity of the two previous methods, Shepherd and Pope (1993) propose two different ways to model migration. One of these is a VPA conducted on a restricted age range, considered free of any contamination by migrating fish. For the Icelandic cod, ages 6 and younger were included in the analysis on the assumption that migrants have generally reached age 7. An extended survivors analysis (XSA) is performed with different restraints on terminal Fs and a weighted average of the resulting Fs is used in the final model. Migration is estimated, in numbers of 3 year-olds, as the difference between the recruitment estimates from conventional VPA and the XSA on the restricted age range.

4. In the same paper, a simple method for estimating a migration is proposed. These authors take large negative residuals from an ANOVA, attempting to explain the logarithm

of the weight at age in the catches in terms of age, year and year class effects, coupled with a high ratio between year class strengths at Greenland and Iceland, as an indication of a migration. The proportions in which residents and immigrants from these yearclasses mix, as 6-8 year old fish, are estimated on the basis of differences in mean weights. The mean weight at age of immigrants from Greenland is obtained from data on their source population. For the residents at Iceland, a crude estimate of mean weight is found by performing an ANOVA similar to the one just described, but excluding from the ANOVA the candidate year classes after they reach the likely age of migration.

The last mentioned method will be used here for the 1984 saithe year class at Iceland, but calculations will be based on lengths rather than weights. It is assumed that a migration occurred in 1991 but, instead of using a mean length estimate for the resident part of the year class from a predictive ANOVA, a set of four mean lengths of age group 7 will be used, *i.e.* 77, 78, 79 and 80 cm. However, performing this type of ANOVA on mean lengths for saithe of ages 3-7 in 1985-94, with zero weight given to seven year olds in 1991, predicts a mean length at age 7 in 1991 of 77.5 cm. This indicates that the lower two of the four values selected are the most realistic.

4. Material and methods

4.1. Biological material

The age-length database for Icelandic saithe at the MRI and some summary data on Northeast arctic saithe from the IMR form the main data basis for this study. For our purposes, the material, for both stocks, can be divided in two, according to how it was collected, *i.e.* in a survey or from commercial catches. In the following, different subsets of the Icelandic age-length combinations, will be considered and compared to the appropriate Norwegian data.

The age readings of some 8027 saithe, collected in the Icelandic groundfish surveys (IGFS) which have been conducted in March annually since 1985, form the basis for the calculation of deviations in MLAs from the long term average MLA of all survey data from 1985 through 1992. The IGFS is a systematic stratified survey, used in the assessment of the main demersal fish stocks at Iceland (Pálsson *et al.* 1989). Age readings from other months and vessels were omitted in order to achieve standardization, *i.e.* with regard to season and selectivity of the fishing gear.

For the present purposes, the survey data were insufficient and, therefore, the material was extended to include also samples from commercial catches. All age-length information on the saithe year classes since 1959 was extracted from the fish data base at the MRI. These data were screened graphically and obvious outliers omitted, *i.e.* the points, lying clearly isolated outside the main range of the data, were deleted. The age-length combinations from this analysis are shown in Figure 4.1. Data were limited or missing for some years early in the period. Since 1974 sampling has been continous and in fair numbers for most years and year classes and that period was, therefore, chosen as the basis for further analysis.

The age was determined from broken sagittal otoliths by trained staff at the MRI. Although no validation study of these age determinations has been undertaken, saithe otoliths are generally considered easily read (Anon. 1995c) in agreement with the consensus on its relative, the cod (Jørgensen 1992).

For Northeast arctic saithe, two sets of mean length data were made available (K. Nedreaas, IMR, pers. comm.). The first gives the mean length at age from four autumn surveys, *i.e.* in 1988, 1989, 1993 and 1994, based a total of 2 880 fish. The surveys covered an area off the Norwegian coast, extending from Møre into the western part of the Barents Sea. In addition, mean lengths at age in samples from commercial catches for the period 1984-1993 were used.

Recent reports of the Arctic Fisheries Working Group and the NWWG of ICES were used as sources of relevant VPA statistics for the two stocks, *i.e.* catch at age, mean weights at age, and fishing mortalities for each age group over the years (Anon. 1993, 1995, 1995b).

4.2. VBGF model specification

Von Bertalanffy's growth function (VBGF), for describing the relationship between age and length, was used as a tool for comparing the growth of Icelandic and Northeast arctic saithe. The likelihood ratio test procedure described by Kimura (1980) was followed. VBGF was fitted to mean lengths at age of pseudocohorts, obtained by pooling data from 4 autumn surveys off the coast of Norway (1988, 1989, 1993 and 1994) and from 8 consecutive IGFS surveys in spring (1985-1992). Mean length at age was modelled by:

$$\bar{l}_{ij} = l_{\infty_i}\left(1 - \mathrm{e}^{-K_i\left(t_{ij} - t_{0_i}\right)}\right) + \varepsilon_{ij} \qquad (4.1)$$

where i denotes stock and j age group; t is the age, adjusted for the half year difference in timing of surveys; l_∞ is the asymptotic length; K is the parameter generally dubbed the growth parameter; t_0 the hypothetical age at length zero; and ε_{ij} is an error term, assumed independent and normally distributed. In order to test hypotheses concerning model parameters, model (1), which allows separate parameters for the two stocks, was compared to constrained versions of the model, *i.e.*:

$$\bar{l}_{ij} = l_{\infty}\left(1 - \mathrm{e}^{-K\left(t_{ij} - t_{0}\right)}\right) + \varepsilon_{ij} \qquad (4.2)$$

with l_∞ , K and t_0 common for the two stocks corresponding to a null hypothesis of complete parameter equality;

$$\bar{l}_{ij} = l_{\infty}\left(1 - \mathrm{e}^{-K_i\left(t_{ij} - t_{0_i}\right)}\right) + \varepsilon_{ij} \qquad (4.3)$$

a model with a common asymptotical length when the null hypothesis is: l_∞ is equal for the two stocks;

$$\bar{l}_{ij} = l_{\infty_i}\left(1 - \mathrm{e}^{-K\left(t_{ij} - t_{0_i}\right)}\right) + \varepsilon_{ij} \qquad (4.4)$$

where the growth parameter is constrained and the null hypothesis: K is the same for both stocks; and finally

$$\bar{l}_{ij} = l_{\infty_i}\left(1 - e^{-K_i\left(t_{ij} - t_0\right)}\right) + \varepsilon_{ij} \tag{4.5}$$

when the hypothetical age at length zero is assumed the same for both stocks, corresponding to H_0: t_0 is common for Icelandic and Northeast arctic saithe.

These hypotheses were then tested by comparing the residual sum of squares from the full model (1) to that of one of the constrained models (2-5) by calculating the test statistic

$$-N\ln\left(\frac{\hat{\sigma}_\Omega^2}{\hat{\sigma}_\omega^2}\right) \tag{4.6}$$

where N is the total number of observations from the two stocks; $\hat{\sigma}^2$ is the mean residual sum of squares from a model fit; Ω and ω denote the full model and one of the constrained models, respectively. This test statistic will under H_0 have an asymptotically χ^2-distribution with degrees of freedom equal to the number of parameters fixed (Kimura 1980).

4.3. Mixture model

In order to estimate the magnitude of the hypothesized migration of pre-spawners or first-time spawners from Norway to Iceland, the following assumptions were made. A given age group was treated as a mixture of two components, one resident at Iceland assumed to experience "typical" growth and the other of immigrants from Norway assumed to have a mean length close to that observed in the Norwegian landings of that age group. We then proceed to use the "mixture model" to obtain a rough estimate of the proportions of the components constituting the mixed population (James 1978; Shepherd and Pope 1993; cf. Appendix).

In our hypothetical example, four values were chosen of a mean length for the resident component, since there is no way of pinpointing that parameter as of today. The values chosen were 77, 78, 79 and 80 cm, all well within the observed range of mean lengths for age group 7 at Iceland. The mean length of the immigrants was kept fixed at 69 cm, which is close to the value observed in the Norwegian data. The mean of the mixed distribution is set at 76 cm, *i.e.* close to the mean length of age group 7 in Icelandic samples in 1991. Estimates of the mixing proportion are calculated from the model using a sample size of 1 500, *i.e.* close to the actual numbers sampled from age group 7 in 1991.

Given this set of assumptions we proceed to estimate the proportion of immigrants in the mixture by the formula:

$$\tilde{p} = \frac{\overline{X} - \mu_2}{\mu_1 - \mu_2} \tag{4.7}$$

and obtain an approximation of the precision of that estimate using a plug-in-estimate for the variance:

$$Var(\tilde{p}) = \frac{Var(\overline{X})}{(\mu_1 - \mu_2)^2} \tag{4.8}$$

where $\tilde{p}$ is the moment estimate of the mixing proportion, $\overline{X}$ is the observed sample mean of the mixture, n the sample size, and μ_1 and μ_2 are the means of the two components (James 1978; cf. Appendix).

4.4. Simulation

To investigate the performance of the approximation of the variance of the mixing proportion, mixing in given proportions was simulated by sampling from two normal distributions, one of residents, and the other of the generally smaller immigrants, under two different model assumptions about the mixing of components.

To study the precision of the estimate of the mixing proportion some assumptions about the varibility of the components have to be made. A coefficient of variation (CV) of 10% for both component distributions is assumed, *i.e.* that the standard deviation is 6.9 cm for the immigrants and somewhat larger for the residents. This value is based on an examination of the data on 7 year olds from both areas. In the Norwegian samples from all of the years 1984-1993, 99% of the observations of the length of age group 7 were contained within a range of 30 cm or less. If lengths are normally distributed, that range should, according to normal theory, have a width of approximately 5 standard deviations. For the Icelandic saithe the coefficient of variation in length from all age-length couples for 7 year olds, since the mid-1960s, was in the range of 5-9% in all years, except 1991, and incidentally also in 1983 for the 1976 year class, when it exceeded 11% (see Appendix Table IV).

Model 1

Components were assumed to be completely mixed and sample size considerations did not enter the model other than the total number of fish was kept fixed at 1 500.

Model 2

Components were assumed to be totally separated in the mixture, with probabilities p and 1-p of a given subsample coming from the immigrant and resident components respectively. When it had been decided from which component to sample, a sample size was drawn at random from a vector of the sizes of samples actually taken from 7 year-olds in 1991, the distribution of sample sizes shown in Figure 4.1. It is, in other words, assumed that residents and immigrants occur separately in similar sized schools. Sampling was continued until the total sample size had reached 1 500 in the first run. In later runs sample size was increased until the same nominal precision, as in the simple complete mixing model, had been achieved.

Component means and numbers sampled were the same as described for age group 7 in 1991 in section 4.3. Proportions simulated were the appropriate estimates from the application of the mixture model. The number of simulations was 10 000 for the first run of both models but in later runs of model 2 the number of simulations was reduced to 2 000. In the simulations components were sampled in propotions from James's formulas, given to an accuracy of 3 decimals.

5. Results

5.1. Growth difference

The standard VPA tables, giving mean weights at age in the catch, were used as data sources to illustrate the growth difference between the two stocks. Figure 5.1 shows growth in terms of annual weight increment as a function of mean weight. Another view of these same data is shown in Figure 5.2 where the mean weight of selected year classes is plotted as a function of age. Here the VPA mean weights at age for the Norwegian saithe are shown to be separated from those of the Icelandic saithe. The figures clearly show a growth difference between the Northeast arctic and the Icelandic saithe. Figure 5.1 further shows the intermediate nature of the Faroe saithe.

Figure 5.3 shows survey MLA's for Icelandic and Northeast arctic saithe together on the same plot, with ages shifted to account for the approximately half year difference in timing of the surveys. Von Bertalanffy's growth function was fitted to these survey mean length data. The model fit showed a difference between the two stocks both for the growth parameter, K, and the asymptotic length, l_∞ (likelihood ratio test, $p<0.01$). A further analysis should perhaps be performed by year classes on data sets of individuals from both/all stocks within a modelling framework, including a larger set of explanatory variables, *e.g.* food availability, stock size and temperature.

5.2. Variability in the size at age data

Deviations in mean length and weight at age from the average for Icelandic saithe are shown in Figure 5.4. The length deviations are derived from IGFS data during 1985-1992, while deviations in weight at age are based on samples from the commercial catch in 1979-1993. For the most part, there is a correlation between the deviations in length and weight. Of particular interest are the year classes of 1976 and 1984 which, due to their large negative deviations, can be followed over several years.

MLAs were calculated on a quarterly basis for saithe sampled from trawl catches in two different areas, with a east-west division along 18°W. The reason for this division is, simply, that an immigration from the east is bound to appear first on the fishing grounds off the eastern part of Iceland. Samples from trawl catches were chosen since they generally yielded the highest number of saithe, were spread fairly evenly in space and time and because the trawl is less selective than the gillnet, the other main fishing gear.

The results are shown in Figure 5.5, where changes in mean length of the year classes 1981-1986 can be followed. It is clear that the the saithe in the eastern area tend to be smaller, but no clear indication of the arrival of immigrants is apparent. The same data, plotted on a monthly basis, did not yield any additional information.

Means, numbers sampled, standard deviations and coefficients of variation of the length distributions from saithe age groups 4-10 for the year classes since 1970 are given in Appendix Tables I-IV. The standard deviations for the year classes 1976 and 1984 were not markedly higher than average for age groups 4 and 5. For age groups 6 and older, on the other hand, they were among the highest on record. This added variability after the age of 6, coupled with the low MLAs for these year classes, is also apparent in the table of CVs. Contrary to the trend for most other year classes, these two show an increase in CV for ages 6 and 7.

It is possible to explain the negative deviations in size over a number of year by shortage of food, *i.e.* intra-specific competion or density dependence. On the other hand, increased variability in lengths after a certain age would not be expected as a result of general food shortage and is more reasonably explained by an immigration. However, it should be borne in mind that the variability of a length distribution is sensitive to other factors, such as numbers sampled from each gear type.

5.3. Catches and Fs at age

From the available VPA data on the year classes of 1962 through 1987 it is observed that catch at age generally peaks at age 6, for a few year classes at ages 4 and 5. Exceptions are the 1962, 1964 and 1984 year classes which are represented in greatest numbers in the catches as 7 year old fish in 1969, 1971 and 1991. The 1984 yearclass was also numerous in 1990 , with over 10 million fish caught during that year also. The 1976 year class shows a secondary peak in the catches at age as 10 year old fish in 1986. Catches at age from year classes of saithe at Iceland since 1962 are shown in Figure 5.6.

Tables of Fs at age were also scrutinized for Schopka's indication of a migration, *i.e.* a drop in F in years and at ages prior to a migration event. The Fs at ages 5 and 6 were also among the lowest on record for both the 1977 and 1984 year classes. In addition F at age 9 for the 1977 yearclass in 1985 is given as 0.213 which is far below the average for 9 year-olds. Fs were only examined as far back as to 1970, thereby omitting the not as recent 1962 and 1964 year classes, since less confidence must be attached to the the results of a historical VPA than for the past two and a half decades.

Table 5.1. Estimates of the mixing proportion (prop.) and its standard error (s.e.) from mixture model and simulation results. Mixture model estimates based on a mixture mean of 76 cm. Immigrant mean 69 cm and CV 10% for both components in all cases. **Model 1** simulates complete mixing of components, **Model 2** components separate within mixture. **n** denotes sample size, **S** number of simulations. For Model 2 sample sizes are at least **n**, depending on how sample sizes were drawn.

		Simulation setup		Resident mean			
		n	S	77	78	79	80
Mixture model estimates	prop.	1 500		0.1250	0.2222	0.3000	0.3636
	s.e.			0.02599	0.02433	0.02294	0.02177
Model 1	prop.	1 500	10 000	0.1249	0.2218	0.3002	0.3639
	s.e.			0.02602	0.02388	0.02301	0.02158
Model 2	prop.	1 500	10 000	0.1236	0.2219	0.2996	0.3638
	s.e.			0.05674	0.06840	0.07548	0.07845
Model 2	prop.	5 000	2 000	0.1253	0.2221	0.2985	0.3631
	s.e.			0.03221	0.03815	0.04069	0.04286
Model 2	prop.	7 000	2 000	0.1249	0.2223	0.3001	0.3636
	s.e.			0.02624	0.03244	0.03414	0.03584
Model 2	prop.	10 000	2 000	0.1243	0.02210	0.2999	0.3636
	s.e.			0.02180	0.02697	0.02900	0.03056

5.4. Model and simulation results

The uncertainty, associated with the estimation of the mean in a mixed distribution, is negligible for sample sizes close to 1 500, the number of 7 year old saithe aged at Iceland in 1991. On the other hand, the variance of the moment estimate of the mixing proportion is considerable, giving a standard error close to 0.025 for all resident means combined with an immigrant mean of 69 cm. Assuming that, at the sample sizes (≈1 500 fish) under consideration, the mean has been accurately determined, and using the rough normal approximation of doubling the standard error, indicates a 95% confidence interval of ±5% for the estimate of the mixing proportion of the components forming the mixed distribution.

Table 5.1 summarizes the values resulting from the application of the mixture model as well as the results of simulations.

From the results of the simulations we observe that the approximate variance formula and the variance from the simulations are in agreement when complete mixing of the two components is assumed. On the other hand, it is clear that if the components are clumped within the mixture, the variation in the estimate of the mixing proportion becomes much larger. The variance of the sample sizes used will determine how large this increase is. In model 2, the variance of the mixing proportion increases as the proportions of the components approch 0.5, the reverse of what is the case in model 1. Thus, given nearly equal proportions in model 2, there is greater probability of a series of samples coming from the same component, thereby offsetting the estimate of the mixing proportion and increasing the variance.

Increasing the numbers sampled in Model 2 gives an indication of how great the sampling effort must be to approach a standard error of 0.025 for the mixing proportion. Some 7 000 saithe sampled would be required with a mixing proportion close to 0.1, at least 10 000 for proportions close to 0.2, and even more as proportions approach 0.5, for this one age group only. The standard error of the simulated proportions decreases as the inverse of the square root of the sample size, as given by elementary statistics.

6. Discussion

It is evident from previous work on the saithe that the species undertakes trans-Atlantic migrations. These migrations are at times of such magnitude that they result in boom or bust in the cathces from the migrating year classes at different fishing grounds in the area (Schmidt 1957, 1958; Olsen 1961; Reinch 1976; Jakobsen and Olsen 1987). Reinsch gives an example of a record long distance migration of a saithe. On the January 23 of 1958 a saithe was tagged off the south coast of Iceland onboard a German research vessel. Some 55 days later, on March 21, this saithe was caught in the Barents Sea off the Nordkyn peninsula. The shortest distance between the release and recapture localities is more than 1 300 nautical miles, *i.e.* the fish had kept a minimum cruising speed of 24 nautical miles per day. These observations, together with evidence from catch data, have led to our effort to describe the underlying evidence and at quantifying one such migration event.

The results of the tagging experiments on NE-Atlantic saithe show that the local stocks are variously connected and, in the present context, that the Icelandic, Faroese and Northeast arctic saithe intermix. A more balanced distribution of tagging effort among areas seems desirable and a more detailed analysis of the returns from the almost 100 000 saithe tagged at Norway would, undoubtedly, give a more solid basis for understanding these migrations.

The previously held view, that the migration of saithe between Norway and Iceland is mainly one-way should be reconsidered. A new analysis of the results given by Jones and Jónsson (1971), as recaptures from spawning grounds, indicates that a migration in the opposite direction is no less likely. The German anlysis of saithe data together with Faroese tag results also indicates a frequent interchange of saithe along the Faroe-Iceland Ridge.

During the last three and a half decades, irregularities in catch in numbers figures from VPA for Icelandic saithe indicate 3 or 4 cases of immigration. Two of these are further supported by deviations in both mean lengths and weights at age. The VPA figures are naturally nothing more than derivatives of the catch statistics and age-length measurements undertaken through the years and their value will, inevitably, rely on good groundwork. Our study uses two sets of VPA data that have been collected by the same two fisheries laboratories throughout the period, and should therefore be consistent and comparable.

Fishing pattern is obviously one of the determinants of all estimates of mean length at age in the catch. Since the fleet seeks out the best concentrations, it is possible that in response to incoming saithe from Norway, these become overrepresented in the catches thereby biasing mean weights and lengths downward.

The observed irregularities in lengths at age for the strong saithe year classes of 1977 and 1984 at Iceland lead to at least two explanatory hypotheses, *i.e.* density dependent growth and immigration of slower growing saithe. The largest deviations in the MLAs were observed for 9 year old saithe in 1985 and a slightly smaller deviation for 7 year olds in 1991, from the strong 1977 and 1984 year classes, respectively. As stated previously, these year classes also showed a negative deviation from the average in both mean weight and length for the younger age groups . Whether this is an indication of density dependent growth (Olsen 1966), or the result of the immigration being spread over more than one year, is difficult to find out for sure. Furthermore, these two explanations are by no means incompatible, the recruitment to a year class can be a success in more than one saithe stock in the NE-Atlantic in a given year (Jakobsson 1992), this year class can then go on to suffer from density-dependence, and, finally, undertake a trans-Atlantic mass migration, detectable in both source and sink populations (Pulliam 1988).

Observations of saithe fry on the outskirts of the Norwegian fisheries jurisdiction in April and May in some years are not in themselves sufficient to make the case for a hypothesis of larval drift from Iceland, since these fry could easily have drifted from spawning grounds in the North Sea. However, capelin larvae have been observed in the same general area, about two months later in the year. These larvae are beyond doubt of Icelandic origin though some uncertainty is attached to their date of birth (Bjørke and Sætre 1994; H. Vilhjálmsson, MRI, pers. comm.). In view of these two independent observations, a larval drift of saithe from Iceland to Norway and a subsequent migration back to Iceland cannot be ruled out.

In the golden days of the Atlanto-Scandian herring bonaza, saithe were a frequent bycatch in the herring seines and pelagic trawls, with amounts of up to 60 tonnes reported in the latter case (Reinsch 1976). This occured most frequently in the overwintering area east of Iceland and north of the Faroes. Jigging for saithe during breaks from the herring fishery, was a considerable source of income for Icelandic herring fishermen, especially in the late 1960s (H. Vilhjálmsson, MRI, pers. comm.)

Accepting, as we have done here for the sake of argument, that import of Norwegian saithe explains, in part at least, the low mean length and mean weight at age 7 in 1991, the next question is that of numbers? A simple attempt at an answer to this, is to use point estimates of MLA observed for saithe at Iceland and Northeast arctic saithe and some assumptions on growth for a purely resident component, and then apply the mixture model. This yielded an approximate mixing proportion of at least 0.1, probably closer to 0.2, in other words: Some 10-20% of age group 7 saithe in the catches at Iceland in 1991 were of foreign origin, probably Norwegian. If we accept this approximate proportion and the VPA stock in numbers estimate of 35 million 7 year olds in 1991, this immigration would amount to some 3.5 - 7 million saithe or, at a mean weight of 3.5 - 4 kg, a biomass of 12 to 25 thousand tonnes.

It is stressed that, due to the nature of the data, these estimates are only tentative. On the other hand, it is felt that the available evidence lends fairly strong support to a hypothesis of an occasional large scale migration. It is hoped that further studies using the mixture model, will pave the way for dealing more effectively with any future immigration of either saithe or cod to Icelandic waters.

All of this is speculative and the assumptions need further qualifications. A key question is whether the Icelandic and Northeast arctic saithe throughout a year can be regarded as coming from the same length distribution. The main flaw in the argumentation is probably tied to the assumption that observations are derived from the same mixed distribution, when they are, in fact, from distributions that are in no way fixed. The fish grow throughout the year, immigrants arrive at some point, and, although that possibility has not been considered in our analysis, may well leave again later in the year.

Another generalization is the assumption of a constant coefficient of variation of 10%, which is on purpose kept generous. Lowering the CV to 8%, which is closer to what has generally been observed for Icelandic saithe, led to a reduction in the standard errors for the proportion of some 15 - 20%, thus indicating better estimation. The sampling effort needed to obtain a higher precision in the estimation of the mixture proportion by the present method is enormous. Setting the desired precision at 2% or less, would require a sample size of some 10 thousand saithe depending on the component means, their variances and proportions. However, if immigrants arrived early in the year and remained in the population sampled by MRI throughout the year, the mixture model would be an acceptable basis for indicating the numbers of immigrants.

The simulations were carried out in order to examine the accuracy of the approximate variance formula for the mixing proportion given by James (1978). If complete mixing of components is assumed model and simulations agree. However, when components of the distribution remain separate, as would seem likely in the case of separate schools, and, given the sample sizes used here, the accuracy of our estimate of the mixing proportion decreases. A theoretical formula for the variance of the proportion could, no doubt, be derived by also considering the variance of sample sizes. This is left as an exercise for others. The application of the mixture model for the evaluation of migrations is, obviously, dependent on the available data on the fish stocks in question, and the Icelandic saithe are probably lacking in that respect. Anyway, the request by Shepherd and Pope (1993) for further work on the precision of the mixture model has been met to some extent.

Because all age-length couples for 7 year olds at Iceland in 1991 were available, the selection of programs available for the analysis of length distributions might have been applied to our problem (MIX, Multifan etc). However, Sparre (1986, in Kolding and Bergstad 1988) has shown that in order to resolve a length distribution into components, the means must be more than two standard deviations apart no matter what method you use. The other migration assessment methods, described in section 3, might also be used to estimate saithe immigration. Although they have given useful estimates for the cod, the surveying, sampling and assessment of these two species are incomparable.

Using the mixture model as suggested by Sheperd and Pope (1993), with the addition of an approximation of the variance of the mixture propotion, seems more to the point. The presence of normal components is not assumed and there are only two components we need concern ourselves with. In such a case the simple and easily understandable method, although in many ways rudimentary, is preferable in a first attempt at describing these relationships.

If migrating individuals come from the upper part of the length or weight distribution of the source population, the use of the mean lengths or weights of the fish remaining at Norway would lead to an underestimate of the mixing proportion, since it would take a greater number of slightly larger fish to explain a given reduction in either mean length or weight at age. On the other hand, if the energetic stress accompanying the migration is high, the growth of the migrants could be retarded which would tend to counteract this effect.

To further establish and quantify these relations more extensive tagging experiments are needed, in particular on the Icelandic saithe. A combination of morphometric and genetic studies should also be considered. Although the limited number of genetic studies conducted on saithe in the NE-Atlantic to date point towards homogeneity among the stocks, the field of fish population genetics is developing rapidly and the application of new methods could yield valuable insights. Otolith morphometry is also promising. In the case of the Greenland migration to the Icelandic cod some work has been done on differences between resident and immigrant otoliths (Easey 1978), if such a difference is also detectable between the saithe stock units under consideration that could be capitalized on with the state of the art automated age reading apparatus. Also, and perhaps least costly, a more thorough analysis of existing data on saithe might yield valuable insights, *i.e.* following the advice given to ecologists by Frank and Legget (1994).

Schopka (1993) points out that the failure, in the early 1980s, of recognizing the full impact of the return migration of the 1973 cod year class from Greenland, was in part due to optimism connected to the recent extension of the fisheries jurisdiction, and led to an underestimation of the F's in operation and an overestimate of the cod's biomass. This is one of the explanations for the poor state of the Icelandic cod stock at present and demonstrates the importance of developing methods to monitor such mass movements of fish stocks. By studying the dynamics of the saithe stock units in the North Atlantic more closely, we might become better able to prevent them from reaching such dire straits as the Icelandic cod and perhaps learn a lesson or two that could be useful when dealing with other related fish stocks.

Most of the results presented in this paper and the conclusions drawn from them can perhaps be described as **weak inference**, something that students in marine science and fisheries biology, and presumably in other disciplines as well, are warned against and drilled in recognising in the scientific literature. Nevertheless, I would like to make a case for this "scientific method" since we are often not in posession of material that allows the much sought after **Stong Inference** (Platt 1964; Elner and Vadas 1990). Some inference is always better than none as long as it is recognised as such. It seems clear from the findings presented in this paper/study and the review of earlier work that more attention should be given to the wanderings of the North Atlantic saithe.

7. References

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8. Figures

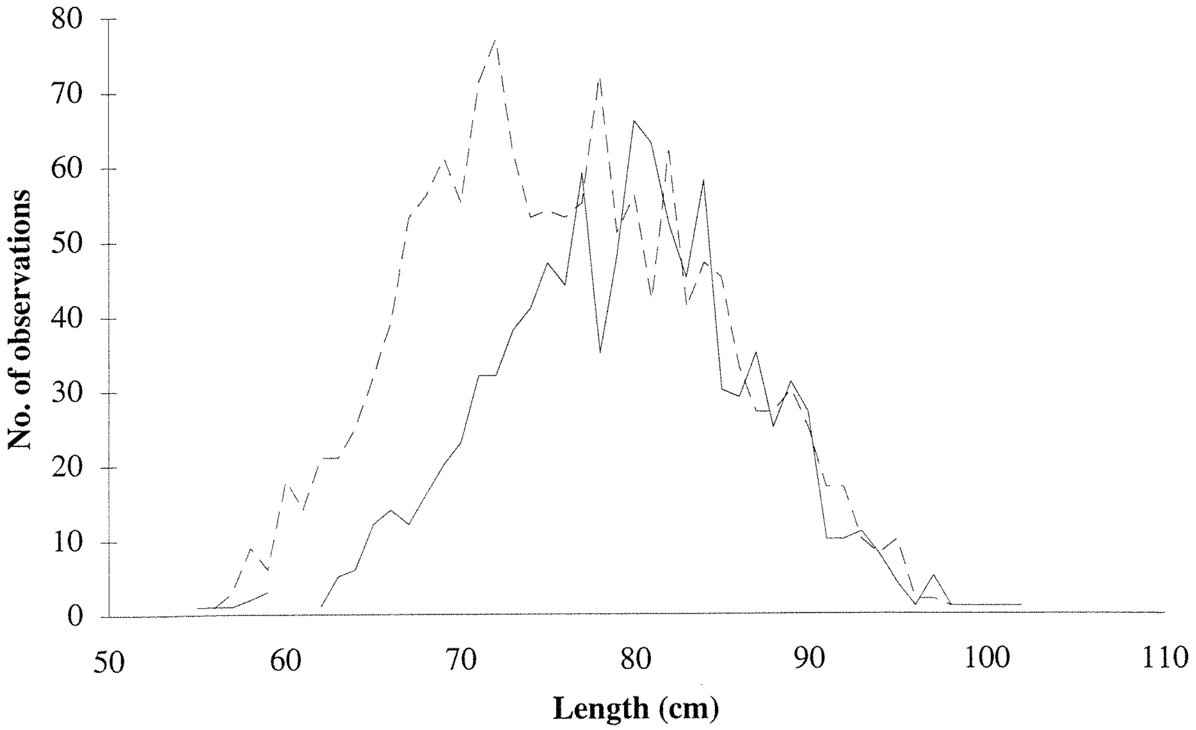


Figure 2.1. Length distributions of saithe age group 7 at Iceland in 1990 (—) and 1991 (---).

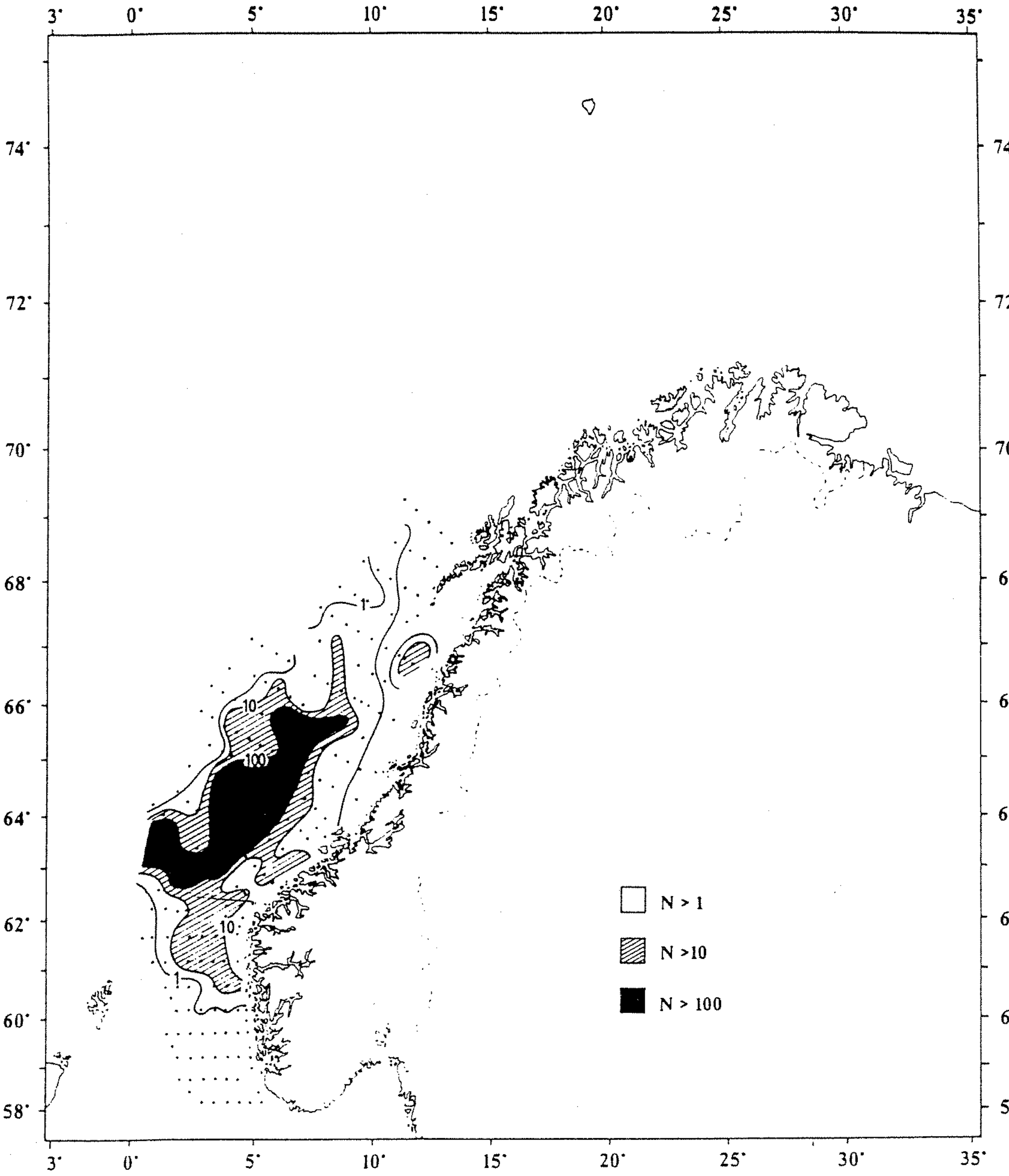


Figure 2.2. Distribution of saithe postlarvae off the west coast of Norway in April-May 1986. The black area represents the highest numbers. Source: Bjørke & Sætre (1994).

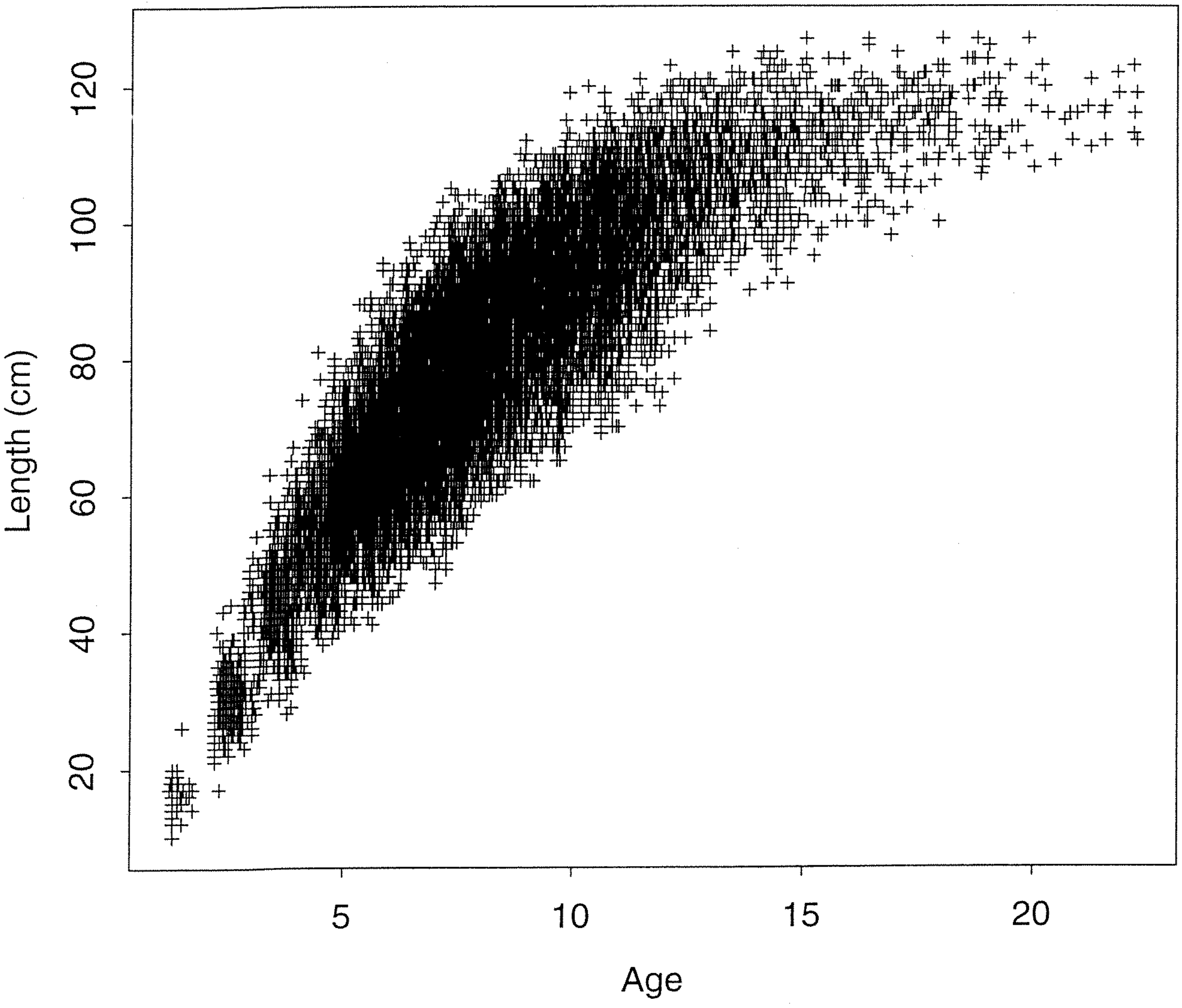


Figure 4.1. Scatterplot of length at age for saithe at Iceland. Year classes since 1962 are included.

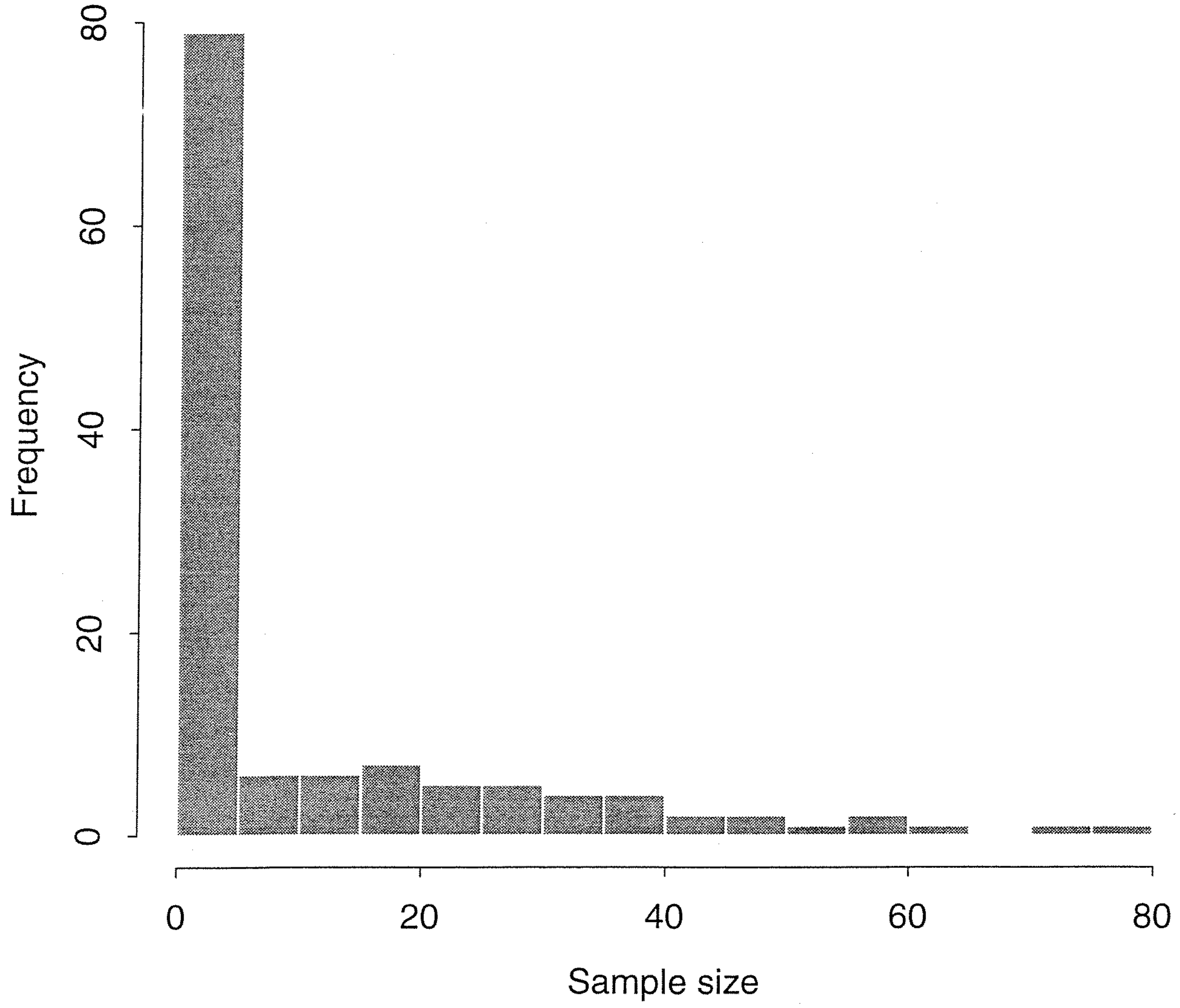


Figure 4.2. Sample sizes of age group 7 in 1991.

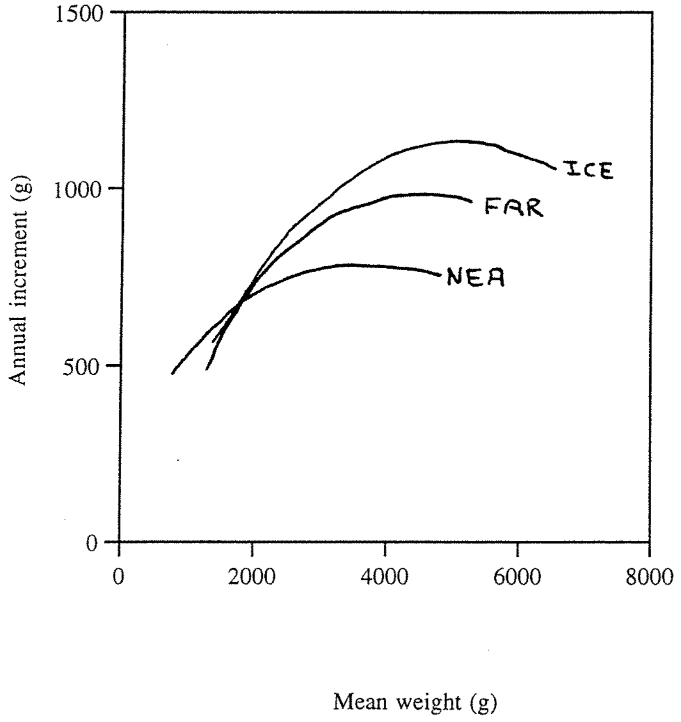


Figure 5.1. Relationship between annual growth increment and mean weight for Icelandic, Faroese and Northeast arctic saithe. Based on average mean weights and their increments for age groups 3-10 in the period 1980-1993. Data from the MRI, the NWWG and the Arctic fisheries WG.

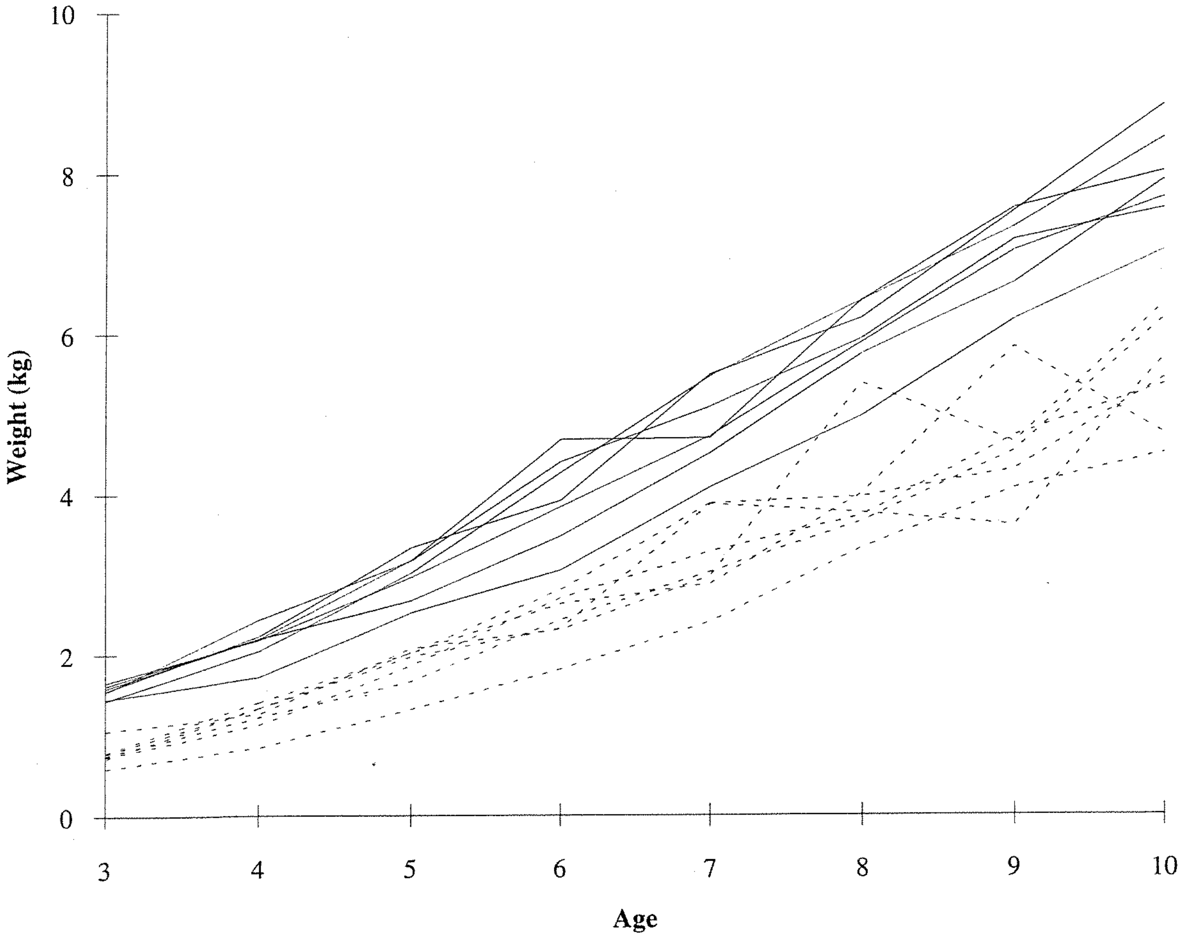


Figure 5.2. Mean weight at age for Icelandic (—) and Northeast arctic (---) saithe for the year classes 1977-1983.

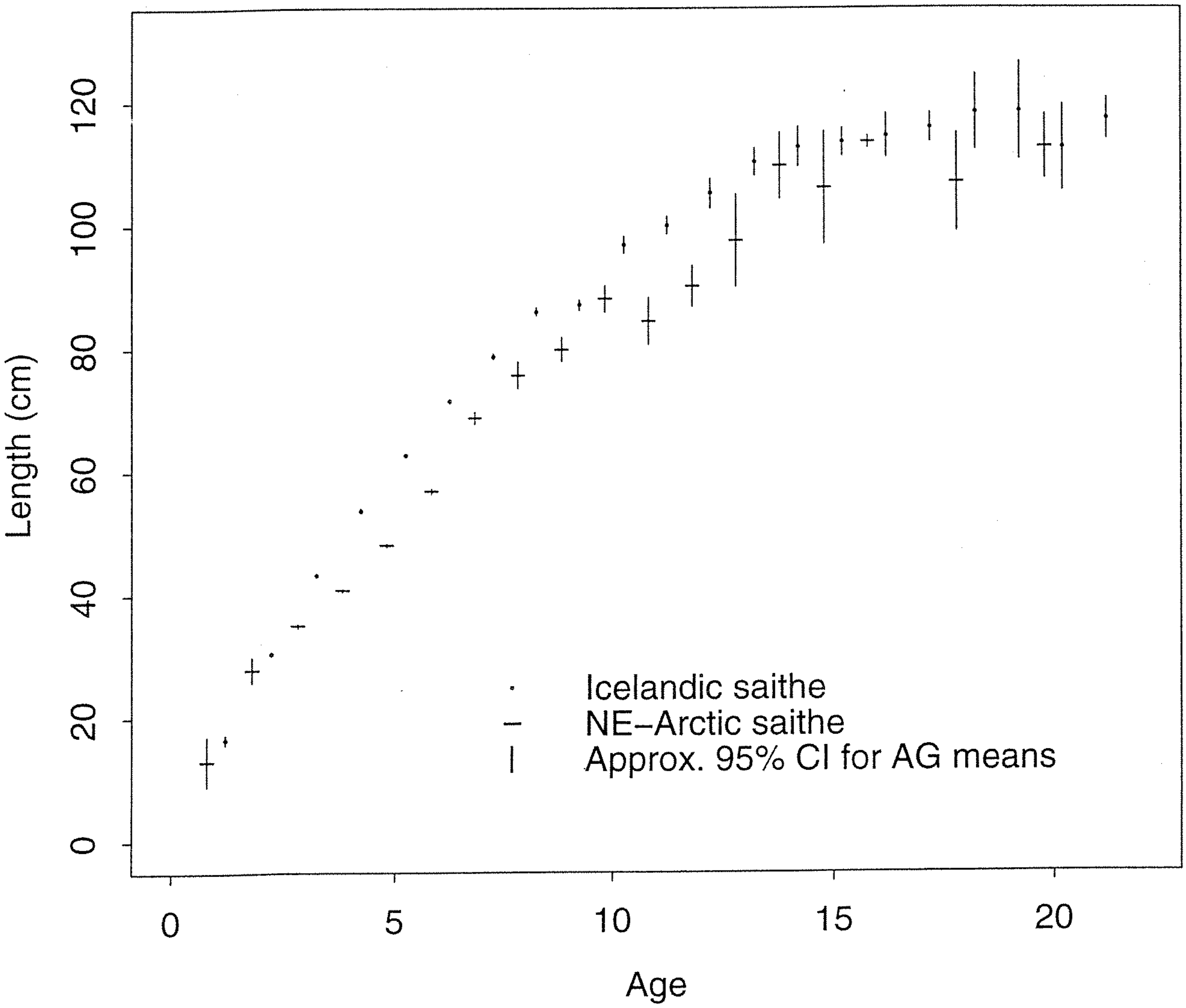


Figure 5.3. Survey MLAs for Icelandic and Northeast arctic saithe. Averaged over 8 and 4 surveys respectively.

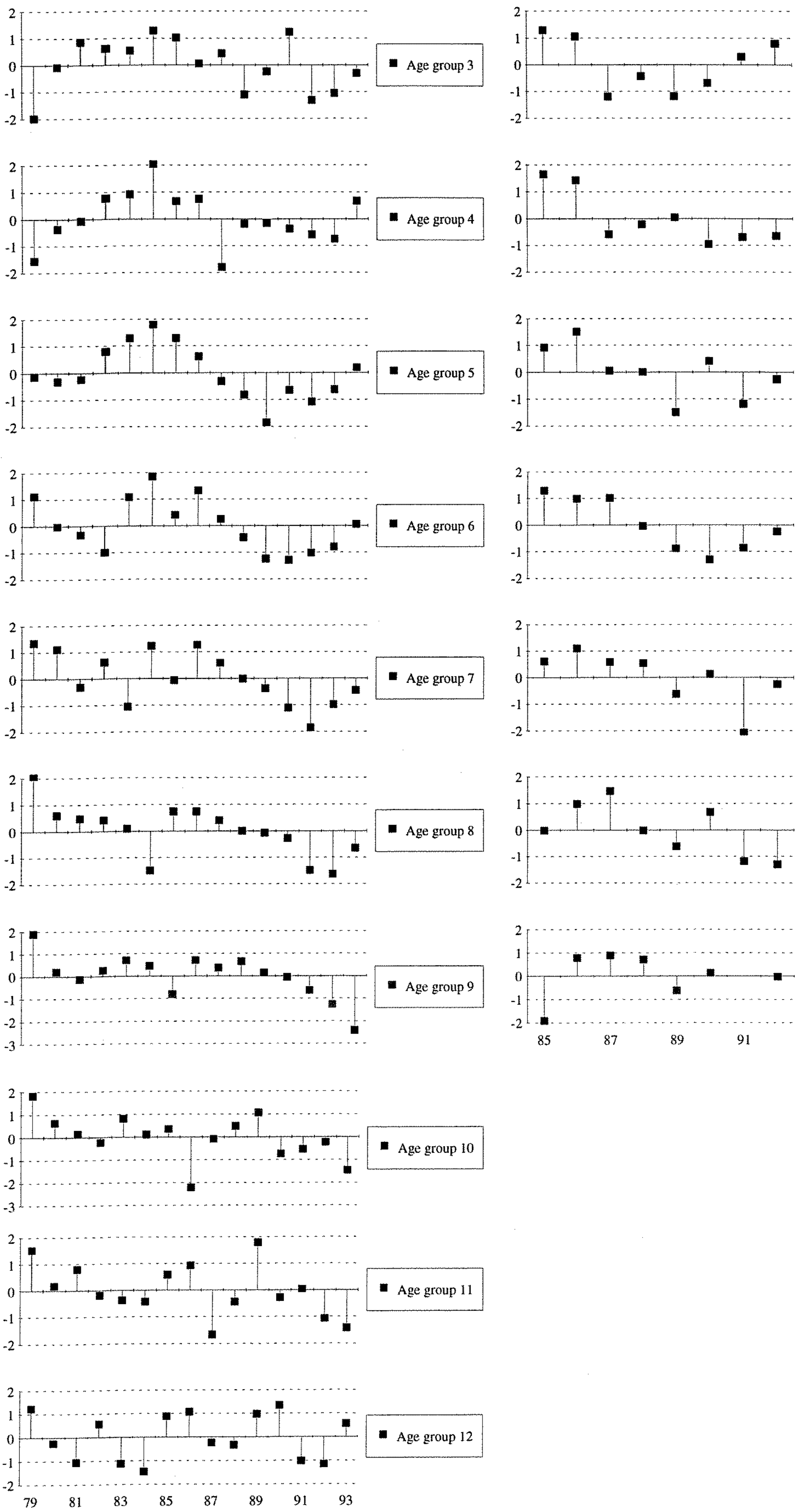


Figure 5.4. Standardized deviations in mean weight and length at age for Icelandic saithe from the average in the period indicated. Deviations in mean weight are based on VPA tables giving mean weight age in the catches, deviations in mean length at age are derived from IGFS data.

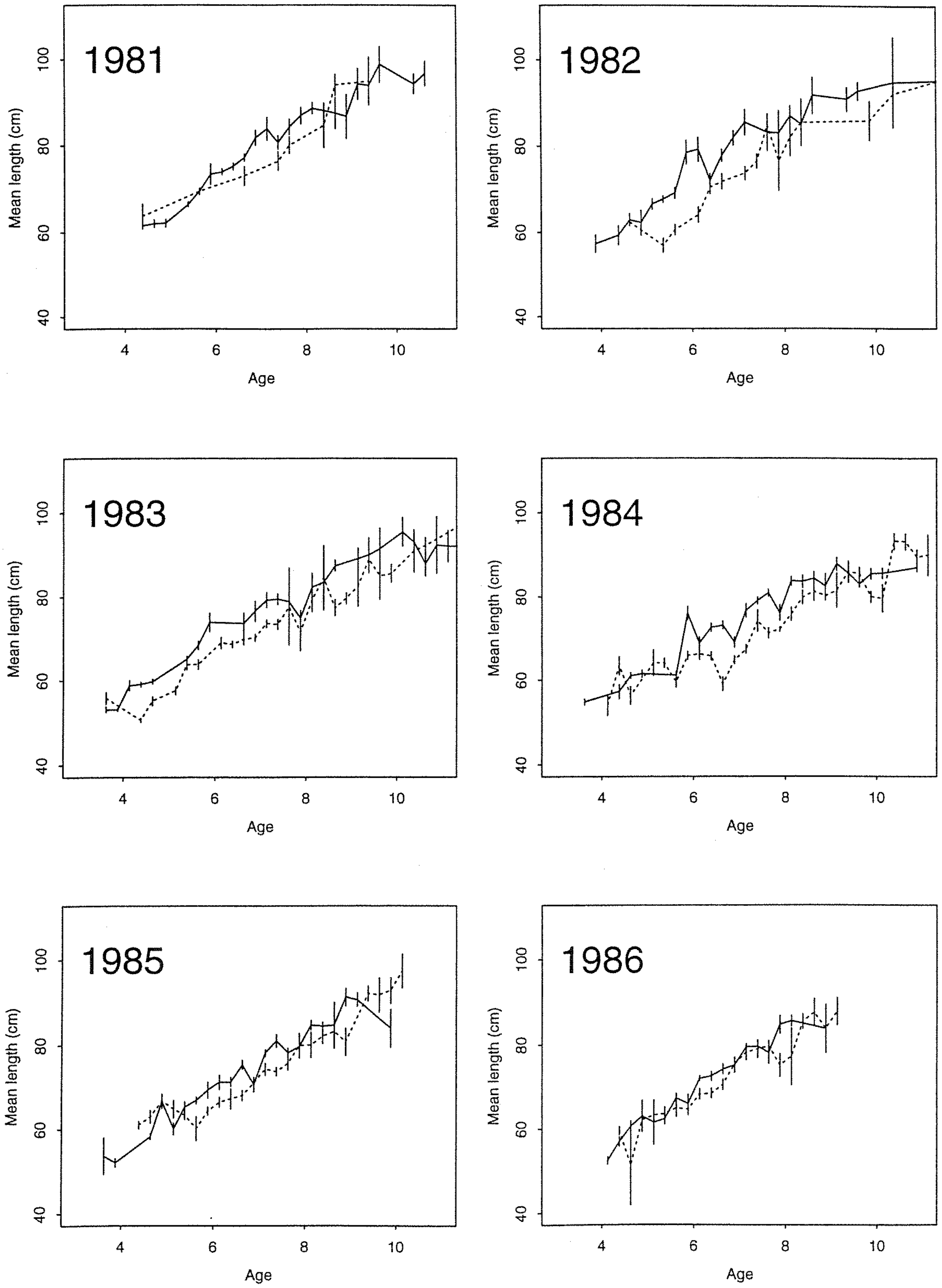


Figure 5.5. Quarterly MLAs for the year classes 1981-1986 west (—) and east (---) of 18°W. Approximate 95% confidence intervals based on the t-distribution are indicated.

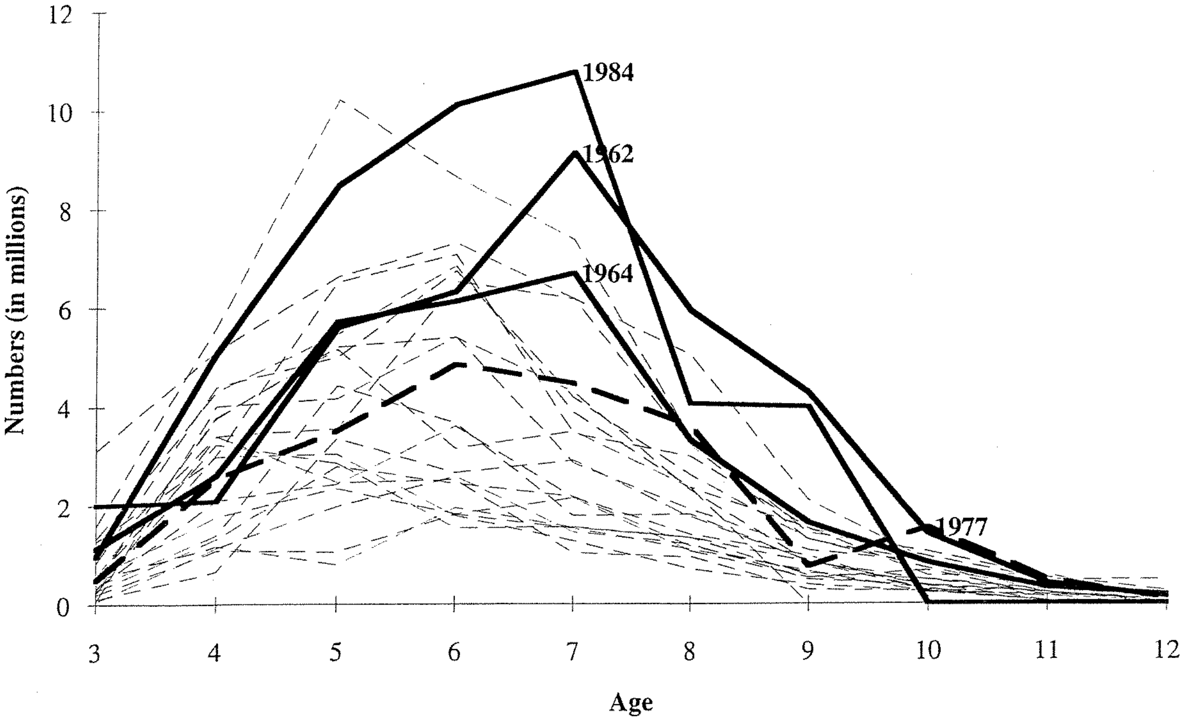
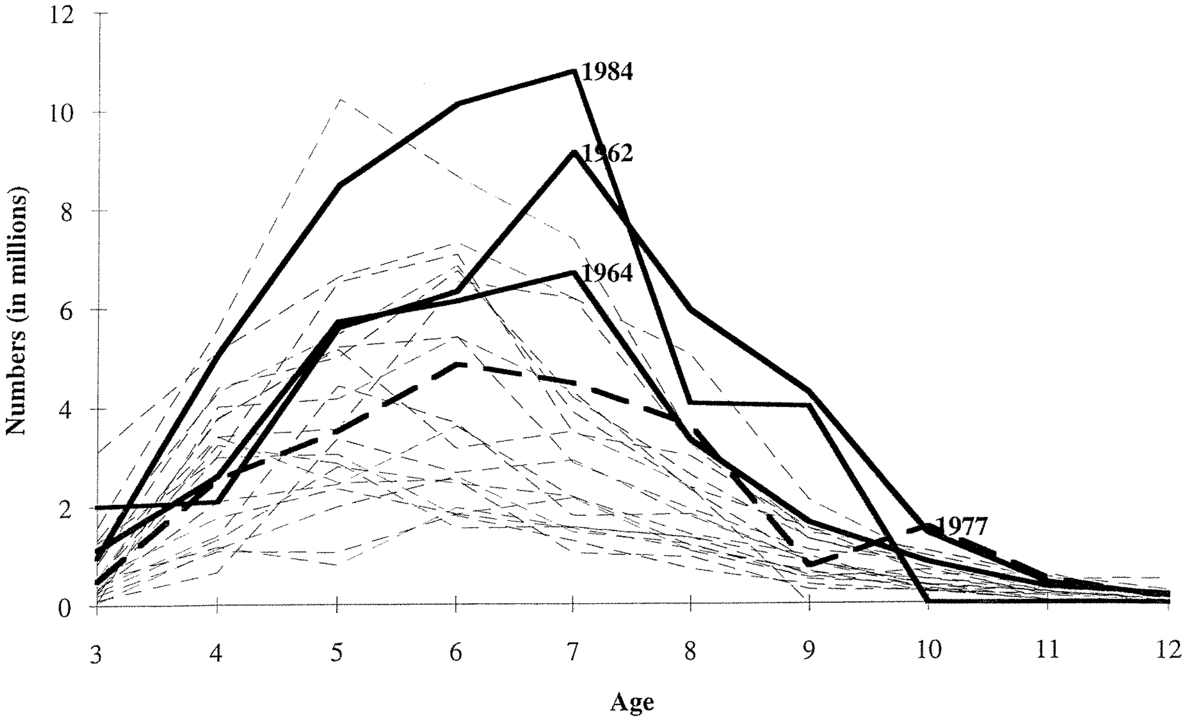


Figure 5.6. Catch at age for year classes of saithe at Iceland since 1962.


12
10
8
6
4
2
0
Numbers (in millions)
3
4
5
6
7
8
9
10
11
12
Age
1984
1962
1964
1977

[redacted]

Figure 5.6. Catch at age for year classes of saithe at Iceland since 1962.

Appendix

The mixture model and its variance

A number of statistical papers have dealt with the mixture model

$$g(x) = \pi_1 f_1(x) + \ldots + \pi_k f_k(x)$$

with π's and *f*'s denoting the proportions and probability density functions of each of *k* components and *g(x)* the probability density function of the resulting distribution mixture and various ways of estimating some or all of the parameters in the model (*e.g.* Day 1969; Dick and Bowden 1973; Hosmer 1973; James 1978; MacDonald and Pitcher 1979; Scnute and Fournier 1980). Few of them state explicitly a formula for the variance of a mixture of two components, which we need in the present case, when attempting to analyse the precision of the moment estimate of the mixing proportion, as suggested by Shepherd and Pope (1993). However, Johnson and Leone (1977), in a textbook example, give the general formula

$$VarX = \sum_{i=1}^{k} \pi_i \sigma_i^2 + \sum_{i=1}^{k} \pi_i (\mu_i - \mu)^2$$

for the variance of a mixture of *k* distributions with π_i, σ_i^2 *and* μ_i the proportion, variance and mean, respectively, of component *i* in the mixture and μ the mean of the mixed distribution itself given by

$$\mu = \sum_{i=1}^{k} \pi_i \mu_i .$$

For a mixture of two distributions the variance expression simplifies to

$$VarX = \pi \sigma_1^2 + (1 - \pi) \sigma_2^2 + \pi (1 - \pi)(\mu_1 - \mu_2)^2$$

when we have replaced the mixture mean with its formula in component means and $\pi = \pi_1$ and $1 - \pi = \pi_2$.

The mixing proportion is given by

$$\pi = \frac{\mu - \mu_1}{\mu_2 - \mu_1}$$

where $\mu=\pi\mu_1 + (1-\pi)\mu_2$ is the mean of the mixed distribution. One way of estimating the mixing proportion, assuming knowledge of the means and variances of the components, given by James (1978), is equating the sample mean with the population mean which gives us

$$\tilde{p} = \frac{\overline{X} - \mu_2}{\mu_1 - \mu_2}$$

the so-called moment estimate of the mixing proportion which has an approximate large-sample variance

$$Var(\tilde{p}) = \frac{\pi(1-\pi) + [\pi\sigma_1^2 + (1-\pi)\sigma_2^2]/(\mu_1 - \mu_2)^2}{n}$$

In the following it will be shown how the variance of the moment estimator for the mixing proportion is derived from the variance in the mixed distribution.

The variance of the mean of a sample from a mixture is

$$Var(\overline{X}) = \left\{\pi\sigma_1^2 + (1-\pi)\sigma_2^2 + \pi(1-\pi)(\mu_1 - \mu_2)^2\right\}/n$$

for a sample of size n. The variance of the mean determines the variance of the mixing proportion completly when we assume component means and variances are known, namly

$$Var(\tilde{p}) = Var\left(\frac{\overline{X} - \mu_2}{\mu_1 - \mu_2}\right) = \frac{Var(\overline{X})}{(\mu_1 - \mu_2)^2} = \frac{\left\{\pi\sigma_1^2 + (1-\pi)\sigma_2^2 + \pi(1-\pi)(\mu_1 - \mu_2)^2\right\}/n}{(\mu_1 - \mu_2)^2}$$

which rearranges to

$$Var(\tilde{p}) = \frac{[\pi\sigma_1^2 + (1-\pi)\sigma_2^2]/(\mu_1 - \mu_2)^2 + \pi(1-\pi)}{n}$$

the formula given in James's (1978) paper.

We note that $Var(\tilde{p})$ can be regarded as the sum of the usual binomial variance and an addition due to the separation of the mixture components and their variances. This addition is the dominant term for the sets of numbers considered here as can be seen after making some simplifying assumtions. A further note is, that as the separation of the components increases this addition becomes smaller while it increases with the variance of one or both components. The variance of the mixture mean, on the other hand, increases with both separation and component variances.

Table I. Mean lengths at age for saithe year classes at Iceland.

	YCL70	YCL71	YCL72	YCL73	YCL74	YCL75	YCL76	YCL77	YCL78	YCL79	YCL80	YCL81	YCL82	YCL83	YCL84	YCL85	YCL86	YCL87	YCL88	YCL89	YCL90
AGE4	61.15	56.59	58.45	62.65	63.14	58.92	59.82	60.43	60.80	59.86	55.53	60.27	60.03	56.12	58.16	58.34	55.97	55.34	57.38	60.49	58.84
AGE5	73.41	69.04	68.05	70.85	68.29	66.73	66.32	69.26	69.11	69.06	69.08	68.43	65.16	64.41	62.42	64.51	62.93	64.94	66.26	67.16	
AGE6	81.45	79.72	78.45	78.49	77.17	73.85	70.39	78.12	78.50	76.67	78.41	75.53	73.17	70.60	69.50	70.93	71.66	74.37	74.02		
AGE7	88.55	86.13	84.07	86.57	79.61	84.65	76.76	84.83	82.99	85.71	82.98	82.64	80.36	79.31	75.94	78.41	79.47	82.93			
AGE8	92.04	91.09	91.28	89.30	90.55	89.41	80.06	90.51	90.88	90.61	89.30	88.43	89.52	86.48	82.73	86.29	86.87				
AGE9	95.96	95.64	92.91	95.81	98.33	95.27	87.55	96.38	95.78	97.38	94.46	94.90	94.14	90.49	84.47	93.38					
AGE10	101.23	99.92	98.79	103.08	100.96	99.76	90.75	100.18	101.15	101.87	100.38	98.03	96.32	93.34	90.29						

Table II. Numbers sampled by yearclass.

	YCL70	YCL71	YCL72	YCL73	YCL74	YCL75	YCL76	YCL77	YCL78	YCL79	YCL80	YCL81	YCL82	YCL83	YCL84	YCL85	YCL86	YCL87	YCL88	YCL89	YCL90
AGE4	528	278	223	179	300	542	249	223	194	361	218	383	270	615	520	460	337	170	682	322	740
AGE5	193	116	139	396	223	606	707	423	208	141	557	778	657	708	937	777	461	779	984	561	
AGE6	109	81	193	409	385	1054	824	326	187	377	767	910	582	884	1616	765	831	689	991		
AGE7	87	188	223	491	277	794	622	206	435	492	707	588	423	1007	1468	852	750	567			
AGE8	205	79	360	184	252	352	360	439	457	363	463	588	483	722	1036	781	524				
AGE9	27	135	68	223	87	55	428	269	187	184	275	336	305	327	1342	502					
AGE10	98	26	67	79	23	166	738	158	68	70	124	247	84	289	810						

Table III. Standard deviations.

	YCL70	YCL71	YCL72	YCL73	YCL74	YCL75	YCL76	YCL77	YCL78	YCL79	YCL80	YCL81
AGE4	5.569	7.503	3.465	4.198	4.522	4.440	5.866	4.489	6.188	5.470	8.623	5.283
AGE5	5.711	6.368	9.097	4.817	5.295	6.703	6.249	5.273	6.204	6.684	8.739	5.085
AGE6	5.860	7.342	5.589	5.630	8.964	5.874	7.867	5.529	6.139	6.921	6.814	5.631
AGE7	5.064	5.648	5.805	6.112	7.637	4.677	8.464	5.477	6.625	6.109	6.603	6.628
AGE8	4.488	5.311	5.060	5.586	5.297	5.965	8.116	6.491	6.130	6.403	7.303	5.638
AGE9	4.670	5.673	7.911	4.514	5.636	7.799	8.652	6.283	5.991	6.517	6.432	5.831
AGE10	5.167	7.260	4.794	4.741	6.491	7.287	6.513	6.274	6.299	6.808	7.368	6.256

	YCL82	YCL83	YCL84	YCL85	YCL86	YCL87	YCL88	YCL89	YCL90
AGE4	5.350	5.437	6.105	5.724	5.359	5.812	5.001	5.368	5.580
AGE5	6.964	6.817	6.602	5.658	5.620	5.746	5.653	5.879	
AGE6	7.229	6.336	8.383	6.651	5.696	5.990	5.810		
AGE7	6.819	7.320	8.467	6.616	6.066	6.038			
AGE8	6.498	7.047	8.008	6.335	6.654				
AGE9	6.176	7.122	7.397	6.627					
AGE10	7.015	7.340	8.262						

Table IV. Coefficients of variation.

	YCL70	YCL71	YCL72	YCL73	YCL74	YCL75	YCL76	YCL77	YCL78	YCL79	YCL80	YCL81
AGE4	0.091	0.133	0.059	0.067	0.072	0.075	0.098	0.074	0.102	0.091	0.155	0.088
AGE5	0.078	0.092	0.134	0.068	0.078	0.100	0.094	0.076	0.090	0.097	0.127	0.074
AGE6	0.072	0.092	0.071	0.072	0.116	0.080	0.112	0.071	0.078	0.090	0.087	0.075
AGE7	0.057	0.066	0.069	0.071	0.096	0.055	0.110	0.065	0.080	0.071	0.080	0.080
AGE8	0.049	0.058	0.055	0.063	0.058	0.067	0.101	0.072	0.067	0.071	0.082	0.064
AGE9	0.049	0.059	0.085	0.047	0.057	0.082	0.099	0.065	0.063	0.067	0.068	0.061
AGE10	0.051	0.073	0.049	0.046	0.064	0.073	0.072	0.063	0.062	0.067	0.073	0.064

	YCL82	YCL83	YCL84	YCL85	YCL86	YCL87	YCL88	YCL89	YCL90
AGE4	0.089	0.097	0.105	0.098	0.096	0.105	0.087	0.089	0.095
AGE5	0.107	0.106	0.106	0.088	0.089	0.088	0.085	0.088	
AGE6	0.099	0.090	0.121	0.094	0.079	0.081	0.078		
AGE7	0.085	0.092	0.111	0.084	0.076	0.073			
AGE8	0.073	0.081	0.097	0.073	0.077				
AGE9	0.066	0.079	0.088	0.071					
AGE10	0.073	0.079	0.092						