BIO 3910

MASTER'S THESIS IN BIOLOGY

NORTHERN POPULATIONS AND

ECOSYSTEMS

The spatial relationship between pelagic fish species
in the Barents Sea

Vegard Haukeland

May, 2008

Capelin (Mallotus villosus): 15-18 cm
(female above)

FACULTY OF SCIENCE
Department of Biology

University of Tromsø

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Acknowledgements

My work on this thesis has been a process of highly progressive learning and intellectual maturing. Combined with times of tough challenges and frustration, it has been a great source of inspiration for further educational development. My interest for the theme has been thriving as I worked on my thesis, and because I still find many questions unsolved, I would like to continue working on this and related problems in the future.

My supervisor, Per Fauchald (NINA), deserves great thanks for worthwhile contribution and support, and for making accomplishment of this thesis possible.

The Institute of Marine Research is acknowledged for providing data for this thesis.

Thanks to my co-workers at NINA for useful help and for social breaks and festivities.

I would like to thank all my friends at the Institute of Biology for long-lasting breaks, parties, skiing trips and strong support.

Also, I would like to thank my family and friends in Oslo for compassionate phone calls, nice vacations and for always being there when needed.

Tromsø, May 2008

Vegard Haukeland

Abstract

Capelin (*Mallotus villosus*) is a pelagic fish species with large interannual stock variations in the Barents Sea ecosystem. Together with polar cod (*Boreogadus saida*) and juvenile herring (*Clupea harengus*), it functions as an intermediate link that transfers energy from zooplankton to higher trophic levels. Capelin is a key prey and important as a food resource both to sea birds, sea mammals and other fish species. In late summer capelin perform a feeding migration from the central part of the Barents Sea and into Arctic water masses in the north and east. Earlier studies have shown that this migration is strongly density dependent. In years of high abundance, capelin has a more aggregated spatial distribution and migrate further compared to years of low abundance. In this study I investigate how this density dependent migration might affect the distribution and habitat selection of two competing species; polar cod and herring. I compare two years with contrasting abundance in capelin and investigate the spatial distribution of the three competing species with respect to oceanographic habitat. As predicted, capelin showed a shift in distribution into colder water masses in the year with high abundance. One of my hypotheses, which suggested increased spatial overlap with polar cod in years with high capelin abundance, was supported. On the other hand, no increase in overlap with herring was detected. Neither did I find any significant displacement of polar cod or herring that could be connected to capelin abundance. I suggest that the overlap between polar cod and capelin would increase the opportunity of ecological interactions, as they probably utilize many of the same resources. Possible interactions between capelin and its neighbouring pelagic species were connected to the competitive exclusion principle and ecological niche theories.

Keywords: *Barents Sea; capelin; coexistence; competitive exclusion; density dependent; migration wave; niche theories; pelagic schooling fish; spatial distribution.*

CONTENTS

1   Introduction

1.1   Spatial relationship between competing species

According to the competitive exclusion principle, introduced by Gause in 1934, no species with the similar ecological requirements can coexist in the same community. This principle makes up one of the frames for this thesis, in which I have studied three pelagic and schooling fish species in a northern marine shelf ecosystem. Due to a latitudinal gradient of marine species richness, diversity will generally be lower in a northern ecosystem than closer to the equator (Cheung et al., 2005). Hence, it might be reasonable to assume that there are fewer but more significant interactions occurring in northern ecosystems. One single set of interactions between two competing species might be easier to investigate when there are few other potentially interacting species to control for. Historically, competition as an interaction has been a highly debated topic, including a small minority of opponents totally denying its occurrence. However, Gause's principle has generally been handled as a fundament for competition theory development among scientists since its introduction (e.g. Amundsen, 2001). Despite the principle's convincing logic; that coexistence of two competing species in an isolated habitat can never be sustainable, extensive research is still necessary when it comes to systemizing the outcome of any interaction in the complex nature. During the last century, scientists have attempted to explain why many species might coexist and consequently how diversity can persist in the long run, despite an occurrence of interspecific competition. These questions have given rise to different niche theories.

1.2   Evolvement of the niche concept

The term niche was introduced approximately 250 years ago, although not obviously in analogy with or preliminary to its present use in ecology (Schoener, 1989). Definitions of an ecological niche were brought to us by J. Grinnell and C. Elton during the first part of the 20th century. As referred in Pulliam (2000), the "Grinnellian" niche concept states that a species occurs wherever conditions are suitable and never where conditions are unsuitable. Under normal conditions of reproduction and dispersal, the species is expected to occupy a geographical region that is directly congruent with the distribution

of its niche. However, Grinnell seems to modify this basic principle by stating that every species occupies a niche, although not necessarily the reverse, there may be some empty niches as well (Schoener, 1989). His interpretation of the concept takes into account both spatial and dietary dimensions, as well as avoidance of predation. In Elton's definition of the concept, a niche need not be restricted to a single species, but may include a group of e.g. predators or prey inside the same habitat. Both Elton and Grinnell consider niches as largely immutable "places" or "recesses" in the community (Schoener, 1989).

G. E. Hutchinson was the first to formally quantify the niche concept in terms of a geometric space. He presented the niche as a "multidimensional hypervolume, defined by the sum of all the interactions of an organism and its (abiotic and biotic) environment" (Hutchinson, 1957). He also introduced the terms *fundamental niche*, which means the entire set of resources which could physiologically be used by any one organism, and *realised niche,* which is its actual position limited by biotic factors such as competition, predation and relationship with its own food resources (Roughgarden & Diamond, 1986). These biotic factors effectively narrow the realised niche to only comprise a fraction of the abiotic habitat which an organism is adapted to occupy. Another aspect is the so-called "limited membership"; in which the species that *does* occur together constitutes a limited subset of what *might* occur together. Causes of the limited membership may be low rates of dispersal and species interactions such as competition and predation. These factors inhibit species from being present in an environment of which it is physiologically adapted (Roughgarden & Diamond, 1986). Important properties of a niche are its position on the resource continuum, its spread, and its overall shape and form (Putman & Wratten, 1984). The spread, or niche width, is a measure of the breadth of exploitation of a given resource by an organism, while the niche position and form relate to the role of the organism within its surrounding community, describing the relationship to organisms utilizing the same resource continuum. The fundamental niche often has a bell-shaped form, while the curve of a realised niche often is skewed or distorted due to interactions with other organisms such as predation or competition (Putman & Wratten, 1984). Contradictory to Grinnell and Elton, Hutchinson defined the niche only with respect to its occupant or species population, and not to the place in the community (Schoener, 1989).

The typical concept used in modern niche theory, known as utilization distribution, is defined for a particular species population and gives the fractional use of resources arranged along one or more dimensions called *niche axes* (e.g. Roughgarden, 1972). It is thus nothing more than a frequency histogram of resource use by some population. This was contradictory to Hutchinson's concept, which allows little representation of distributional properties of resource use. Hutchinson's interpretation of the competitive exclusion principle was that two species, when they coexist, must in some sense be occupying different realised niches, i.e. their realised niches do not intersect and there will be no overlap. Modern niche theory relates niche overlap to the competition coefficient and thereby coexistence. A little overlap allows coexistence, but somewhat more does not (Schoener, 1989).

1.3 Niche theories and a marine pelagic shelf environment

Three pelagic fish species from a common trophic level were included in this observational study. The species investigated were capelin (*Mallotus villosus*), polar cod (*Boreogadus saida*) and juvenile herring (*Clupea harengus*). All of these are migrating species with large stock fluctuations (e.g. Gjøsæter, 1998; Dalpadado et al., 2000). Capelin is a key species and by far the most important food source for higher predators in the Barents Sea (Sakshaug et al., 1994). The annual production of biomass through consumption is larger than the standing stock itself (Gjøsæter, 1998). Capelin, juvenile herring and polar cod possess the role as main consumers of zooplankton in the same area (Hamre, 1994; Hop et al., 1997). These schooling fish species occupy the link between zooplankton and marine top predators in the Barents Sea, i.e. they serve as intermediaries in energy conversion from zooplankton production to higher trophic levels. It is typical for a northern shelf ecosystem that this intermediate link is occupied by relatively few species that constitute a high total biomass (Sakshaug et al., 1994).

The Barents Sea capelin stock is subject to large interannual fluctuations (Hamre, 1994). Both overexploitation and heavy predation from juvenile herring on capelin fry have triggered two recorded collapses of the stock, whereas predation by cod *(Gadus morhua*) is demonstrated to delay the stock's recovery after a collapse (Hjermann et al., 2004a). Hamre (1994) found an indirect link between capelin and temperature, in which

capelin fry suffers from heavier herring predation as a response to warmer ocean water in the previous years. Consequently, he concluded that the dynamics of this ecosystem are governed by the inflow of warm Atlantic water, which determines distribution, recruitment success and growth of capelin as well as of the other key species investigated in his study. This view of temperature as a parameter that indirectly determines capelin dynamics was supported by Hjermann et al. (2004b), who showed that increased predation on capelin fry is a delayed result of increased drift of herring offspring northwards in years with high North Atlantic Oscillation (NAO) index. The same authors tried to combine herring predation, cod predation and harvesting as mortality factors, and found that survival of capelin larvae mainly is affected by herring predation, while survival in later life stages were dependent on the two latter factors (Hjermann et al., 2004a). Mortality factors were found additive, and not compensatory, perhaps explaining some of the violently oscillating pattern of the stock. Capelin are only weakly influenced directly by climate (Gjøsæter, 1998).

There is an inverse relationship between zooplankton abundance and capelin biomass, indicating that grazing by capelin has a negative effect on zooplankton abundance (Gjøsæter et al., 2002). A large capelin stock may graze down the medium-size zooplankton fractions, which will recover when the capelin stock is low (Dalpadado et al., 2003). Fauchald et al. (2006) investigated whether these food depletions caused by increased grazing pressure would affect the capelin migration pattern. They suggested that capelin would follow a density dependent migration wave (DDMW), and migrate further and have a more aggregated spatial distribution during years of high capelin abundance compared to years of low capelin abundance. A strong relationship was found, with speed and amplitude of the migration wave increasing with capelin abundance.

Pelagic schooling fish like herring and capelin perform extensive seasonal migrations between feeding and spawning areas (Hamre, 1994; Gjøsæter, 1998). Three pelagic migrating fish species, with overlapping feeding strategy, may have the potential of spatial interaction and competition, i.e. there is a risk of niche overlap. Rapid and unpredictable changes in migratory patterns of capelin will presumably have large consequences for ecosystem dynamics (Fauchald et al., 2006), and because of the

sudden northward DDMWs, it is reasonable to predict an adverse interaction with polar cod, which are feeding in the same area.

A species typically has normally distributed values of growth and survival rates along axes of abiotic factors, with a range of tolerance limited by an upper and a lower lethal limit (Putman, 1994). Inside this range of tolerance there is a critical maximum and minimum, beyond which an organism, though not dead, is ecologically inviable. The preferred range is a narrower range of conditions, concentrated around the species' physical optimum. In a marine environment, abiotic factors that set fundamental niche frames for a fish species' distribution may be physical conditions like temperature, salinity and stratification of the water column. However, Hutchinson's source-sink theory explains how a species may be present in a habitat unsuitable for growth and reproduction, caused by large reproduction that triggers migration out of the abiotic suitable habitat due to food depletion therein (Pulliam, 2000). As mentioned previously, capelin is not very sensitive to changing abiotic conditions and oceanography does not contribute significantly to form the realized spatial niche of capelin. It is therefore not likely that a source-sink effect forces Barents Sea capelin to migrate into a physically unsuitable habitat.

Taking into consideration the competitive exclusion principle and niche theory in general, it is reasonable to suggest that distribution of the main pelagic schooling fish species in a marine ecosystem will be affected by interspecific competition. The theme of this thesis was to figure out how a large stock of a dominant species affects distribution of its neighbouring species. Understanding the outcome of the potential interaction, i.e. possible competition for food and space with polar cod caused by capelin DDMW, and also how this migration affects the juvenile herring distribution in the south, was of essential importance.

1.4   Hypotheses

In an ecosystem-based fisheries management approach, understanding how shifts in abundance and distribution of a species affect neighbouring species is of significant interest, e.g. for researchers providing authorities with recommendations for catch

quotas. It was put effort into assessing coexistence tolerance and relating my findings to the competitive exclusion principle and general niche theory. A large skewing of the distribution of the neighbouring pelagic stocks may confirm the importance of standing theories.

During this observational survey, where three pelagic species in a northern marine shelf ecosystem were studied, some hypotheses have been tested; a large capelin stock will:

I)   Inhibit the polar cod's extension southwards and suppress it into colder water masses. Similarly it will inhibit extension of juvenile herring from the south.

II)   Concentrate the extension of polar cod and juvenile herring to smaller areas.

III)   Increase the spatial overlap between capelin and the neighbouring species.

IV)   Not lead to any shift in the distribution of the neighbouring species.

1.5   The larger project framework of this study

This thesis took part in a research project with focus on spatial aspects of the Barents Sea ecosystem dynamics. The project included several trophic levels, both from habitats above sea surface (seabirds) and habitats in the pelagic section of the water column. It is crucial to understand how a single key species acts as a link in the dynamics of the ecosystem, through migration and variations in density. An investigation of the species' interactions with its potential competitors, whose niches may be partly overlapping, will be the first approach to this understanding. Spatial relationship between pelagic fish species might influence the densities of species at other trophic levels. Influence from one species to another is not dependant on a direct interaction between the actual species, but may be a result of a complex system of links in the dynamics of the ecosystem. Marine mammals that are dependant on zooplankton may be suffering from growth in the stock of a pelagic species, because competition for this resource may be intensified. Sea birds are probably directly affected by these huge shifts, as pelagic fish constitutes their key prey. A main problem is to determine which way the interaction works, whether it is a shift at low trophic level that will influence those higher up (bottom-up) or eventually the opposite (top-down). A cascading top-down effect is also discussed as a possible outcome (Frank et al., 2007).

This study was limited to investigate the direct interactions between some main pelagic schooling fish species, but it will hopefully be a contribution to approach understanding of the Barents Sea ecosystem dynamics.

2   Materials and methods

2.1   Study area

Data for this study was collected from the Barents Sea, which is a 1.4 million km^2 sub arctic ocean. The Barents Sea is a rather shallow shelf sea in the northernmost Atlantic, and it is bordered by the Norwegian and Kola coast lines in the south, the Svalbard archipelago in the northwest, Franz Josef's Land in the northeast and Novaja Zemlja in the east. Its mean depth is 230 meters, and except of Bjørnøyrenna, a channel running east-westwards south of Bjørnøya with depths up to 600 meters, almost all of it is shallower than 300 meters. Most important banks, with depths shallower than 200 meters, are Svalbardbanken between Bjørnøya and Hopen, Storbanken northeast of Hopen, and Sentralbanken, halfway between Svalbard and Novaja Zemlja. These are all highly important fish banks.

The Barents Sea waters consist of three different water masses; Atlantic Water (T>3.0°C, S>35.0), Coastal Water (T>2.0°C, S<34.7) and Arctic Water (T<0.0°C, S=34.3-34.8) (Loeng, 1991). The warm, but relatively fresh Coastal Water, flows westwards along the coast of Norway, disrupted by the coastal banks on its way. The warmer and saltier Atlantic Water is flowing into the Barents Sea with the Norwegian Atlantic Current. It enters the Barents Sea through Bjørnøyrenna and divides into two branches, one flowing eastwards parallel to the Norwegian-Russian coastline, and the other one turning northeastwards along the Hopen trench until it meets the colder and lighter Arctic water masses, which come from northeast, mainly entering the Barents Sea through the strait between Novaja Zemlja and Franz Josef's Land (Loeng, 1991). The borderline between the cold Arctic and warm Atlantic water masses is known as the Polar Front. It is sharply defined in the west and more diffuse further east, and is strongly influenced by the bottom topography. Ingvaldsen et al. (2001) found that there are large seasonal and interannual variations in transport of Atlantic water to the Barents Sea, with inflow fluctuating up to 10 Sv. Variability was partially linked to the local atmospheric pressure field.

Ice formation takes place north of the Polar Front during winter, but its interannual variability in formation and extension is highly variable. When melting takes place in late spring, a sharp transition layer, or pycnocline, is produced between the light melt water and the saltier Arctic water. The stratification is completely broken down only during years with very heavy ice formation, when larger amounts of bottom water are formed by cooling and increase in salinity resulting from brine rejection to the water (Midttun, 1985).

2.2 Ecology of species investigated

The three species investigated, capelin, herring and polar cod, are all schooling pelagic fish species in the Barents Sea ecosystem.

Capelin (*Mallotus villosus*) is a short-lived species and constitutes the largest pelagic fish stock in the Barents Sea. The stock size has shown huge fluctuations between years since regular estimation started with annual cruises in the early 1970's. Abundances have ranged from an estimate of more than 7 million tonnes in the mid 1970's to close to extinction after the collapse in 1986 (Michalsen, 2003). The capelin stock stays in the Barents Sea during all life stages, but performs extensive seasonal migrations. During winter and early spring, mature capelin migrate from a central position in the Barents Sea and southwards to the spawning areas. Its eggs are spawned on the seabed in shallow areas along the coast of northern Norway and east to Kola in April-May, and the 0-group capelin is distributed further north and eastwards beyond 50°E in August-September (Gjøsæter, 1998). Most capelin die after spawning, but for the remaining survivors, feeding-migration towards the north and northeast takes place in summer and autumn. The position of both spawning areas, nursery areas and feeding areas vary with oceanographic conditions (Gjøsæter, 1998). Gjøsæter et al. (2002) found that capelin growth is strongly correlated with the abundance of zooplankton, as various size groups of these constitute the food for all age groups. Juvenile capelin feed on nauplii of copepods and cyclopoids, and large, mature fish generally prey on adult copepods, euphausiids, and hyperiids (Orlova et al., 2002). Diet has been found to vary significantly between years due to availability and competition situation.

Capelin growth has been proven to be influenced positively by temperature (Gjøsæter & Loeng, 1987). This is primarily not an effect of temperature tolerance by itself; it is most probably linked to zooplankton production and thereby food availability. In a study by Fauchald et al. (2006) it was suggested that the capelin feeding migration in summer is triggered by food depletion, caused by increased capelin abundance. The sharpness of the food gradient perpendicular to the migration front is determined by the aggregation of fish along this front, and the speed and amplitude of the migration wave is increasing with increased capelin abundance. Only a weak correlation was found between sea temperature and capelin distribution in this study.

Capelin is a key prey for cod and other fish species, as well as sea birds and sea mammals (Sakshaug et al., 1994). According to a study by Dolgov (2002) capelin was found in the stomach of 21 species of fish and 18 species of birds. Because of its key role as an important forage fish species, the large fluctuation in capelin abundance influences species at several trophic levels in the Barents Sea ecosystem.

The Norwegian spring-spawning herring (*Clupea harengus*) has a high migratory capacity (Nøttestad et. al. 1999), and mature fish is found from east of Iceland and northwards along the central parts of the Norwegian Sea when feeding. *Calanus finmarchicus* and *C. hyperboreus* constitute the main prey for herring (Fernø et al., 1998). Spawning takes place along the western coast of Norway, and the larvae are transported northwards along the Norwegian coast and into the Barents Sea. Juvenile herring is feeding on zooplankton in the Barents Sea until the age of three to four years, before it migrates westwards to join the spawning stock (Dragesund, 1970). Predation pressure from juvenile herring on capelin larvae when present in the Barents Sea, is found to be significant, although the exact impact of this predation is not fully understood (e.g. Huse & Toresen, 2000; Hallfredsson & Pedersen, 2007). In warm years with larger inflow of Atlantic water, stronger year classes of cod and juvenile herring enter the Barents Sea from the south (Hamre, 1994). When the herring grow up, capelin fry will suffer from heavier predation. Distribution of adult capelin might be affected as a delayed response to predation and competition from cod and herring (Gjøsæter & Loeng, 1987). Competition between herring and capelin will occur because they are both feeding on zooplankton, i.e. sharing the same niche with respect to feeding.

Polar cod (*Boreogadus saida*) is a small and relatively short-lived pelago-sympagic species (Gulliksen & Lønne, 1991). Pelago-sympagic organisms are pelagic organisms with a temporal stay in the ice-habitat, as it is often found schooling between sandwiched ice flows in the drift ice. Spawning takes place in the free water masses, often beneath the ice and in early spring. The eggs are hatched at an age of 1.5-2 months (Gjøsæter, 2003). The diet of adult polar cod is found to be differing for those individuals found in the open water, the perennial sea ice and the first-year sea ice (Lønne & Gulliksen, 1989). Diet of individuals in the open water is dominated by copepods such as *Calanus finmarchicus.* Fish in the first-year ice also merely feeds on pelagic crustaceans like calanoid copepods, while diet in the multi-year ice consists both of pelagic organisms and sympagic amphipods like *Apherusa glacialis* and *Onissimus spp*. During a research by Hop et al. (2002) in Kongsfjorden at the Spitsbergen west coast, it was found a shift from diet dominated by copepods to a diet dominated by amphipods when the polar cod reached a size of 8-10 cm. This shift coincides with a change from pelagic to benthic distribution, and may reflect availability of suitably sized prey. The similar tendency of shift in diet was found by Lønne & Gulliksen (1989) and might signalize a general movement into the multiyear ice zone as the fish grow up.

According to their highly overlapping diet, it is reasonable to expect direct competition as a significant interaction between capelin and polar cod in the north and capelin and herring in the south. Ushakov (2002) also manifested this in a review, although competition was found to be most extensive in the capelin-polar cod interaction, due to large feeding area overlap.

2.3 Data collection

The data sets used in this study were collected during scientific cruises that were carried out in cooperation between the Norwegian Institute of Marine Research (IMR) and the Russian Polar Research Institute of Marine Fisheries and Oceanography (PINRO). Research vessels from both nations are participating in this yearly event, and it is attempted to achieve sufficient data coverage from most parts of the Barents Sea by letting the ships follow a given system of transects (Figure 1). Sampling is carried out in
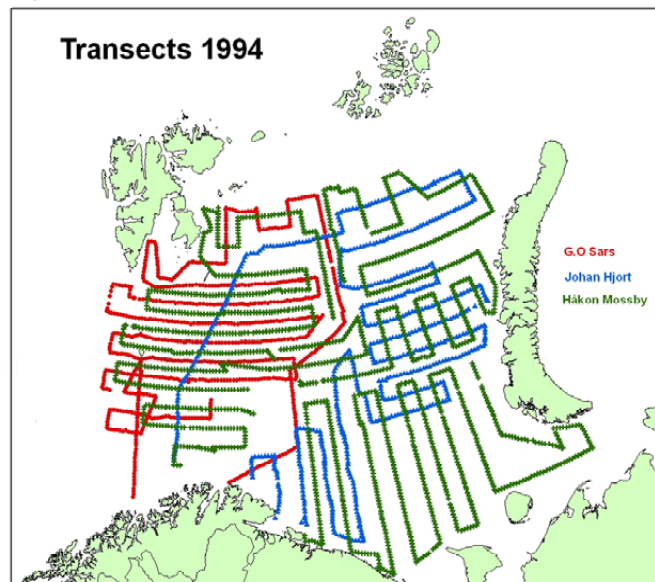
a)
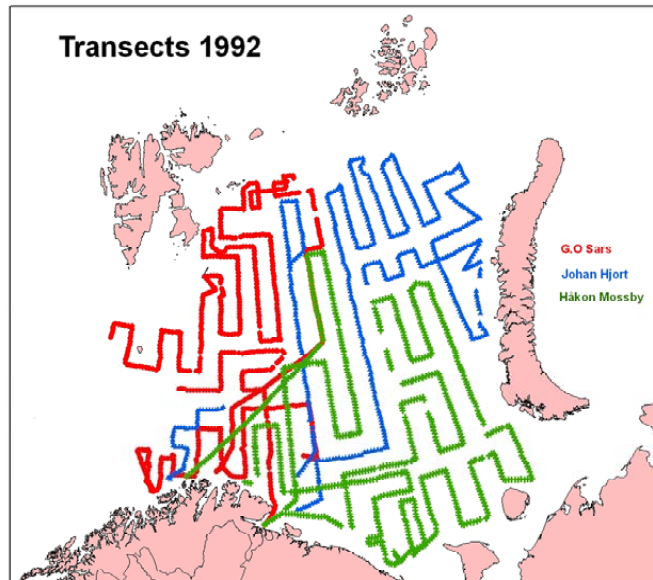
b)

Fig. 1: Transects followed by the research vessels. Data samples were averaged for each 5 nautical miles.

the autumn (September-October), because factors affecting the measurements like weather conditions, fish distribution and migration, are found most suitable at that time of the year (Gjøsæter et al., 1998). These collections, including the use of acoustic

measurements, started in 1972 for capelin and 1983 for herring, and they are providing researchers with an overall picture of the distribution of the fish species**.**

The datasets that are collected during the autumn cruises are of quite extensive proportions. CTD data were taken from the ICES' (International Council for Exploration of the Seas) database, while acoustic data are provided directly by IMR and PINRO. For various reasons, some data are lacking in this common base. Autumn scientific cruises are costly and time consuming, but they are essential in providing stake holders, researchers and authorities with information about the state of the Barents Sea, with regard to stock sizes and year class distributions of commercial species. Research results based on these data make the basis for negotiators when catch quotas are to be determined.

2.4   Acoustic abundance measurement method

The echo integrator was developed in the mid 1960's, making it possible to use echo sounders more quantitatively for measurements over large areas. The acoustic method has since developed into a sophisticated way of mapping the Barents Sea ecosystem, and it is object to annual improvements. The time lag between the transmission and reception of a given echo corresponds to the depth of the target. Transmissions from the echo sounder are averaged for each 1 or 5 nautical miles. In my study, intervals of 5 nautical miles were used. Hence, at a typical vessel speed of 10 knots and a pulse repetition frequency of about one per second, several hundred transmissions are averaged. Modern equipment normalizes the values with respect to calibration of data so that the output is an estimate of backscattering area per unit sea surface, represented by an S_A-value (square meters per square nautical mile) (Aglen, 1994). An S_A-value is a relative measurement of density, and it is found by the equation $S_A = \rho \cdot \sigma$, where ρ is the area density of targets and σ is the average back-scattering cross-section per target. Modern acoustic systems provide information on the distribution of the target strength of the scatters, i.e. the ability of a fish to reflect sound, dependent on size of swim bladder etc (Toresen et al., 1997). Total S_A-values might then be split among the different fish species, so that by the end of the study, there is a record of separate S_A-values for each category of fish. Only S_A-values were used in this study for quantitative

measurements of the fish stocks, but the actual number of fishes, N, can be found by multiplying ρ by the actual area, $N = \rho \cdot A$. If the mean weight w of these fishes is known, the biomass, B, can be calculated by $B = N \cdot w$ (Gjøsæter et al., 1998).

Although the acoustic measurement method has been considerably improved since its introduction in the surveillance of the Barents Sea ecosystem, it still suffers from a number of limitations. Fish that form dense schools may cause underestimation within the beam due to sound extinction, instrument saturation or misinterpretation of the school as bottom. Errors in estimation might also be caused by migration of schooling species (Aglen, 1994). Consequently, the interpretation of the acoustic data is often quite uncertain, and the observations drawn from the echo sounder must be brought to verification. Each of the averaged interval values must be examined and allocated into categories, e.g. species or groups of species (0-group and mature fish). This allocation is based on the identification of different types of recordings with the help of sampling gear, of which trawl is the most common. Trawl samples are taken at regular intervals along the transects, and additional hauls are taken whenever the characteristics of the echogram change (Gjøsæter et al., 1998). For the main species a subsample of 100 individuals is selected, and length, weight, sex, age and stomach filling are recorded for each single fish.

2.5 CTD stations

Parallel to the acoustic survey and stock estimations, abiotic conditions were measured along the transects. CTD-data (Conductivity, Temperature and Density) were collected at all stations in addition to several exclusive CTD-stations in between. Samples for these variables were collected at specific depths. I used temperature and salinity data from surface (0 m) and 100 m depth, because these two depths were found beneficial with respect to having one measurement above, and one beneath, an eventual pycnocline when also taking into consideration the shallow depths of the Barents Sea. Signs of stratification would probably be detected by this method of sea water property data sampling. Inverse distance weighting (IDW) was used as interpolation technique to picture out temperature and salinity gradients horizontally at these two depths, in the years of interest. IDW is a method of interpolation that estimates cell values by

averaging the values of sample data points in the neighbourhood of each processing cell. The closer a point is to the centre of the cell being estimated, the more influence, or weight, it has in the averaging process. The function used for this purpose is $w(d)=1/d^{\,p}$, where $w(d)$ is the weight of a given point at a given distance d and the exponent p is a measure of the power, i.e. the significance of known points on the interpolated values, based on their distance from the output point (ESRI ArcMap 9.2). A high power puts more emphasis to the nearest points, and the surface will appear more detailed (less smoothed). The most common choice is $p=2$, which was also used in this study. Using this level of power would provide a fairly smoothed surface, but still reveal any important details. Salinity values were more homogeneously distributed at 100 m depth than at the surface, and a finer scale was therefore used to detect differences at this depth.

2.6   Selection of years for investigation

Two different years were compared in this study, and the degree of fulfilment of three main criteria was paid attention to when selecting these two years (Table 1). Firstly, years with respectively high and low capelin abundance were sorted. Because the main theme of the investigation was the effect of stock size on distribution of capelin itself and the other species, capelin abundance was also the most important focus. Secondly, large scale oceanographic conditions had to be controlled for. Because I wanted to find the effects from capelin abundance alone, I emphasized to keep the physical divergence between years within a relatively small range. Thus, any differing in distribution across the environmental gradients could be explained solely from abundances. A combination of mean temperature and the total capelin stock is found in Figure 2. Ultimately, I attempted to find years with a sufficient data cover. Completely optimal years could not be selected with respect to equal physical conditions, due to inadequate data coverage in the easternmost parts of the Barents Sea. Consequently, there has been a trade-off between finding two years of approximately similar physical conditions and two years with widely differing capelin stock. The two years that were selected for investigation in this research, 1992 and 1994, do have a fairly adequate coverage of transects in the Russian section of the Barents Sea (Figure 1), combined with the assumption that the physical conditions do not diverge too severely (based on measurements from the Kola

transect, Figure 2). Total Barents Sea capelin biomass was estimated to 5,214,000 tonnes in 1992 and 254,000 tonnes in 1994 (ICES). Any autocorrelation regarding distribution between years is unlikely, because capelin migrates at a large scale interannualy. The stock distribution of each fish species (based on transformed S_A-values) was visualized in maps, worked out by the IDW interpolation technique which was explained in section 2.5.

| | **1992** | | | | | **1994** | | | | |
	Dist (km)	Mean	Min	Median	Max	Dist (km)	Mean	Min	Median	Max
Capelin	64671.84	4.377	0	0.113	56.368	88229.28	0.164	0	0	4.971
Polar cod	64671.84	0.903	0	0	70.110	88229.28	0.678	0	0.002	23.578
Herring	64671.84	1.838	0	0	28.056	88229.28	0.315	0	0	24.161
	N					N				
Temp 0 m	951	5.162	-0.969	5.613	9.316	753	5.090	-0.665	5.149	9.885
Temp 100 m	951	2.682	-1.376	2.499	8.130	753	2.259	-1.552	2.205	7.324
Sal 0 m	951	34.229	30.620	34.478	35.050	753	34.342	31.557	34.576	35.011
Sal 100 m	951	34.865	34.270	34.887	35.161	753	34.872	34.272	34.927	35.101

Table 1: Descriptive statistics of fish densities (S_A-values) and CTD-data (temperature by degrees C and salinity). Dist (km) means total length of the transects. N equals number of CTD stations. CTD-values are missing for some of the fish data.
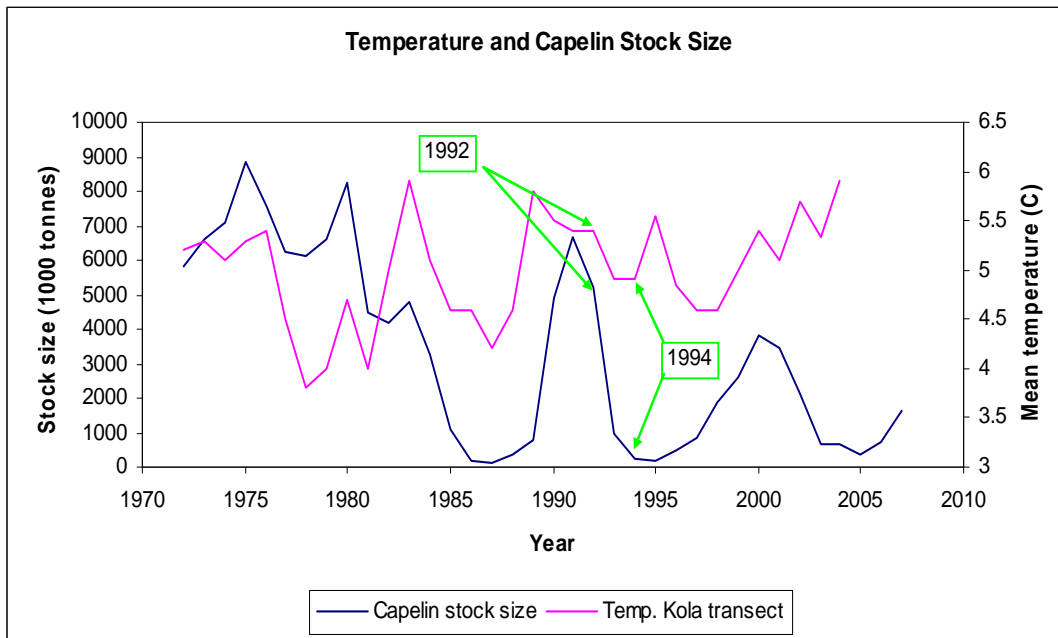

Fig. 2: Mean sea temperature (0-200 m depth) along the Kola transect compared to the total estimated Barents Sea capelin stock. Temperature data provided by PINRO.

2.7 Aggregation of data

This is a large scale study, investigating interactions between stocks in a vast geographical area. According to Jelinski and Wu (1995), the size of the observational window must match the scale of the phenomenon or pattern of interest. Pelagic schooling fish has a highly heterogeneous spatial distribution at small scales (see e.g. Fauchald et al., 2000). Small-scale patterns were not of interest in this study, and this eventual noise had to be filtered away. As mentioned previously, data samplings were carried out along transects, and the requirement of large scale interpretation of the samples was met by aggregation of data points. Aggregation was performed by calculating the sum of all data inside a circle with a given radius. These circles were following each other continuously along the transect. The number of data points would increase when the vessel was turning, and consequently give a more accurate estimate of that particular circle. Migration patterns at a scale of several hundred km were investigated in this study, and aggregation circles with a radius of 50 km were supposed to be proper. This resolution would probably provide us with any significant findings.

The species had a very skewed and patchy distribution, and therefore the data set used in this study contains a high number of zeroes. Zero-inflation and spatial correlation are typical properties of marine spatial data, due to schooling and aggregative responses towards abiotic features (Cianelli et al., 2008). The zero-inflation was reduced by the aggregation of the data. To reduce the skewness, all data were transformed to a log-scale.

Zero-values complicated the log-transformation of the data. To overcome this problem, I added a small constant to the data set before the transformation. This constant was set to equal the lowest S_A-value found in the entire data set which was 0.002.

All CTD-values inside the given 50 km radius of each circle were averaged before connecting the oceanographic values to the aggregated S_A-values in the same area.

2.8   Analyses performed in this study

Presentation of the data was initiated by giving an overview of the descriptive statistics. Firstly, a general description of the density distribution of each fish species was presented. This overview would give an idea of the patchiness and concentration for each year, together with the proportion of completely empty areas and the percentage of the area in which a given share of the biomass was concentrated.

Next, it was a necessary purpose to detect the spatial presence of each of the different fish species relative to the oceanographic conditions. I.e., at which partitions of the scales of the oceanographic conditions were the species present in each of the years? Approaching this visualization of data spread has been achieved by systematizing the data values larger than zero into quartiles. The quartile distributions on the axes of oceanographic values have been presented by box plots, also including mean values. Any skewness, overlap and deviation between the two years would then easily be revealed.

The third step was to measure the distribution of fish with respect to the density of capelin. In other words, I attempted to find the distribution of densities of capelin experienced by the two other species and capelin itself. A high degree of overlap when capelin density was also high could reveal an increased potential of competition between species. This presentation might also signalize high degree of intraspecific competition when the capelin stock itself was densely packed. Box plots with distributions over a density scale were used for this presentation as well.

Posterior to mapping out the density distribution of the stock's S_A-values along oceanographic scales, I analysed the distribution of fish in relation to the oceanographic variables handled as niche parameters. To what degree would each independent abiotic variable explain the distribution of fish? I expected relatively high covariance between some of the explanatory variables, resulting in co-linearity. By chance, different variables might emerge as important in different years when implementing them in multiple models. Hence, it would be difficult to interpret change in environmental niches between years, and I therefore adopted a separate analysis of each of the variables. Two covarying variables might not only be a problem, they can also be

handled as replicates supporting any pattern that elsewhere might have been considered to be insignificant.

A non-linear relationship between fish abundance and oceanographic parameters was expected, and this would claim a more sophisticated tool than a generalized linear model. Generalized additive models (GAMs) were used to provide us with a more proper picture. A generalized additive model is a generalized linear model with a linear predictor involving a sum of smooth functions of covariates. The model allows for rather flexible specification of the dependence of the response on the covariates rather than detailed parametric relationships (Wood, 2006). Smoothing will include the use of penalized regression splines, and the degree of smoothing will be a trade-off between bias and variance. If the smoothing line fits many of the data poorly, the number of splines is too low, and if the smoothing line tends to be overfitted, i.e. it fits the noise as well as the signal, then the number of splines selected is too high. Generalized cross validation (GCV) was used to select an appropriate number of splines for each of the parameter's regression line. GCV was automatically executed by the mgcv package under R (Wood, 2006), also providing the estimated degrees of freedom.

3 Results

3.1 Distribution of density

According to my expectations based on the criteria for selection of the two datasets, capelin was found to be present in a larger proportion of the area in 1992, which was the year with highest total capelin abundance (Figure 2). In 1992, no capelin was found within ca 45 percent of the total investigated area, while 45 percent of the total fish stock was found within 10 percent of the area (Figure 3a and 3b). In 1994, no fish was observed in 57 percent of the total area and approximately 75 percent of the observed stock was found within 10 percent of the area (Figure 3a and 3b). Both total distribution and concentration was larger in 1992, which was also expected when taken into consideration that total biomass was approximately 100 times larger than in 1994. As can be interpreted from the curvature in Figure 3b, a given proportion of the capelin stock was found in a larger share of the total area in 1992. Also, the histogram in Figure 3a revealed that a larger proportion of the capelin was found in more densely packed areas in 1992 than in 1994. The herring density distribution had close to the same pattern as capelin with respect to deviance between the two years (Figure 3c), although its distribution was concentrated to a smaller share of the investigated area in both years (Figure 3d). Herring was absent in approximately 68 percent of the total area in 1992, and about 65 percent of the individuals were detected inside 10 percent of the total area. In 1994, the entire stock was concentrated within 10 percent of the area, i.e. there were no herring observed in 90 percent of the area this year (Figure 3c and 3d). The stock's distribution was more extensive in 1992, when total stock was larger. A higher share of the stock was found in densely populated areas in 1992 than 1994 (Figure 3c). Polar cod showed less divergence between years regarding overall density distribution, but had an opposing pattern when compared to the other species (Figure 3e and 3f). Zero-values were found in approximately 60 percent of the area in 1992 and 50 percent in 1994. 90 percent of the stock was observed in 10 percent of the area in 1992 and 80 percent in 1994. The frequency histogram in Figure 3e reveals no special divergence between years with respect to density distribution.
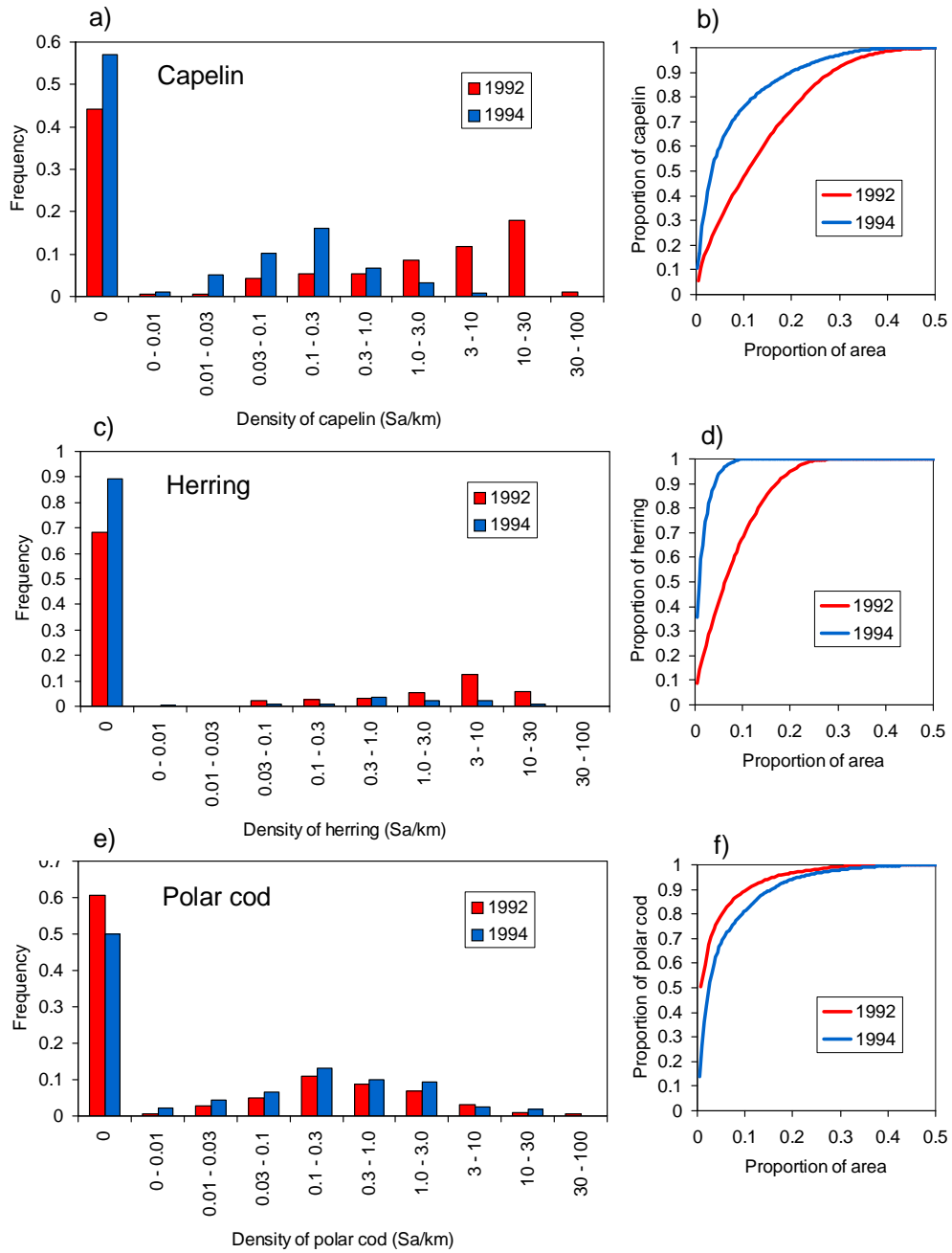
Fig. 3: Left: Frequency histogram of fish density. Right: Cumulative proportion of fish as a function of proportion of area surveyed.

3.2   Distribution of fish in relation to environment

Regarding distribution of the fish species relative to oceanographic conditions, my findings revealed significant interannual divergence for some of the parameters. For capelin, the bulk majority (the 25-75 interpercentil) of the 1992 stock had no overlap with the same interpercentil of the 1994 stock, with respect to surface temperature (Figure 4a). I.e., a vast majority of the capelin presence was observed in colder water masses in 1992 (majority present at SST<4°C) than in 1994 (majority present at SST>4°C), which can also be discovered when comparing Figure 5a and 5b with 6a and 6b, respectively. Similar observations apply to polar cod and herring as well (Figure 4a), but are not just as obvious when comparing the maps (Figure 5c-f and Figure 6a-b). The median of the polar cod distribution is only marginally skewed into waters with lower SST in 1992. Briefly summarized, the species were on average present in areas with colder surface water masses in 1992, when the capelin stock was large. When studying the presence on 100 meters depth temperature scale (Figure 4b), only capelin has a clear repetition of the pattern found at the SST scale. This may be explained by little proportionality between distribution of temperatures at the surface and 100 meters depth, although temperatures were generally lower deeper in the water column (Figure 6c-d).

For distribution across a surface salinity scale, most of the trends from the temperature diagrams were detected once more (Figure 4c). Herring and capelin were present in areas with less saline surface water in 1992 than in 1994. This is likely because cold water masses are less saline, and detects a possible colinearity between these two variables (compare Figure 7a-b to 6a-b). Any difference for the polar cod could hardly be detected, probably because they will at any circumstance only be present in low saline Arctic water masses. Salinity values at 100 meters depth were almost homogeneous all over, with areas of slightly fresher water close to the Norwegian coast and in the north, to the east of Svalbard (Figure 7c-d). A larger proportion of the capelin was distributed across the less saline deep sea waters in 1992 than in 1994 (Figure 4d, 5a-b and 7d). Herring showed an opposing pattern (Figure 4d), as the stock's distribution extended further from the Norwegian coast and into the central Barents Sea (Figure 5e-f and 7d). These descriptive statistics detected no obvious change with respect to the polar cod (Figure 4d, 5c-d and 7d).
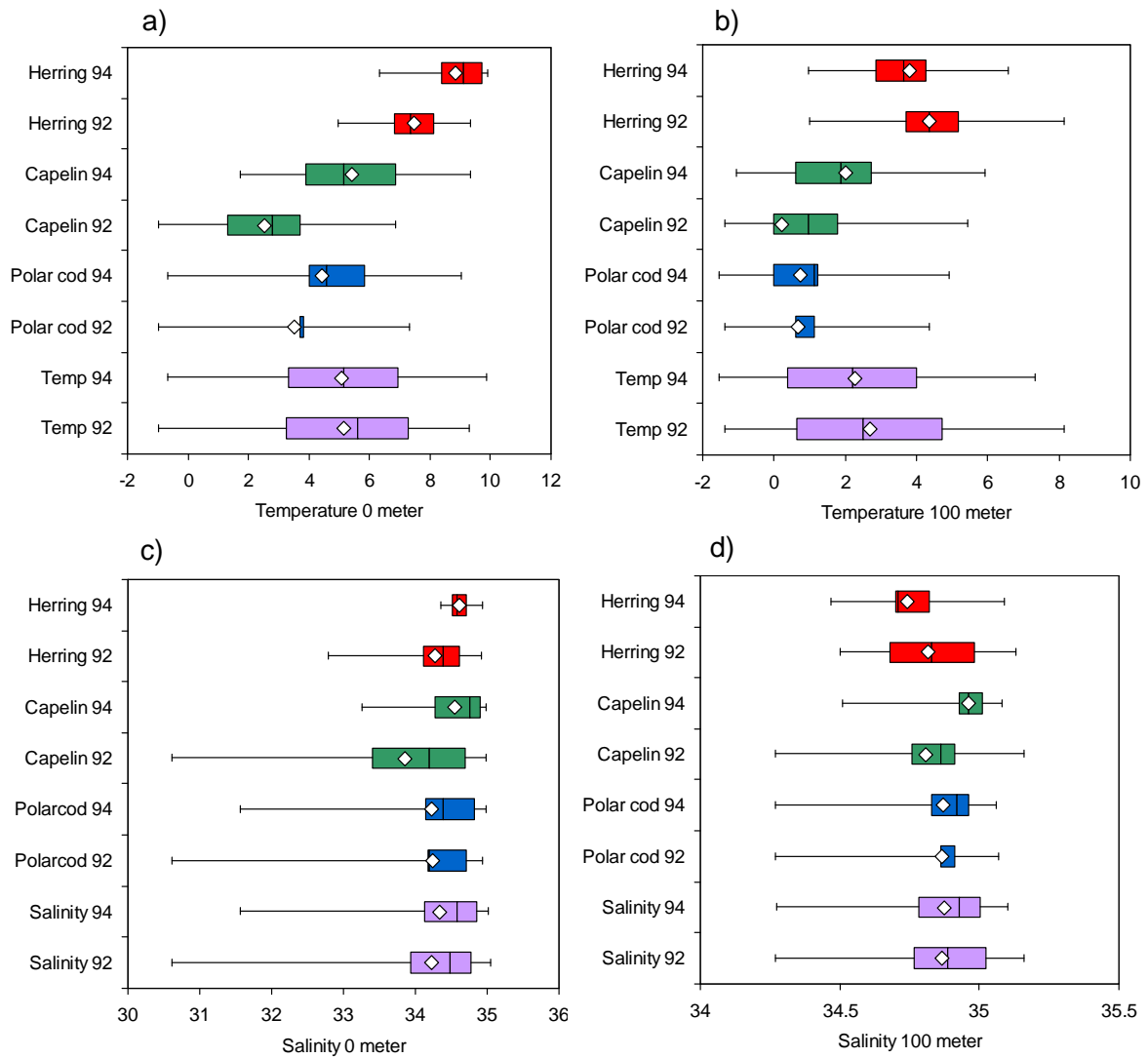
Fig. 4: The distribution of fish with respect to oceanographic values. Box plots containing quartiles (min, 25%, median, 75%, max) show the oceanographic conditions experienced by the fish stocks. Mean values are indicated by "diamonds". Purple boxes are distributions of the oceanographic variables.
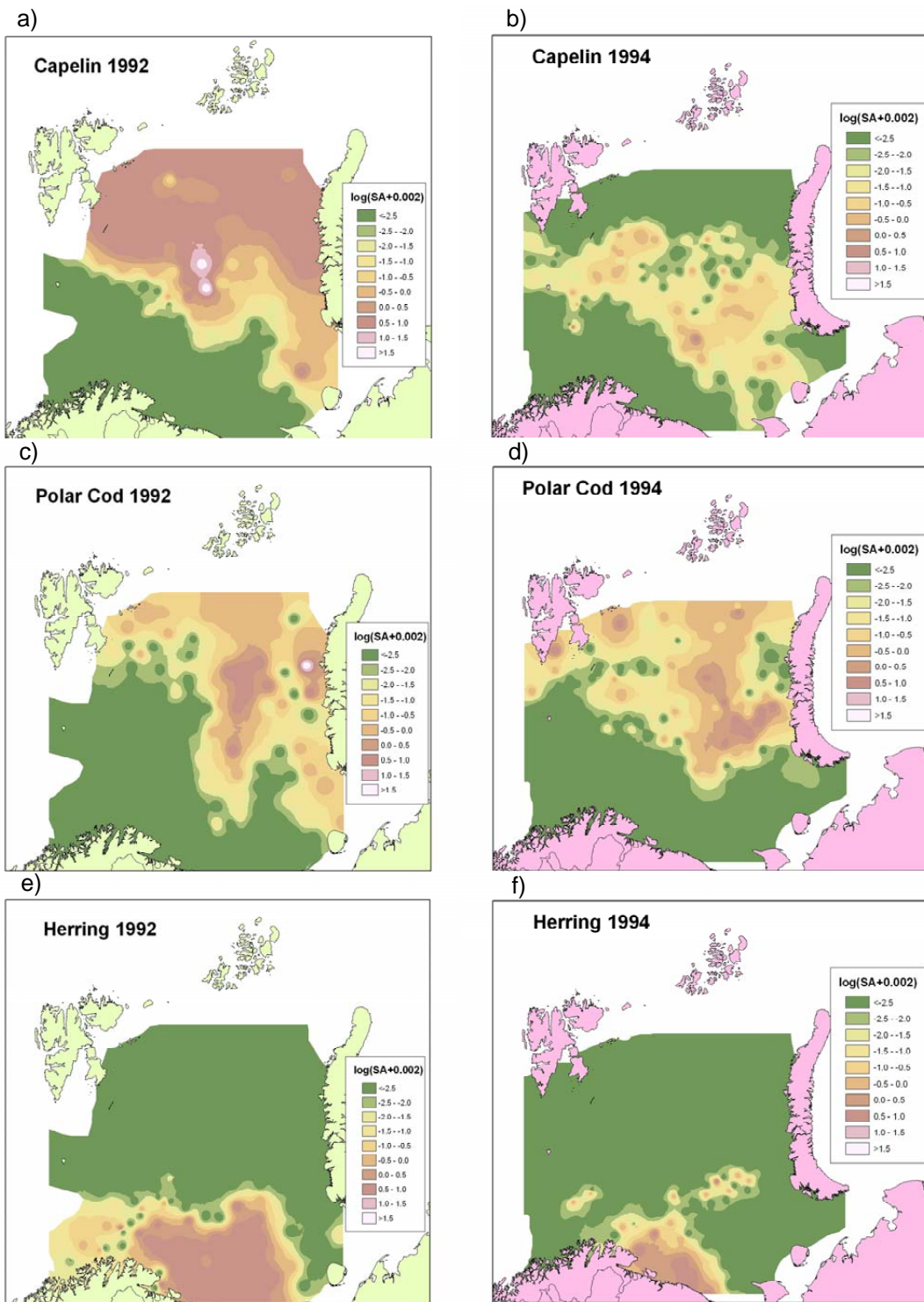
Fig. 5: Interpolated (IDW) distribution of fish density (log-transformed SA-values).

a) Sea Surface Temperature 1992

b) Sea Surface Temperature 1994

c) 100 m Depth Temperature 1992

d) 100 m Depth Temperature 1994

Fig. 6: Interpolated (IDW) temperature measurements August-September. Data from ICES.

Fig. 7: Interpolated (IDW) salinity measurements August-September. Data from ICES. Notice the different scales.

3.3 Distribution of fish in relation to capelin density

Figure 8 provides us with the distribution of the different species with respect to capelin density. Thus, the figure depicts the distribution of the capelin densities that individuals, both from the ca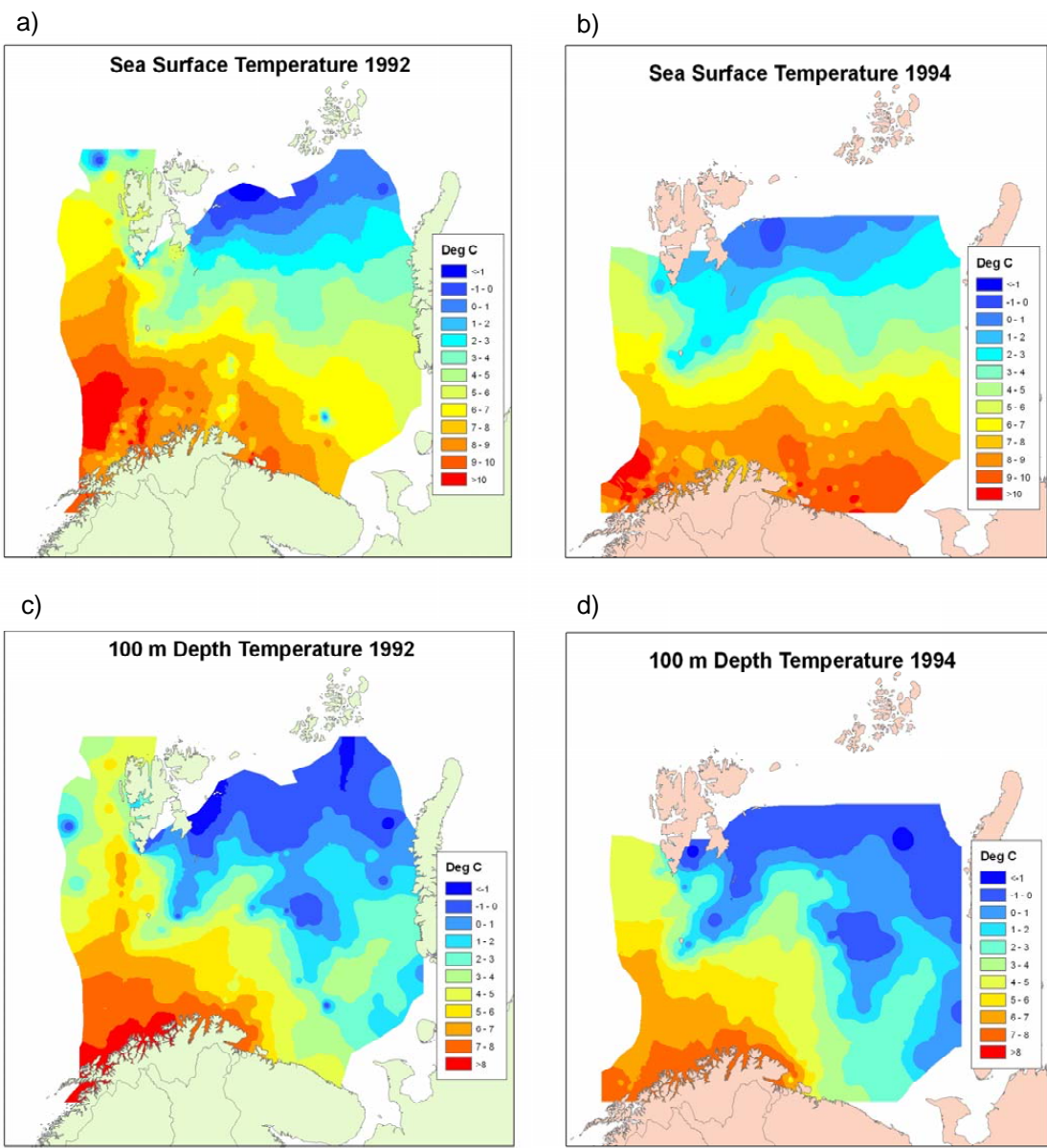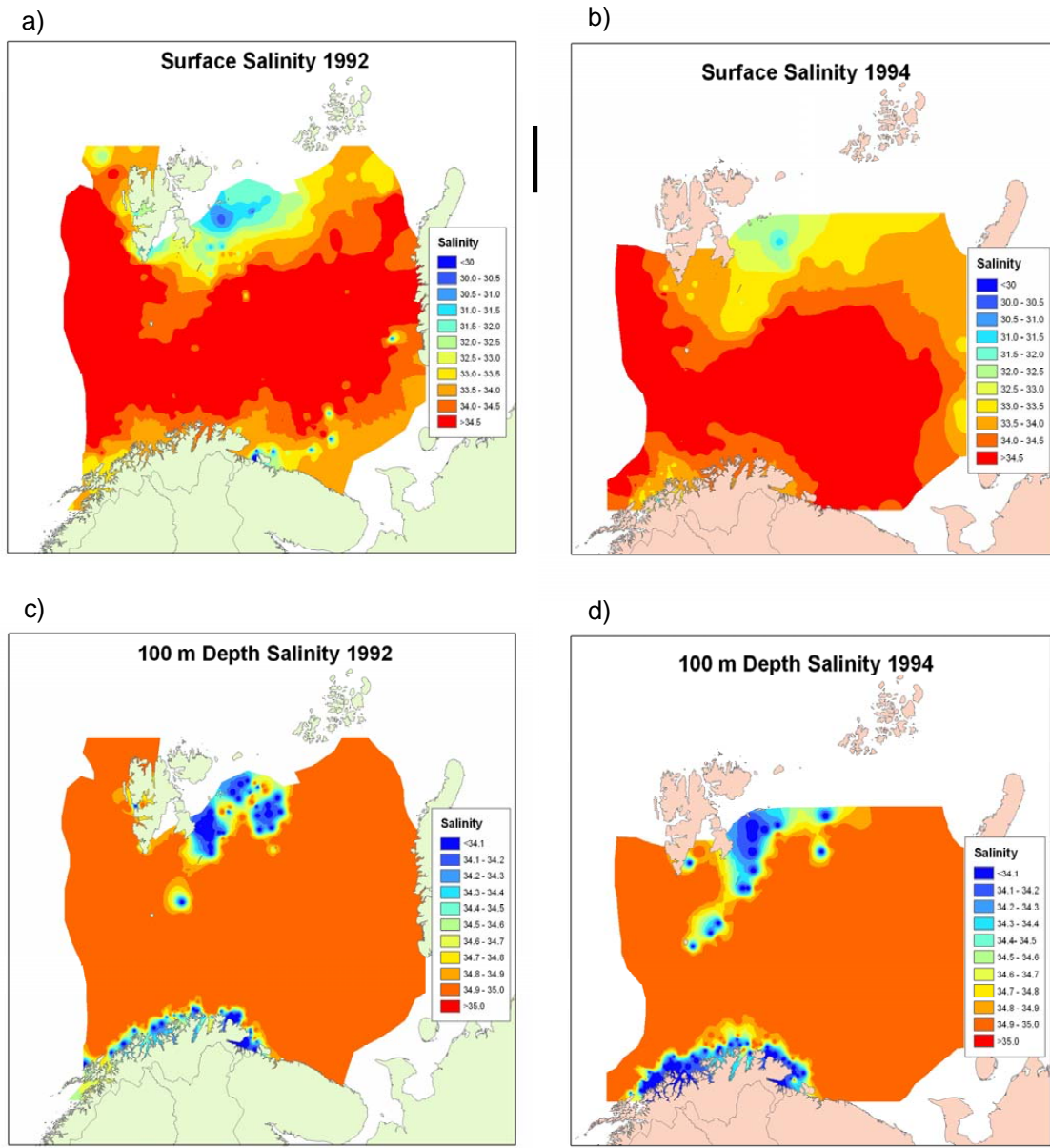pelin stock itself and from the two other species, will experience. If most of the observations of polar cod and herring are done in areas with high capelin density, it signalizes a high spatial overlap. An approximation of the potential strength of interspecific and intraspecific competition might be predicted from these descriptive data. In 1994, polar cod was mostly observed in an area with low capelin density, including large areas in the north where there was almost no capelin present at all (Figure 5b and d). In 1992, most of the polar cod present was concentrated to areas with rather high capelin abundance, increasing the probability of significant ecological interactions. Contrary to polar cod, the majority of the herring stock experienced a capelin density equal to zero in both years. However, the mean values show that capelin densities were slightly higher in areas where herring was also present in 1994 than in 1992. The plots in Figure 8 also illustrate that capelin was much more densely packed in 1992 than in 1994. The plots called "Cap dens" show the distribution of capelin densities for all of the investigated area. The plots called "Capelin" show the distribution of capelin with respect to capelin density. A randomly selected individual would probably experience a much higher density of its own species in 1992. Because the probability of encountering other individuals was enhanced by several magnitudes this year, the scene might have been set for intensified intraspecific competition.
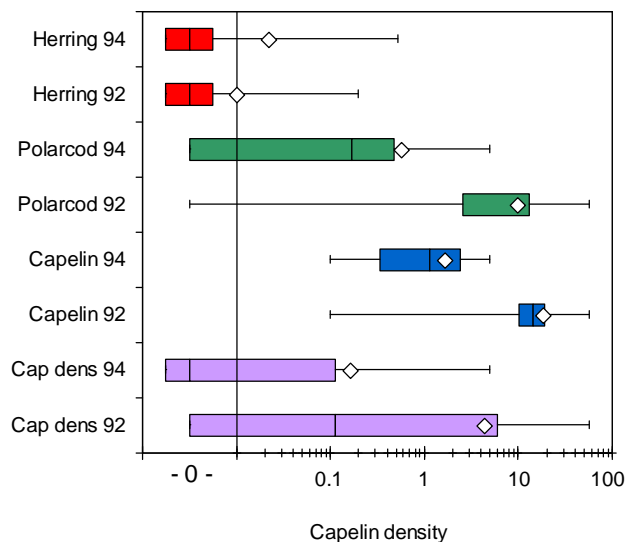
Fig. 8: Distribution of fish in relation to capelin density represented by box plots (min, 25%, median, 75%, max). Diamonds represent mean values. Distributions to the left of the vertical zero-line indicate the proportion of the total area with zero capelin density. The purple box plots show the capelin density distribution for each of the two years. The red and green box plots show the distribution of the neighbouring fish species with respect to capelin density. The blue plots show the distribution of capelin with respect to capelin density.

3.4 Analyses of density and oceanographic factors

As we could see in Figure 4a, fish was observed at surface temperatures ranging from -1 to 10 degrees C. The GAM analyses revealed high deviance explained for some of the variables, although it was in the intermediate or low range for most of them (Figure 9-12). Both the highest and lowest explanation was detected with respect to capelin. For this species, the deviance explained ranged from only 3.91 percent for surface salinity to 78.7 percent for surface temperature. Temperature explained more than salinity for all species. I found generally higher degree of explanation in 1992 than in 1994, mainly caused by the shift in capelin distribution in relation to oceanography. The number of degrees of freedom varied from 1 (surface salinity) to 6.38 (100 m temperature).

The strongest connection that was found, was between capelin and surface temperature (Figure 9a-b). Whereas the smoothed regression line took form like a bell-shaped curve in 1994, with a density maximum around 4.5 degrees, the situation was radically different in 1992 when the stock was larger. In 1992 density was very high in cold Arctic water masses, but declined sharply when temperature exceeded 3.5 degrees. This very obvious shift in relative distribution of capelin was repeated with respect to 100 m depth temperatures, as the patterns of the smoothed curves were closely related (Figure 10a-b). However, this close connection was not surprising, as I expected covariance between these two variables at a large scale. Surface salinity did hardly explain the density of capelin at all, and GAM did not seem to be beneficial compared to a linear model, probably because there were too few data points in areas with low salinity (Figure 11a-b). Regarding salinity at 100 m depth, any clear pattern could not be extracted (Figure 12a-b). As for surface salinity, data points were few in low salinity waters also for this variable. Based on these few points, a higher density was found in less saline waters in the northern Barents Sea in 1992. A better explanation might have been detected if the salinity scales had been transformed.

Contrary to capelin, polar cod showed no clear shift in distribution for any of the variables (Figure 9-12 c and d). The smoothed curve showed a general decrease towards warmer surface waters, but with an intermediate increase around 4 degrees in 1994 (Figure 9c-d). This was repeated with respect to 100 m depth temperature, but with the

intermediate increase in density at about 1 degree in 1994 (Figure 10c-d). Surface salinity explained very little of the polar cod distribution, and the relationship was linear (edf=1) with density decreasing for increasing salinity (Figure 11c-d). A non-linear relationship was found for salinity at 100 m depth; the general trend was still decreasing density for increasing salinity, but with an intermediate increase when salinity values approached 34.9 (Figure 12c-d). Any shift between the two years though could hardly be detected, most likely because the salinity at this depth is homogenous in most of the area (Figure 7c-d).

Herring densities were clearly related to surface temperatures in both years, with densities increasing sharply when temperatures exceeded 4-6 degrees (Figure 9e-f). However, densities were higher at the high end of the temperature scale and lower at the low end of the scale in 1992 than in 1994, probably because temperatures were higher in the south-eastern Barents Sea in 1992 (Figure 6a-b). Temperatures at 100 m depths hardly explained anything in 1994, but was clearly positively correlated to density in 1992 (Figure 10e-f). My data set did not have adequate coverage in areas of low surface salinity (Figure 11e-f). I could therefore not conclude on any significant trend when relating this variable to stock density. Salinity at 100 m depth had low significance when related to herring density. Deviance explained by this variable was also very low (Figure 12e-f).

Density vs Surface Temperature

a) **Capelin 1992**

Edf: 5.71

p-val: 2e-16

Dev. exp: 78.7%

b) **Capelin 1994**

Edf: 2.85

p-val: 2.46e-8

Dev. exp: 17.2%

c) **Polar Cod 1992**

Edf: 1.38

p-val: 2e-16

Dev. exp: 36.2%

d) **Polar Cod 1994**

Edf: 4.52

p-val: 1.15e-11

Dev. exp: 26.2%

e) **Herring 1992**

Edf: 2.80

p-val: 2e-16

Dev. exp: 46.8%

f) **Herring 1994**

Edf: 3.31

p-val: 2e-16

Dev. exp: 38.7%
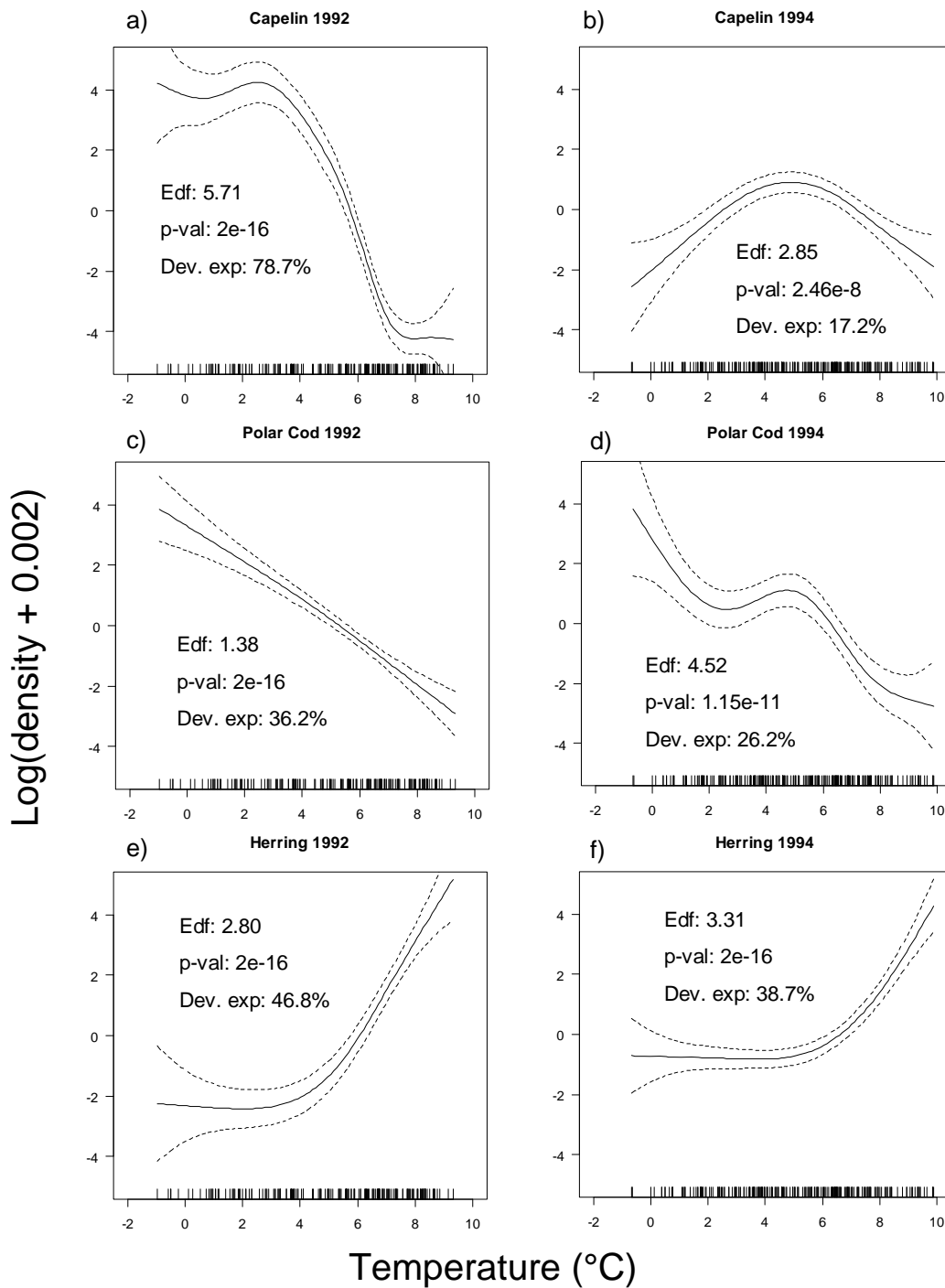
Log(density + 0.002)

Temperature (°C)

Fig. 9: GAMs including fish densities (transformed *SA*-values) for different suface temperatures. Number of splines were selected by mgcv.

Density vs 100 m Depth Temperature

a) **Capelin 1992**

Edf: 3.53

p-val: 2e-16

Dev. exp: 68.7%

b) **Capelin 1994**

Edf: 3.14

p-val: 2.06e-8

Dev. exp: 18.5%

c) **Polar Cod 1992**

Edf: 3.09

p-val: 2e-16

Dev. exp: 41.7%

d) **Polar Cod 1994**

Edf: 6.38

p-val: 2e-16

Dev. exp: 40.1%

e) **Herring 1992**

Edf: 3.28

p-val: 7.51e-13

Dev. exp: 32.9%

f) **Herring 1994**

Edf: 2.03

p-val: 0.00285
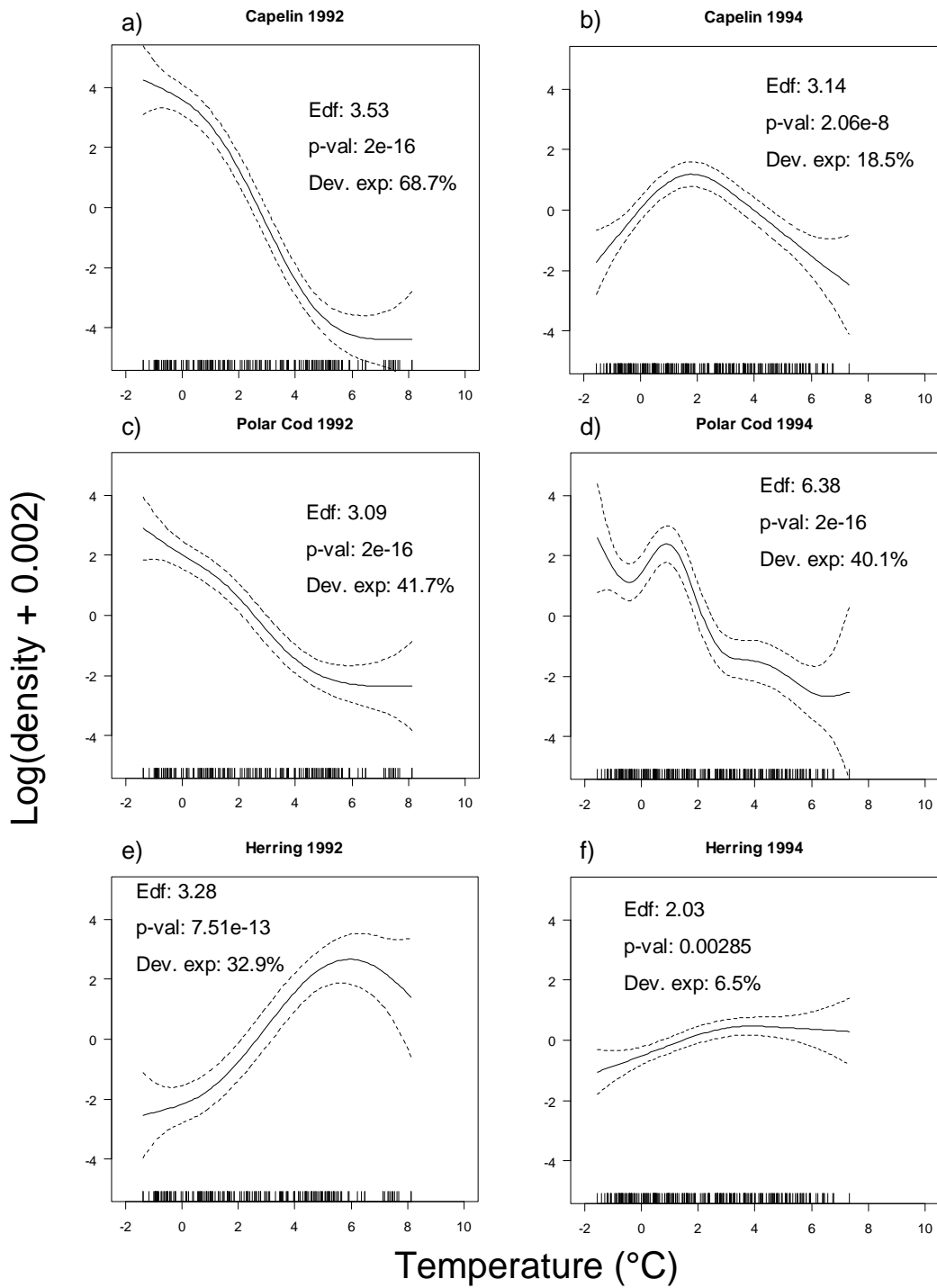
Dev. exp: 6.5%

Log(density + 0.002)

Temperature (°C)

Fig. 10: GAMs including fish densities (transformed *SA*-values) for different 100 m depth temperatures. Number of splines were selected by mgcv.
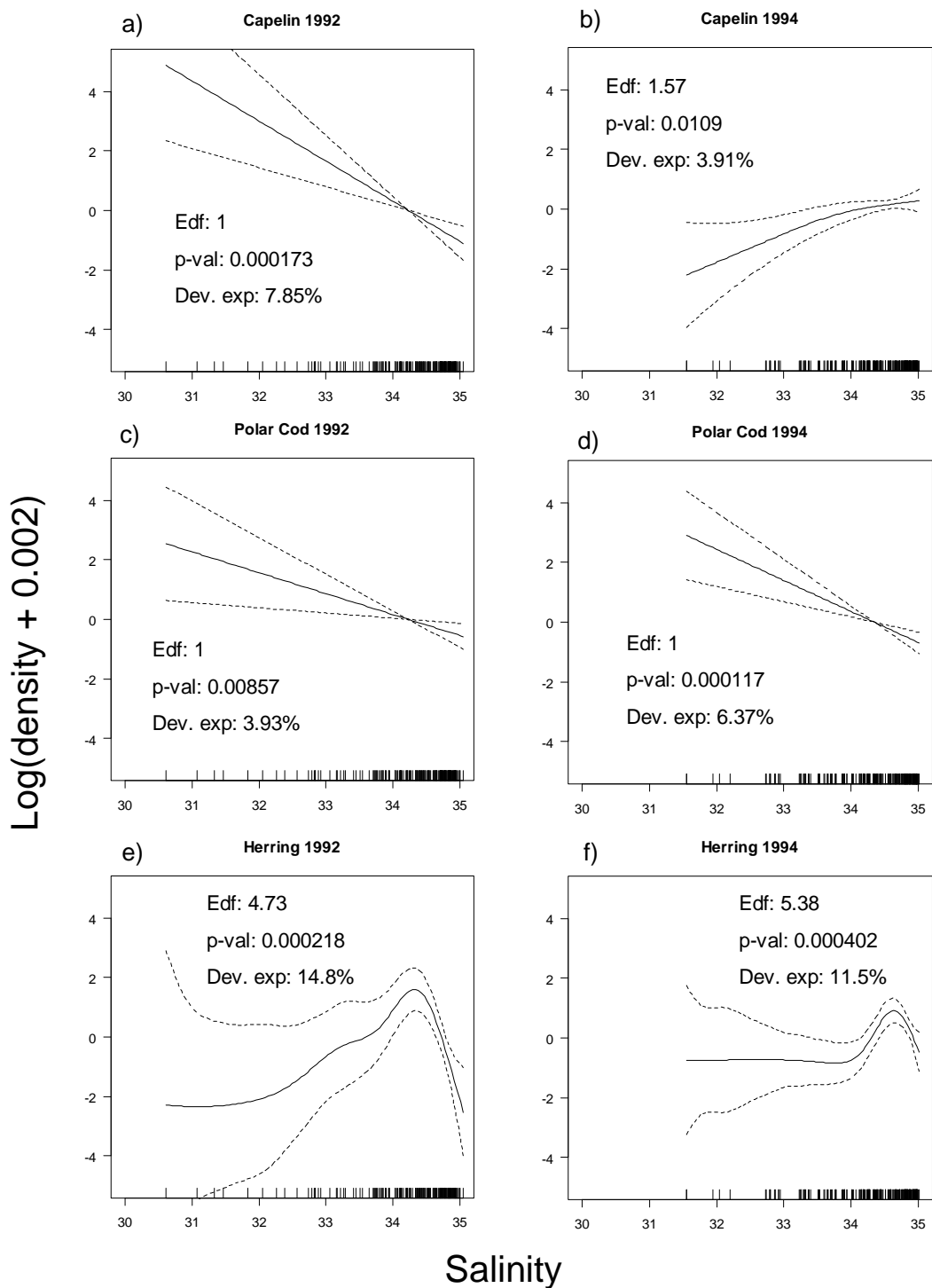
Density vs Surface Salinity

Fig. 11: GAMs including fish densities (transformed *SA*-values) for different surface salinity values. Number of splines were selected by mgcv.

Density vs 100 m Depth Salinity

a) **Capelin 1992**

Edf: 4.09

p-val: 0.00893

Dev. exp: 9.53%

b) **Capelin 1994**

Edf: 4.53

p-val: 1.43e-6

Dev. exp: 16.6%

c) **Polar Cod 1992**

Edf: 4.06

p-val: 1.51e-6

Dev. exp: 21.0%

d) **Polar Cod 1994**

Edf: 4.40

p-val: 5.33e-5

Dev. exp: 12.7%

e) **Herring 1992**

Edf: 3.41

p-val: 0.0154

Dev. exp: 7.53%

f) **Herring 1994**

Edf: 2.18

p-val: 0.00989

Dev. exp: 4.33%
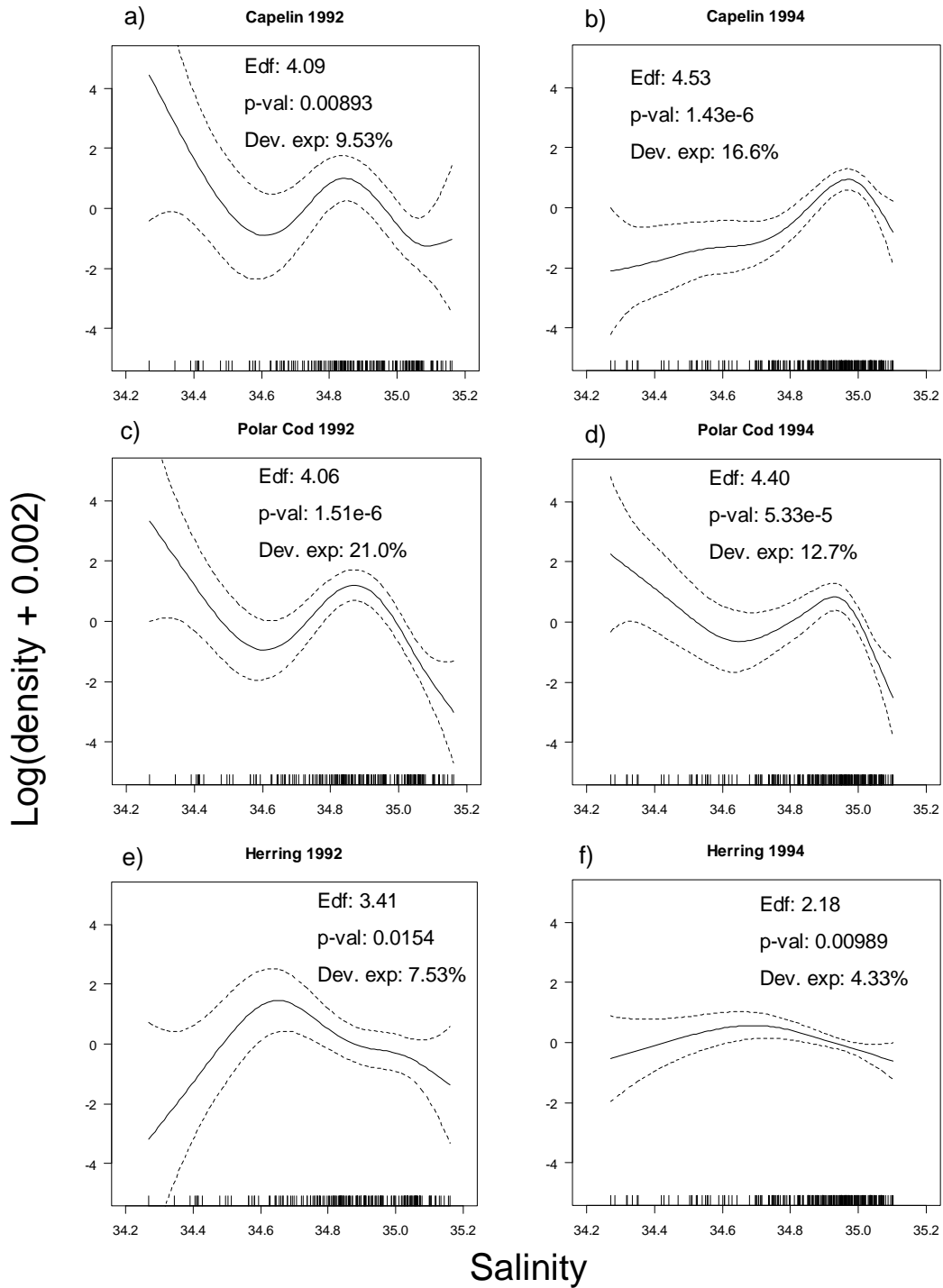
Log(density + 0.002)

Salinity

Fig. 12: GAMs including fish densities (transformed *SA*-values) for different 100 m depth salinity values. Number of splines were selected by mgcv.

4   Discussion

4.1   Main findings

In analogy with Fauchald et al. (2006), the present study demonstrates a strong northward migration pattern in years with high capelin abundance (Figure 5a-b). As the capelin stock increased with a magnitude of nearly a hundred times, a large share of the stock invaded colder water masses. Any further extension southwards could not be detected. According to Gjøsæter et al. (2002), there is a close relationship between capelin growth, capelin abundance and zooplankton biomass. It is therefore reasonable to assume that a shift in density distribution is caused by intraspecific competition and a depletion of resources. The capelin migration northwards in 1992 resulted in a higher degree of spatial overlap with polar cod, and a vast majority of the polar cod was found in waters densely populated by capelin this year (Figure 8). Probably this increasing coexistence factor gave rise to intensified interspecific competition. Polar cod gave no clear sign of migration further northwards as a response to the capelin density dependent migration wave. Concentrations increased in the eastern parts of the Barents Sea (Figure 5c-d), close to Novaya Zemlya, but I found no clear migration perpendicular to any of the oceanographic gradients, as I did for the capelin. The smoothed regression line of the GAM analyses shows a hump at about 5°C and 1°C in 1994 (Figure 9d and 10d), in the surface and 100 m depth temperature analyses, respectively. Any exact reason to why this hump occurred in 1994 and not in 1992 has been difficult to approach, but it could be caused by increased patchiness or a greater extension of ocean areas with these temperatures in 1994. My first hypothesis, which suggested that a northward capelin migration would suppress the polar cod into colder water masses, did not seem to be strengthened. It did neither seem likely that a large capelin stock inhibited the movement of polar cod southwards, as polar cod was detected at lower latitudes in the south-eastern Barents Sea in 1992 compared to 1994. The polar cod's distribution was not diminished in 1992, and my second hypothesis was consequently not supported. My third hypothesis, which suggested increased overlap with capelin, was supported. Any clear signal of influence on polar cod distribution by capelin could not be found in this study. However, this single study has not brought

evidence for the absence of such influence, and my material is probably too confined to assert any strong support of my fourth hypothesis.

With respect to interaction between capelin and herring, almost total avoidance seemed obvious in both years (Figure 5a-b, 5e-f and 8). A large capelin stock had no DDMW southwards, and did by no means suppress juvenile herring further south. The herring stock was significantly larger in 1992 than in 1994, and distributed further to the north in 1992 (Figure 5e). We might assume that herring would have migrated even further to the north if it was not hampered by the large capelin stock. The temperature gradient might as well have functioned as a buffer against further herring migration. Anyhow, support for the first and second hypothesis with respect to herring did not appear likely. Neither was there any support of the hypothesis about increased overlap. There was a large divergence in distribution between the two years, but intuitively it seems reasonable to explain this by another DDMW northwards from the herring. Although it might be true that increased capelin abundance will not affect herring distribution, I could not claim support for my fourth hypothesis in this study.

According to my density distribution results of the species in relation to capelin density, polar cod accepted coexistence with capelin whereas herring did not. The long term effect from capelin on polar cod was not investigated, and it is not known whether polar cod might stand out a long term occupation of its territory by capelin. This would depend on the degree of interspecific competition, which is not fully understood. In the review by Gjøsæter (1998) it was stated that capelin is the only fish stock capable of utilizing the zooplankton production in the central and northern areas including the marginal ice zone. He asserted that polar cod is not a specialised zooplankton feeder and consequently would not be able to compete with the capelin or take its place in the food web. His assumption is contradictory to findings by Lønne & Gulliksen (1989), who investigated diet of polar cod in the western Barents Sea. Its diet mainly consisted of copepods like *Calanus finmarchicus* and *Calanus glacialis*, together with the amphipod *Parathemisto libellula*. Copepods were also found to be important prey items in the marine ecosystem research by Hop et al. (2002). Gjøsæter (1998) also based his assertion of very little competition to the fact that no significant rise in the polar cod stock has been found when the capelin abundance has been low. The avoidance of capelin by herring, or vice versa, might indicate that there would elsewhere be a strong

interaction between the species (cf. Hjermann et al., 2004a). If so, coexistence may not be possible to any extensive degree.

4.2 Density distribution and the abiotic niche axes

My analysis was an attempt to explain the level of utilization of resources, in my case abiotic resources such as water masses with different oceanographic characters. A specified abiotic environment may be looked upon as an adequate resource to fish if it favours growth of individuals, reproduction and maintenance of the stock. The abiotic environment may influence directly on the fish by setting limits to e.g. growth or exceeding its limits of physical tolerance (Gjøsæter & Loeng, 1987), or it may influence by affecting the distribution of nutrition-rich water masses and thereby food items for the fish. Parameters in marine zooplankton populations, which constitute the main food source of the species treated here, are influenced by advection of water masses (Melle & Skjoldal, 1998). Dalpadado et al. (2003) linked variability in the zooplankton biomass to physical factors like temperature and water mass distribution. They found that more zooplankton, like *Calanus finmarchicus*, is advected into the northern parts of the Barents Sea during warm years, but also that different temperatures will have an impact on the distribution and growth of different zooplankton species. Distribution of the most important amphipod species in the polar pelagic fauna, *Themisto libellula*, is greatly determined by the amount of Arctic water present in the Barents Sea, and it seems intolerant to warmer water masses (Dalpadado, 2002). Direct measurements of zooplankton were not performed in the present study. However, because oceanographic conditions are so important for the distribution and abundance of this resource, I argue that there must be a clear connection between fish species' growth conditions and migration patterns, and oceanography. The influence from abiotic conditions to food distribution, justifies the conversion of oceanographic variables into resources that might be utilized partly or completely along niche axes.

Some of my niche parameters did not explain much of the deviance from year to year. One could look at realized niches in terms of a frequency histogram of resource use, as described in the modern niche theory. The proportion of utilization of one abiotic resource, the realised niche, will be significantly limited compared to the fundamental

niche (Schoener, 1989). This was very evident when comparing capelin density to sea surface temperature SST (Figure 9a-b). Utilization of the water masses was larger at the high end of the temperature scale in 1994, although the stock had collapsed this year. The DDMW northwards in 1992, probably caused by food depletion (Fauchald et al., 2006) and maybe avoidance of coexistence with herring, hampered capelin's presence in warmer water masses, which it elsewhere is physiologically adapted to. Polar cod showed no clear shift in presence from one year to the next, except of the conspicuous hump at around 4-5 degrees in 1994 (Figure 9c-d). Its utilization of water masses with different SST did not seem to be influenced by the density of capelin in the same area. However, the distribution of polar cod with absence of capelin is a hidden scenario, and I may not conclude that polar cod distribution is unaffected by capelin. Likewise to the south of the capelin area, we do not know how far north the large herring stock of 1992 would migrate if it was not confronted with the capelin. Surprisingly, herring had lower density in waters with SST below approximately 5 degrees in 1992 than in 1994, despite their northward migration in 1992 (Figure 5e-f and 9e-f). It is most probably due to diverging temperature distributions between the two years (Figure 6a-b).

The analysis at 100 meters depth mainly confirmed the patterns of niche utilization that I detected with respect to SST. One could use these findings to defend the assumption that the species do in fact experience close to the same pattern, because they are normally present in the zone between 0 and 100 meters. The salinity variables only explained a fraction of the density distribution, and because of their covariance with temperature, they did probably not contribute much as independent niche axes. Any further interpretation of the role of salinity would therefore be redundant.

The only very obvious shift in utilization of an abiotic resource was found for capelin. In an ideal situation, when there are no limiting factors such as competition, predation pressure or food availability, no trade-off will be necessary when selecting an appropriate abiotic habitat. The fundamental niche axis might then be fully exploited, i.e. the resource utilization frequency might be 100 percent. On the other hand, when a large stock is threatened from inhibiting biological factors, it might not fully occupy its optimal abiotic habitat, and only a share of the fundamental niche axis will be utilized (Putman & Wratten, 1984). The two situations described had some parallels to the situations in 1994 and 1992, respectively. In 1994, when food availability was adequate

and there was no competition or predation pressure from herring, it probably maintained its position in the central Barents Sea, where temperatures might optimize growth conditions. A large 1992 capelin stock was probably forced to only utilize the cold share of the water masses to which it was adapted. Food depletion prohibited most likely any complete use of its fundamental niche.

4.3   Confounders and limitations to this study

This study was limited to include only two different years with no replicates for large and small capelin stocks. From a scientific point of view this is seldom enough to conclude on any effect, because we might not consider whether the outcome is random. Ideally, several years with low and high capelin stock together with close to identical oceanographic conditions, should have been investigated. The simpler way was chosen not to make this study too comprehensive. However, very clear patterns detected in a large scale study are unlikely to be set off randomly. Marine ecosystems are complex, and it would be impossible to control for any factor that might have an effect in an observational study. Despite the lack of replications, the data sets showed very clear shifts with respect to capelin, and the northward DDMW was probably not a random outcome posterior to food depletion.

The herring stock is a potential confounder in this study. Parallel to a strong capelin stock, herring was very abundant in 1992, and the degree of influence to capelin migration from herring is not easy to determine. Important confounders that are not handled at all in this study include other major predators on capelin. In a study by Dolgov (2002) and a review by Ushakov and Prozorkevich (2002), capelin was described to possess a key role as prey in the Barents Sea ecosystem. Its main predator is cod, while it is also considered to be a significant part of the diet for sea birds, marine mammals and a number of fish species (e.g. haddock, greenland halibut, long rough dab and thorny skate). None of these predators were controlled for, although their consumption rates vary significantly between years (Dolgov, 2002). Predation pressure from these species is likely to have an effect on capelin migration, and this effect probably fluctuates.

4.4 Connecting my findings to standing theories

The capelin's migration into colder water masses probably increased the chance of ecological interactions with polar cod, and this situation brings us right to the core of the competitive exclusion principle. As mentioned previously, this principle states that no competing species might coexist in the long run. Whether capelin and polar cod are competing species, may be an object of discussion. Anyhow, I find it reasonable to argue in favour of competition occurrence along some niche axes, because they both feed on calanoid zooplankton and occupy pelagic water masses. This assumption is also in analogy with Ushakov & Prozorkevich (2002), who referred to the particularly inherent competition found in the eastern and north-eastern Barents Sea. Based on the fact that competition only may occur during the annual period of intense feeding posterior to the zooplankton bloom, I was not able to conclude on whether the coexistence might be sustainable or not. A direct interpretation of Gause's principle would result in the conclusion that capelin and polar cod are not able to coexist, because they have somewhat similar ecological requirements. However, modern niche theory attempts to explain why species seem to handle sustainable coexistence in the real environment. According to modern theories, some niche overlap may occur as long as each species only has a partial utilization of the resource (Schoener, 1989). In this way two species may coexist although they do compete for some of the resources.

The niche width (described in Putman & Wratten (1984)), was only investigated with respect to abiotic environment and not to food resources directly for each year. Each single species of calanoids, euphausiids and amphipods, the most common food components to capelin (Orlova et al., 2002), must have been shared at a given ratio between the two fish species when coexistence increased. Partitioning of resources will probably increase the strength of intraspecific competition relative to that of interspecific competition (Amarasekare, 2003). This was probably valid for polar cod, for which the stock size was not significantly altered between years. However, capelin intraspecific competition must have magnified several times as well in 1992. A reasonable assumption to their mutual tolerance might be that they only partially utilized their shared resources. In such case, their realized niches were limited by competition, and they might in addition have had some niche overlap. The suggestion of limited utilization of a species' fundamental niche is supported by Hutchinson's theory,

whereas the allowance of some niche overlap is in accordance with modern niche theory.

Any outcome of the long term coexistence was not monitored, and it would not be consistent to conclude that coexistence is sustainable in the long run. There might as well have been responses to the interaction which could not be detected in this study. One could also suggest that a premise for coexistence are the strong fluctuations in capelin stock and the short feeding season. Under these conditions, coexistence between capelin and polar cod will always be a time-limited event, and is possibly by no means sustainable. I suggested that capelin would withdraw from colder water when the stock again decreased. Although not very obvious, there has been found a direct relation between water temperature and length growth of capelin (e.g. Gjøsæter & Loeng, 1987), and it is reasonable to assume that capelin will turn to areas of optimal growth conditions when food availability has recovered in this area.

4.5   Conclusions

This large scale study revealed a migration wave into colder water masses by capelin in a year with high capelin abundance. Supported by findings in earlier studies, I suggest that this migration wave was triggered by food depletion in the central Barents Sea. Capelin density did not increase in warmer water masses, i.e. there was no migration southwards. An explanation to this might be the large distribution by juvenile herring in 1992, which is a strong competitor to capelin. Avoidance between capelin and herring was almost total both in 1992 and 1994. Polar cod showed no kind of avoidance from capelin when capelin migrated northwards, and I expect that competition for their food resources must have taken place during their dense coexistence. The coexistence might be explained by overlapping niches or limited utilization of resources by each species. However, divergences in feeding behaviour by the different species between years were not investigated in this study. Degree of competition and overlap with respect to feeding might therefore only be based on previous knowledge. Future research ought to include feeding behaviour, as well as a longer time span of monitoring. This would help us to understand whether coexistence might turn into a stable annual event or if it is dependent on large and continuous oscillations in the size of fish stocks.

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