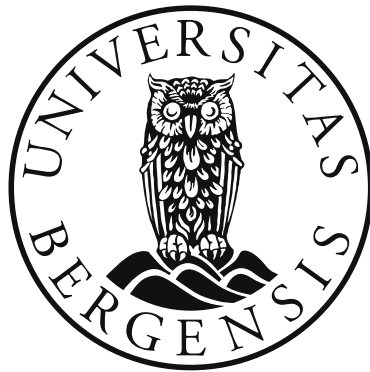# Dynamics of the Barents Sea pelagic compartment: species distributions, interactions and response to climate variability

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*In memory of my beloved father and*

*mother who passed away far too early.*

# Acknowledgements

# Summary

Long, consistent and uninterrupted monitoring resulting in time series of biological and environmental data are needed to understand the relations between environment and species, and species interactions, which also affect fish stock production and thereby fisheries (Dragesund et al. 2008). Traditional fishery science in the Barents Sea has mainly focused on the commercially important species (e.g. cod, haddock, capelin and herring). However, the conducted surveys provide a substantial amount of data on additional species, and thereby the opportunity to study a wider range of species, species interactions, community structure and ecosystem processes required for an ecosystem-based management (Michalsen et al. 2013, ICES 2016). This aspect has been the focus of this thesis, which aim is to 1) evaluate monitoring data for use in ecosystem studies, 2) understand past and current changes in the pelagic compartment of the Barents Sea ecosystem, and 3) determine the effects of the recent warming on the pelagic compartment and its components.

Since 1965 the international 0-group fish surveys and since 2004 joint Barents Sea ecosystem surveys have provided an early estimate of year class strength and huge amounts of additional data. The thesis is based on pelagic catch data and information from these autumn surveys reported in a series of nine papers. The monitoring data were quality checked and only pelagic trawl station of satisfactory quality were used to establish time series of 0-group fish abundance (9 species) and biomass (4 species), biomass and abundance of juveniles and adults lumpfish, biomass of krill and jellyfish and spatially resolved biomass time series of pelagic compartment. Through this work, the databases have been updated and now data are available for the scientific community. An evaluation of sampling equipment and the observation methods indicated limitations of past and current monitoring that may have lead to increased variance and biases. Further development of survey equipment and observation methods are suggested, including modifications of current or development of a new pelagic trawl, use of acoustic recordings of krill and the further development of "DeepVision" and software for automated image analyses. Nevertheless, despite samplings limitations these time series gives new insight into the spatial and temporal dynamics in the pelagic compartment and improves opportunities to study key interactions in the pelagic food web.

The period from 1980 to 2015 can be broadly divided into four segments based on differences in oceanographic and biological (krill, jellyfish, 0-group fish and lumpfish abundance time series) variables with break points in 1986, 1994 and 2004. The period 1980-2015, which is the period considered here, is characterized by warming from a cold and relatively low-productive system to a warm (but variable temperature condition) and slightly more productive, to a record warm (with largest areas of warm waters) and high-productive pelagic system.

The pelagic organisms, such as zooplankton, fish egg and larvae drift with ocean currents into the Barents Sea directly and immediately respond to change in water flux, temperature and distribution of water masses. Krill, jellyfish and 0-group fish (such as cod, haddock, herring and capelin) showed interannual variations in abundance and distribution, but demonstrated a general trend over the sampling period as it increased from a cold 1980s to the record warm 2000s. These organisms were found mostly in the warm Atlantic and mixed water masses. In addition to larger occupation area, 0-group capelin showed also northwards distribution shift, which was correlated with increased temperature and areas of Atlantic and mixed waters. The northward shift may have reduced the overlap with young herring, which in turn can have had a positive effect on capelin recruitment, as herring predation on capelin larvae may significantly reduce capelin recruitment success. 0-group polar cod abundance and distribution decreased during the period. Poor recruitment in recent decades and poorer body condition during and after the spawning may have already resulted in reduced abundance in response to the warm climate. Variable recruitment of fish stocks is a major source of variability in stock development and for the dynamics of the Barents Sea ecosystem. The biomass of 0-group fish contributes directly to the pelagic biomass and the plankton-feeding component and subsequently as juveniles and adults over the following years. Among small non-commercially fish Ammodytidae, Cottidae and Myctophidae were abundant in early 1990s, while Stichaeidae, Ammodytidae and Agonidae in recent decade. However, these small fish made up a small fraction (0.02 %) of the total biomass of the pelagic community.

To investigate the large scale spatial organization and biomass fluctuations of the pelagic compartment, monitoring data for the shorter period 1993-2013, including pelagic catches (krill, jellyfish, 0-group fish and small fish) and acoustic measurements (pelagic fish stocks) were aggregated into small grid cells and larger geographic areas. The estimated total biomass of the investigated pelagic compartment, not including mesozooplankton, ranged between about 6 and 30 million tonnes wet weight with an average of 17 million tonnes over the period 1993-2013. Krill was the dominant biomass component (63%), while pelagic fish (capelin, polar cod and herring) made up 26% and 0-group fish 11% of the biomass on average. During 1993-2013, the total biomass of the pelagic compartment remained relatively stable within each of two main periods (before and after 2004), but increased by a factor of two from around 11 million tonnes in the first to around 23 million tonnes in the last period (i.e., after 2004). The pronounced increase likely reflected the warming and was driven mainly by an increase in krill, presumably due to increased advection. Variable recruitment of fish had a strong influence on the variation in pelagic biomass, first as 0-group fish (including demersal species such as cod and haddock) and subsequently over the following years manifested as strong or weak year classes of the dominant pelagic species. The biomass distribution showed a broad-scale pattern reflecting differences in distribution of the main pelagic fishes (capelin in the north, polar cod in the east, and herring in the south) and transport of krill and 0-group fish with the Atlantic water flowing into the southern Barents

Sea. The highest average biomass values were found in the Southwestern and South-Central subareas (about 4 million tonnes in each), with krill as the main component. Biomass was also high in the North-Central subarea (about 3 million tonnes) where capelin was the major contributor.

In conclusion, it is evident that the pelagic compartment has undergone large changes in the two last decades in going from a colder to a warmer temperature regime and from a low to a high productive pelagic compartment. The results presented support the general expectations under a climate change; increased production in the northern marine systems, and contraction and decline of arctic species while boreal species expand their distributions.

# 1   Contents

## Objectives and structure of the thesis

Long, consistent and uninterrupted monitoring and time series of biological and environmental data are needed to understand the relations between environment, fish species and stock interactions, which affect fish stock production and thereby future fisheries (Dragesund *et al.* 2008). Traditional fishery science has mainly focused on the commercially important species (e.g. cod, haddock, capelin and herring). However, the conducted surveys provide a substantial amount of data on additional species, and thereby the opportunity to study a wider range of species, interactions and ecosystem processes required for an ecosystem-based management (Michalsen *et al.* 2013, ICES 2016). This aspect has been the focus of this thesis, which aimed to 1) evaluate monitoring data for use in ecosystem studies, 2) understand past and current changes in the pelagic compartment, and 3) determine the effects of the recent warming on the pelagic compartment and its components.

The thesis is based on pelagic catch data and information from the joint IMR-PINRO autumn surveys reported in a series of nine papers, with the main conclusions presented in chapters 3-4 in this synopsis. The various papers contribute to the major aims as follows:

- To evaluate monitoring data for use in ecosystem studies the monitoring data were quality checked; only ordinary pelagic trawl station of satisfactory quality were used to estimate time series, while temporal and spatial data (of satisfactory quality) were used to describe the status and changes of the ecosystem components (Papers I, II, III, IV, VII and VIII).

- To understand past and current changes in the pelagic compartment large-scale spatial and temporal variability in biomass of pelagic species were examined and relationships to climate variability, fish densities and individual sizes were explored (Papers IV, V, VI, VII and VIII).

- To determine the effects of the recent warming on the pelagic compartment integrated and multivariate analyses including pelagic stocks, pressures and drivers were performed, the changes in the ecosystem were documented, and how this relates to climate warming documented were examined (VIII).

The changes in the pelagic compartment reported in a series of nine papers (see below). Four papers deal with 0-group fish and consider aspects of sampling and abundance estimation methods, distribution, thermal habitat, and ecological significance (Papers I, IV, V and VI). Three papers deal with macro plankton, where two of them deal with sampling and ecological importance of krill (Papers II and IX), and one deal with jellyfish and their spatial overlap with 0-group fish (Paper III). One paper deals with lumpfish and their response to climate warming (Paper VII).

| 0-group fish | Macro plankton | Pelagic spesies |
|---|---|---|
| **Paper I:** time series (1980-2006) of abundance of nine fish species, SSB and temperature | **Paper II:** krill biomass time series (1980-2009), distribution, climate, capelin predation | **Paper VII:** lumpfish biomass time series (1980-2012, juveniles and adults, density, fish length, temperature |
| **Paper IV:** biomass time series (1993-2009), year classes strength, sub areas, SSB, climate | **Paper III:** jellyfish biomass time series (1980-2010), distribution, climate, 0-group fish, overlap | |
| **Paper V:** cod haddock, herring and capelin, distribution, thermal habitat, climate | **Paper IX:** krill sampling, methods, biomass, three time series | |
| **Paper VI:** polar cod, redfish, distribution, thermal habitat, climate | | |

**Pelagic compartment**
**Paper VIII:** spatially resolved biomass time series (1993-2013), 0-group fish, macro plankton, pelagic fish species, small non-commercial fish, distribution, warming

This thesis starts with a short introduction of the Barents Sea ecosystem and monitoring. Further, I discuss methods and methodological considerations related to sampling, data flow and estimation of species abundance and biomass, and the degree of influence of methodological aspects. I also suggest a way forward to limit the shortcomings and how to reach absolute abundance estimates. Furthermore, Furthermore, I present new sets of time series and document changes in the pelagic compartment. To understand these changes I study species thermal habitat and how climate variability impacts species density, length and geographic distribution. Finally, I estimate the biomass contributions of the major species or groups in the pelagic compartment and investigate how recent warming and other drivers influence biomass variation of major pelagic components at different spatial and temporal scales.

# List of publications

This thesis is based on the following papers and manuscripts. The papers are referred to in the text by their Roman numerals.

**Paper I.** Eriksen, E., Prozorkevich, D., Dingsør, G., 2009. An evaluation of 0-group abundance indices of Barents Sea fish stocks, *The Open Fish Science Journal*, 2: 6-14

**Paper II.** Eriksen, E. and Dalpadado, P. 2011. Long-term changes in krill biomass and distribution in the Barents Sea: are the changes mainly related to capelin stock size and temperature conditions? Polar Biology 34(9):1399-1409, doi 10.1007/s00300-011-0995-0

**Paper III.** Eriksen, E., Prozorkevich, D., Trofimov, A., and Howell, D. 2012. Biomass of scyphozoan jellyfish, and its spatial association with 0-group fish in the Barents Sea. PLoS ONE 7(3): e33050. doi:10.1371/journal.pone.0033050

**Paper IV.** Eriksen, E., Bogstad, B., Nakken, O. 2011. Ecological significance of 0-group fish in the Barents Sea ecosystem. Polar Biology 34:647–657, doi 10.1007/s00300-010-0920-y

**Paper V.** Eriksen, E., Ingvaldsen, R., Stiansen, J.E., and Johansen, G.O. 2012. Thermal habitat for 0-group fishes in the Barents Sea; how climate variability impacts their density, length and geographical distribution. ICES Journal of Marine Science, 69(5): 870–879, doi:10.1093/icesjms/fsr210

**Paper VI.** Eriksen, E., Ingvaldsen, R. B., Prozorkevich, D. and Nedreaas, K. 2015. The effect of recent warming on polar cod and beaked redfish juveniles in the Barents Sea. Regional Studies in Marine Science 2: 105–112.

**Paper VII.** Eriksen, E., Durif, C.M.F., and Prozorkevich, D. 2014. Lumpfish (*Cyclopterus lumpus*) in the Barents Sea: development of biomass and abundance indices, and spatial distribution. ICES Journal of Marine Science; doi:10.1093/icesjms/fsu059

**Paper VIII.** Eriksen, E., Skjoldal, H.R., Gjøsæter, H., and Primicerio, R. Spatial and temporal changes in the Barents Sea pelagic compartment during the recent warming. Submitted to "Progress in Oceanography"

**Paper IX.** Eriksen, E., Skjoldal, H.R Dolgov, A.V., Dalpadado, P., Orlova, E.L., and Prozorkevich D.V. 2016. The Barents Sea euphausiids: methodological aspects of monitoring and estimation of abundance and biomass. ICES Journal of Marine Science. doi: 10.1093/icesjms/fsw022

# 1 Introduction

## 1.1 The Barents Sea ecosystem

The Barents Sea is a large high latitude shelf sea located between 70 and 80°N in the northeastern Atlantic (Figure 1). This ecosystem consists of a large and relatively deep shelf area (approximately 1.6 million km² in area and mean depth of 230 m; Ozhigin *et al.* 2011). Two archipelagos, Svalbard and Franz Josef Land, are located in the northern Barents Sea. The bottom topography is complex with several large and small banks, basins and deeper trenches that steer the currents and govern the distribution of water masses (Loeng 1991). Two deeper connections exist to adjacent Seas with Bear Island Trough in the western part to the Norwegian Sea and the St. Anna Trough in the northeast towards the Arctic Ocean via the northern Kara Sea. In the south, the Barents Sea borders to mainland Norway and Russian and in the east to Novaya Zemlya.
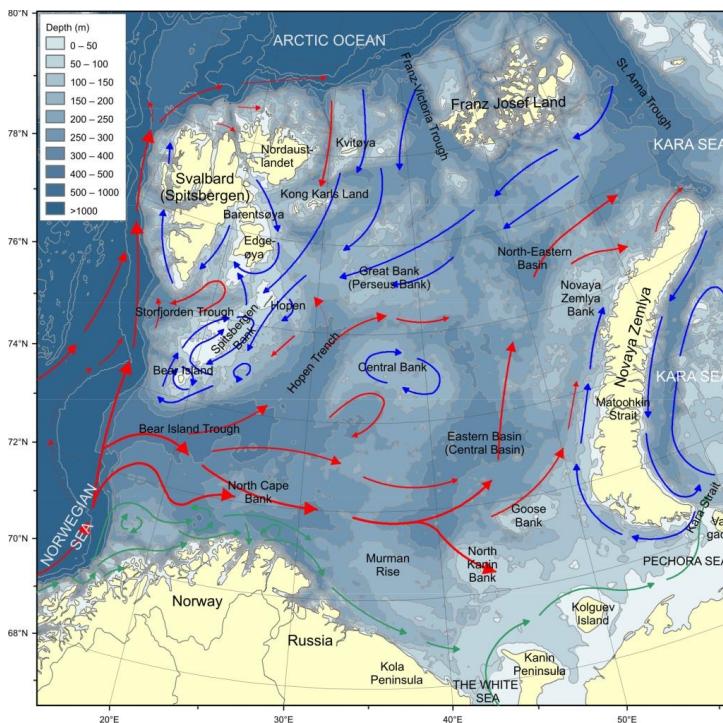


Figure 1. The Barents Sea. Red arrows show Atlantic water currents, blue arrows Arctic currents and green arrows currents of coastal waters.

The Norwegian Atlantic Current (partly as a continuation of the Gulf Stream) flows north through the eastern Norwegian Sea and splits into two main branches, one flowing into and through the Barents Sea from southwest to northeast, the other flowing around the western and northern flanks of the Barents

Sea as the West Spitsbergen Current (Figure 1; Skagseth *et al.* 2008, Ingvaldsen and Loeng 2009, Ozhigin *et al.* 2011, Boitsov 2012). The warm Atlantic water leads to relatively mild conditions in the western and southern parts while more Arctic conditions prevail in the northern and eastern parts of the Barents Sea, which is therefore a biogeographical transition zone between boreal and Arctic provinces (Ozhigin *et al.* 2011). Sea ice covers most of the northern parts of the Barents Sea each winter. The freezing and melting of ice have profound effects on the hydrographic conditions, leading to a separation of deeper cold layers due to ice formation in winter (through brine excretion and convection), and a lighter upper layer caused by ice melt in summer. The melting of sea ice and the associated stratification allows for marginal ice zone phytoplankton blooms which progresses from south to north as the sea ice retreats during spring and summer (Skjoldal and Rey 1989).

The Barents Sea climate varies on time scales of years to several decades (e.g. Ingvaldsen and Loeng, 2009). Over the last decades, there has been a general temperature increase in the Barents Sea. This is partly due to a strong inflow of Atlantic water associated with strong heat flux from the sea to the atmosphere, contributing to lower air pressure over the Barents Sea, which is part of a positive feedback as southwesterly winds maintain a strong inflow (Sandø *et al.* 2010, Smedsrud *et al.* 2010, ICES 2016). Strong inflow is furthermore associated with a wide distribution of Atlantic water and a push-back of sea ice causing a lower extent of sea-ice cover in winter. During the last decade, warmer water of Atlantic origin has spread northwards; thereby increasing the warm Atlantic part of the Barents Sea and decreasing the cold Arctic part (Johannesen *et al.* 2012, ICES 2016).

The strength of the inflow of Atlantic water varies also within years. The inflow in spring and summer influences the annual production in the Barents Sea by advection of plankton (among other the key prey species *Calanus finmarchicus* and *Thysanoessa inermis*), fish eggs and larvae (among others the key Barents Sea species cod *Gadus morhua*, herring *Clupea harengus* (Yashnov 1955, Marti 1956, Ponomarenko 1973, Skjoldal and Rey 1989, Orlova *et al.* 2011, 2014). Summer and early autumn are the main feeding period for many fish and other consumers, and macroplankton, pelagic and demersal fish, sea mammals and sea birds forages on plankton and fish (juveniles and adults) which aggregate in the pelagic layer (Marti 1956, Ponomarenko 1973, Hamre 1994, Dalpadado and Bogstad 2004, Hop and Gjøsæter 2013, Orlova *et al.* 2013).

The phytoplankton primary production provides the basic organic carbon source, which all other Barents Sea food web components depend on. The level of primary production is higher in the southern Barents Sea, occupied by Atlantic water, than in the northern part covered with seasonal ice (Reigstad *et al.* 2011, Hunt *et al.* 2013, Dalpadado *et al.* 2014). Zooplankton forms the main links between the phytoplankton primary producers and higher trophic levels of the food chains (Dalpadado *et al.* 2002, 2014). There are several hundred zooplankton species in the Barents Sea including copepods, pteropods, chaetognaths, and a variety of gelatinous forms such as ctenophores, small hydromedusae and larger

jellyfishes. Copepods are the most important group in terms of biomass and abundance and constitute major prey for many fish, especially smaller pelagic species but also younger stages (larvae and juveniles) of larger species (Drobysheva 1994, Orlova 2002, 2005, Dalpadado *et al.* 2002, 2009). Krill and amphipods are important components among the larger forms of macrozooplankton. The most important krill species are *Thysanoessa inermis*, which are abundant in the western and central and parts, *Thysanoessa raschii*, found in the south-eastern part, and the *Meganyctiphanes norvegica*, which is advected into the western Barents Sea (Drobysheva 1994, Dalpadado and Skjoldal 1991, 1996, Orlova 2014). Krill play a vital role in the Barents Sea food web (Drobysheva 1994, Drobysheva and Yaragina 1990, Dalpadado and Skjoldal 1996, Orlova *et al.* 2001, Dolgov *et al.* 2011). Two species of scyphozoan jellyfish commonly occur in the Barents Sea: the lion's mane jellyfish *Cyanea capillata* and the moon jelly *Aurelia aurita* (Naumov 1960; Zelickman 1970, 1972). Jellyfish are important consumers, both as grazers of phytoplankton and as predators of zooplankton, fish eggs, larvae, and juveniles (Purcell *et al.* 1985, Purcell *et al.* 2000, Arai 2009). From the perspective of top-down control, the collective predation rates of jellyfish can be high and directly or indirectly control the population size of other zooplanktonic organisms, including larval fish (reviewed by Purcell 1985, 1991, 1992, Nielsen *et al.* 1997). However, jellyfish in the Barents Sea have been less studied and their amount, role and impact are poorly understood.

The Barents Sea serves as a nursery area for the offspring of several fish stocks, which spawn during winter-spring along the coast. By late summer the larvae have grown into 0-group juveniles and are widely distributed in the southern and central parts of the Barents Sea where they live as plankton feeders before the demersal species such as cod and haddock settle to live closer to the seafloor in late autumn (Marti 1956, Bergstad *et al.* 1987, Eriksen and Prozorkeich, 2011). Most 0-group fish occupy the upper pelagic layer (0-50 m) in summer-autumn, being prey for larger fish (0-3 years old cod and haddock, herring, and capelin), and several species of seabirds and marine mammals (Marti 1956, Yudanov 1962, Sonina 1967, Bergstad *et al.* 1987, Gjøsæter 1998, Dolgov *et al.* 2001 a,b).

The stocks of small pelagic fish include capelin (*Mallotus villosus*), young herring (*Clupea harengus*), blue whiting (*Micromesistius poutassou*) and polar cod (*Boreogadus saida*), which constitute the bulk of pelagic fish biomass in the Barents Sea (ICES 2016). These pelagic stocks overlap spatially to some extent, although blue whiting are distributed mainly in the western and central Barents Sea, young herring in the western, central and southern areas, capelin in the central and northern areas, and polar cod in the eastern and northern areas (Marty and Fedorov 1963, Zilanov 1968, Heino and Godø, 2002, Gjøsæter 1998, Dolgov *et al.* 2003, Hop and Gjøsæter, 2013). These stocks also prefer different depth layers; polar cod and blue whiting are mainly found in the lower part of the water column near bottom, herring often occupy the upper pelagic layer, while capelin is found at all depths. These species are

mainly plankton-feeders and follow the plankton production, constituting important links between lower and higher trophic levels in the Barents Sea ecosystem (Skjoldal and Rey 1989, Dolgov *et al.* 2011).

In addition to these species, small demersal fishes can be present more or less regularly also in the pelagic part of the system (Eriksen *et al.* 2012c, Johannesen *et al.* 2012, Wienerroither *et al.* 2013). This includes poachers (family Agonidae), sculpins (Cottidae), pricklebacks (Stichaeidae), and snailfishes (Liparidae). All these groups of small demersal fishes feed on a variety of benthic prey such as crustaceans and polychaete worms but they also feed to various degrees in the pelagic realm (Rass 1949, Andriashev 1986, Ponomarenko 1995, Mukhina 2005, Byrkjedal and Høines 2007, Kristoffersen and Salvanes 2009). However, these species have been poorly studied and their abundance and role in the ecosystem is largely unknown (Eriksen *et al.* 2012c).

## 1.2   Monitoring of the Barents Sea

The Barents Sea has been monitored and investigated for more than 50 years in a collaborative effort between Norway and Russia. This has provided an extensive knowledge base for this sea area (Sakshaug *et al.* 2009, Jakobsen and Ozhigin 2011). Monitoring of the ecosystem is vital for an operative and up-to-date fishery science to support the principles and criteria of precautionary, ecosystem-based and bio-economic management approaches laid down by the Joint Norwegian-Russian Fishery Commission (Alekseev *et al.* 2011). The successful fisheries management of the Barents Sea is based on comprehensive monitoring dating back to 1954 (Røttingen *et al.* 2007).

### 1.2.1   Surveys

The international 0-group fish survey (0-group survey) was established in order to obtain an early estimate of the year class strength of the commercially important fish species, and has provided important data for the fishery forecasting since 1965 (Alekseev *et al.* 2011, Eriksen and Prozorkevich 2011). The applied methods and approaches for monitoring, estimation of year class strength/abundance, data exchange and combination of national data bases have been continuously improved over the last decades. For example, standard equipment ("Harstad" trawl) and trawling procedures recommended by ICES (Anon. 1980, more information see below) have since 1980 been used on both Norwegian and Russian vessels during the 0-group survey. In addition to abundance and year class strength, the survey provides time series of oceanographic and biological conditions important to understand ecosystem changes in the Barents Sea. All captured organisms have been sorted, recorded, and today, most taxa are identified to the species level, although with some exceptions (e.g., euphausiids, amphipods, jellyfish, and some small fish) due to difficult species identification and time constraints on board.

The joint Norwegian-Russian acoustic capelin survey has been carried out annually in September-October since 1972. Acoustic data (echo intensities) are integrated continuously along the survey lines,

and mean values of acoustic back-scattering per nautical mile (nm) are recorded for mapping and calculations of fish abundance and biomass. Trawl hauls ("Harstad" trawl) are carried out if the acoustic signatures change their characteristics and/or biological data are needed to identify acoustic recordings and/or to obtain additional biological information (e.g., individual length, weight, maturity stage, stomach data, and age; Aglen and Gavrilov 2011). This survey provides abundance estimates of capelin used for the capelin stock assessment by ICES (Gjøsæter *et al.* 2002, ICES 2014). In addition to capelin, the survey provides abundance indices of other pelagic ecosystem components such as young herring (since 1985), polar cod (since 1986), and zooplankton (since 1986).

Since 2004, both the 0-group survey and the acoustic capelin survey was included in the Joint Norwegian-Russian ecosystem survey, designed and jointly carried out by the Institute of Marine Research (IMR, Norway) and the Polar Research Institute of Marine Fisheries and Oceanography (PINRO, Russian Federation). The joint Barents Sea Ecosystem Survey (BESS), which is a new concept in the monitoring of the sea, provide simultaneous observations of physical and chemical oceanography, plankton, benthos, fish, seabirds, and sea mammals in August-September (Michalsen *et al.* 2011, 2013, Eriksen and Gjøsæter 2014). The timing of the ecosystem survey in autumn allows access to most of or the whole Barents Sea as sea-ice is at its seasonal minimum. This is also the period when migratory species such as capelin have reached their maximum northern distribution at the end of their seasonal feeding migration. At this time the 0-group fish of commercially and ecologically important species are large enough to be caught by pelagic trawl, while settlement to the bottom of 0-group of demersal species has not yet begun (Eriksen and Gjøsæter 2014).

Ecosystem monitoring, the near-synoptic sampling of a range of ecosystem components, allows for ecological studies that increase the understanding of the processes of the Barents Sea ecosystem.

### 1.2.2 Trawling procedure

The "Harstad" trawl is designed to capture small fish and standard equipment for 0-group fish survey, capelin survey and later ecosystem survey (Anon. 1980, Eriksen and Gjøsæter 2013). The standard trawling procedure consists of tows on predetermined positions at 25-35 nautical miles (nm) apart. A pelagic "Harstad" trawl with 20 by 20 m mouth opening and with 7 panels and a cod end was used. The trawl is designed with decreasing meshes towards the cod-end (un-stretched mesh sizes ranging from 20 cm in the front to 6 cm in the rear part). The trawling procedure consists of predetermined tows at three or more depths, each of 0.5 nm, with the head-line at 0 m, 20 m and 40 m and with a trawling speed of 3 knots. Additional tows at 60 and 80 m, also of 0.5 nm, were made where a dense concentration of fish was recorded deeper than 40 m on the echo sounder (Anon. 1980, Eriksen and Prozorkevich 2011). If the number of depth layers at station is 1 and the head-line at 0 m, it means that the trawl was towed for ca 0.5 nm at the surface (0 meter depth) covering the water layer between 0 and 20 m. If the number of

depth layers at station is 2 and the head-line at 20 m, it means that trawl was towed ca 0.5 nm covering 0-20 m and ca 0.5 nm at 20-40 m, and so on.

### 1.2.3   Biological sample processing on board

The trawl catches are processed immediately. The following information on the fishing station are recorded (Mjanger *et al.* 2011): year, nation, vessel, month, day, station's number, series and type, geographical position, bottom depth, gear type and number, vessel log reading, trawled speed and distance, fishing depth (number of depths steps), gear conditions and opening (not always).

The trawl catch is sorted and all captured organisms identifies to lowest possible taxonomic level. Pelagic fishes (capelin, herring, blue whiting and polar cod) and 0-group fishes identifies to the species level, and other species among plankton and small non-commercial fishes identifies to family or genus level due to difficulties in species identification and time constraints on board. For each species or groups (family or higher level) the following information is recorded: species or groups catch amount (weight and number) size of length measurement sample (weight and number) and biological information (age, stomachs etc) depends on species (Mjanger *et al.* 2011). The pelagic species (between 30 and 100 specimens depends on species and number in catch is length and weight measures individually (Mjanger *et al.* 2011). 100 specimens (since 2014, 30 specimens) of each 0-group fish species and 30 specimens of small non-commercial fishes length measured, while pooled weight was obtained for species or species groups. Krill and jellyfish were only weight measured. Since 2014, processing procedure for krill and jellyfish changed and should these organisms should be identified to species level if it's possible. However, the procedure was not followed by all participants of unknown reasons (Eriksen *et al.* 2014).

# 2 Methods and methodological considerations

A crucial aspect of monitoring of dynamic marine ecosystems is to obtain information on temporal and spatial trends in species abundances. Results obtained from scientific trawl catches at monitoring stations may give relative abundance indices, such as number of individuals or biomass per trawled distance averaged across strata. However, to understand the energy flow in the ecosystem and roles of different species for this flow, estimation of total abundance or biomass is required.

## 2.1 Methodological aspects related to the sampling

All sampling methods and equipments have their limitations, which affect sampling efficiency and introduce bias. Here I discuss sampling limitations in the monitoring of pelagic compartment of the Barents Sea and how this influence the quality of the time series derived from the sampling. In particular, I discuss the sampling of 0-group fish and krill, which form the basis of the time series based on the monitoring program I have been responsible for in the last 10 years, the pelagic trawl targeting 0-group fish.

*0-group fish*

Most of the data I have used in this thesis are based on pelagic catches taken by the "Harstad" trawl. The "Harstad" is designed for small fish with decreasing meshes towards the cod-end (un-stretched mesh sizes ranging from 20 cm in the front to 6 cm in the rear part) and this may lead to 1) small fish escapes through coarse meshes in the front (Godø *et al.* 1993), 2) herding of fish backwards until they eventually encounter meshes that are small enough for retention (e.g. Lee *et al.* 1996, Heino *et al.* 2011) and 3) snagging, when fish entangled in the meshes of the net (Engås *et al.* 2013). Godø *et al.* (1993) and Hylen *et al.* (1995) showed that the "Harstad" trawl was highly selective for 0-group cod and haddock, and capture of fish smaller than 65 mm was much lower than their experimental trawl and concluded this applies to other species as well. An unknown fraction of the catch escapes through coarse meshes in the front, which will differ between species and length groups (Godø and Valdemarsen 1993; Hylen *et al.* 1995, Engås *et al.* 2013), and this lead to underestimation of fish abundance and probable overestimation of mean fish length. Herding of several fish species were studied and found that flatfish displayed a strong, consistent herding response (Somerton and Munro, 2001), while pacific cod and walleye pollock did not display herding response to stimuli produced by the doors or bridles (Somerton 2004). No documentation of herding for 0-group fish is available. 0-group capelin has been observed entangled in the meshes but falls off during hauling of the net, indicating the snagging. To compensate for loss of smaller fish through the meshes, the correction factors (dependent on species and fish length distribution) have been established and used in the annual calculations of 0-group fish abundance (Hylen *et al.* 1995, Mamylov 2004, Prozorkevich 2004, Dingsør 2005, see below).

*Krill*

Sampling of krill is difficult due to their intermediate size between macrozooplankton and micronekton, a high degree of patchiness often varying with depth, temperature or migration (Zelickman 1961, Zelickman *et al.* 1978, Someoto, 1983, Nicol 1986, Hanamura *et al.* 1989, Skjoldal *et al.* 2013) and behavioural avoidance of sampling gears (Sameoto *et al.* 1980, 1983; Wiebe *et al.* 1982, 2004, 2013; Timofeev 1988). Trawling is challenged by the escapement of small krill through the mesh opening of the trawl (Orlova *et al.* 2008, 2009, Krag *et al.* 2014), leading to pelagic trawls catches biased towards the larger krill (Paper IX). Paper IX examined three monitoring data sets on krill sampled with a pelagic trawl, a plankton net attached to a bottom trawl, and a multiple-net plankton sampler MOCNESS, and considered likely errors associated with sampling design (timing, geographical and vertical coverage and sampling effort) and gear (e.g. mesh size, filtering volume). Results indicated a high degree of patchiness in the distribution of krill, even at the large scale of sampling with the pelagic trawl (large sampling volumes and high sampling effort). There are reports of pelagic swarms of *T.raschii* in the North Atlantic (Zelickman 1961; Zelickman *et al.* 1978), and of *T.inermis* both in the North Atlantic (Zelickman *et al.* 1978).

Krill migrate to the upper layers to feed during the night in summer and early autumn when the larger portion of krill is found in the pelagic layer (Zelikman *et al.* 1978; Drobysheva 1994). To give a more representative sampling of krill night samples only were used in this thesis. However, krill that stay deeper than 60 m during the night will not be recorded and can lead to an underestimate of the amount of krill.

The behaviour of krill within the trawl is largely unknown, and there could possibly be some herding effect of krill responding to contact with or otherwise sensing the net wall, by moving in the direction of the centre of the trawl. Hence, the krill monitoring in the Barents Sea is associated with many methodological challenges associated with sampling design, effort and gear and patchiness.

*Jellyfish*

Catchability of jellyfish by "Harstad" trawl is unknown, however for the large scyphomedusa, *C. Capillata*, the bell (diameter of 20-60 cm) is larger than the mesh size of trawl and thus I assume that *C. capilata* may be captured by all panels of the trawl. Smaller and less robust species, such as *A. aurita* were probably sieved through trawl meshes and reliably captured by the last panel only, but will however be partially or totally damaged in the cod end, and thus their proportion in catch may be limited. Paper III conclude that the use of the identical trawling procedure over more than 30 years allows for the use of these data in studies of inter-annual changes of jellyfish, and these data represents mostly *C. capillata.*

Yet, due to the methodological consistency over years it is concluded in papers I-IV, VI-IX that data from the standard pelagic samples provides important information about abundance and/or biomass that can be used in analyses of abundance variability and trends.

## 2.2    Data processing and quality control

The quality of the collected biological data greatly influences the precision of estimates, analyses, results, and conclusions based on these data. After each survey, there is a data exchange between IMR and PINRO. Since the data infrastructure is different at IMR and PINRO, the data are converted to institute-specific formats before they are entered into the respective databases. Before computer storage was common, hand-written data were exchanged. IMR and PINRO were responsible for digitizing the historical hand-written data, which were entered into two separate databases before exchanged. All these steps in the data treatment have the potential for introducing errors.

Krill, amphipods and jellyfish have not been the major target for the routine monitoring surveys in the Barents Sea, and the data on these organisms were largely missing from the electronic database. These data have now been updated and are available for the two institutes and the wider scientific community (Paper II and III). Furthermore, both errors and missing data were observed in the 0-group databases. Therefore, a quality control of the databases was required and has been performed (Paper I). All records in each database were compared with the hand-written data and after that the two databases at IMR and PINRO were compared. The joint database was updated and errors were corrected in 2006-2009 (Paper I). The quality control continues as an ongoing routine process.

## 2.3    Considerations on estimation of abundance and biomass

To understand ecosystem functioning and document status and changes in the ecosystem long, consistent and uninterrupted time series of biological and environmental data are needed. The conducted surveys (Section 1.2.1) provide a substantial amount of data. Ordinary fishing station with pelagic trawl hauls of satisfactory quality and gear in good conditions (Sections 1.2.2 and 1.2.3) were used to estimate abundance time series for the period 1980-2015 and biomass time series for the period 1993-2013.

Abundance of 0-group Barents Sea capelin *Mallotus villosus*, Norwegian spring spawning herring *Clupea harengus*, Northeast Arctic cod *Gadus morhua*, Northeast Arctic haddock *Melanogrammus aeglefinus*, Northeast Arctic saithe *Pollachius virens*, redfish *Sebastes* spp., Greenland halibut *Reinhardtius hippoglossoides*, long rough dab *Hippoglossoides platessoides*, and two populations (western and eastern) of polar cod *Boreogadus saida* were calculated using the stratified sample mean method of swept area (Dingsør 2005) and the Barents Sea 0-group strata system, which consists of 23 strata (see Appendix). Abundance per unit area were estimated by the standard procedure using tow

length, number of depth layers and capture area of trawl (width of 20 m) and given both with and without correction for capture efficiency (Paper I). A constant horizontal opening of 20 m was assumed when calculating the abundance at monitoring stations, due to limited information on trawl geometry during towing at the time (Dingsør 2005, Paper I).

Correction factors have been established and used in the annual calculations of 0-group fish abundance (Hylen *et al.* 1995, Mamylov 2004, Dingsør 2005) to compensate for low sampling efficiency (Paper I, IV, VIII, see above). Capture efficiency of the trawl for 0-group cod, haddock, saithe, polar cod, herring and capelin length group were taken in to consideration and the correction factors (dependent on species and fish length distribution) are used in the annual calculations of 0-group fish abundance (Dingsør 2005, Eriksen and Prozorkevich 2011, Paper I). The capture correction factor for biomass of 0-group cod (3.8), haddock (2.8), herring (5.9) and capelin (5.0) was found by calculating the ratio between abundance indices (with and without capture efficiency, Paper IV). For other 0-group fish and small fishes (poachers, sculpins, snailfishes, pricklebacks, and sandeels the species specific and length dependent catch efficiencies are unknown. Based on fish length (1-5 cm) it was assumed that these fishes may be captured efficiently by last panel of the trawl only, and the correction factor of 5 (similar to capelin) were used in the annual estimates of abundance and biomass (Paper IV and VIII). The correction is fairly large (biomass is scaled up about 3-6 times the recorded biomass) and ignores variation in size (length) of the 0-group fish among years, but the uncertainty of the 0-group biomass estimates is difficult to quantify without additional trawl experiments and knowledge (Paper VIII).

The estimates of krill biomass were based on night catches only (most krill migrate up to feed at night in the upper pelagic layer) combined with tow length and an assumed effective filtering area ($10m^2$, based on the fine-meshed trawl sections before the cod end, Paper II). Small individuals will pass through while larger krill (>15 mm) are retained in the finer-meshed last segment of the trawl. The loss of small individuals leads to underestimation of the total biomass of krill, while there is some uncertainty associated with the swept area and herding. It is possible that some krill stay deeper than the covered area of 60 m, further reason the underestimation of the biomass. Overall these shortcomings, I assume that krill biomass estimates most likely underestimated.

For the estimates of large jellyfish (primarily *Cyanea capilata*) no correction factor for low capture efficiency was used due to the large size of the medusa (Paper III). Paper VIII combined data of all captured organisms, including krill, jellyfish, 0-group fish, pelagic fishes and other small fishes and therefore the jellyfish wet weight biomass values have been reduced (factor 0.04, assuming water content of 96 %, Lowndes 1941, Cushing *et al.* 1958, Postel *et al.* 2000, Doele *et al.* 2007) to make it more comparable to fish wet weight biomass values.

In Paper VIII, data from the 0-group fish, capelin and BESS surveys for the 21-year time period 1993-2013 was analysed and the biomass data (kg wet weight per $nm^2$) from the survey stations and the acoustic recordings have been gridded as average values for 60 nm x 60 nm grid cells covering the whole Barents Sea. Pelagic fish (capelin, polar cod, herring, blue whiting) estimates are obtained acoustically by applying information on species composition and age and size distributions from trawl sampling as part of routine fish stock surveys with capelin as a target species (Aglen and Gavrilov 2011). These spatial acoustic estimates were used in Paper VIII, where biomass estimates based on gridded data ($60*60$ $nm^2$) agreed closely with the data reported by ICES. Pelagic catches were used to estimate lumpfish abundance and biomass estimates, due to lack of knowledge about catchability by the trawl and large size (10-60 cm) no correction factor was used.

Clearly, the correction used for low catch efficiency is a crude approximation to total biomass estimates, but the correction builds on the best available knowledge and information on catchability. All estimates present the minimum biomass due to avoidance, vertical and spatial coverage. The degree of influence of these sources of errors is not well known and cannot be quantified at present (Paper IV and VIII).

## 2.4   Way forward to absolute estimates

In recent years, alternative trawling procedures have been tested to improve the sampling methods. Some small organisms are caught (snagged) on the meshes while trawling, especially 0-group capelin, but fall off during hauling of the trawl. To prevent snagging and escape of organisms through the meshes, trials (in 2013 and 2014) were carried out with ruffled fine-mesh inner nets (8 mm) in the back part of the "Harstad" trawl (Engås *et al.* 2012, 2013, 2014, Underwood *et al.* 2014). Underwater observations showed that the inner nets were in continuous motion while towing and hindered loss of fish through the meshes and prevented the trawl from becoming clogged by fish and other organisms (Engås *et al.* 2014). Additionally, a new codend with a fish-lock was tested which prevented fish from swimming forward during towing and haulback (Engås *et al.* 2014). These promising results demonstrate that further development of a new pelagic trawl (capturing both krill and 0-group fish) may improve the capture efficiency of the trawl and thus lead to reduced uncertainties of abundance estimates.

The routine trawl method used up to now does not provide vertical resolution for the species caught due to sample collection in a single codend. Also, less robust species are often damaged in the codend, complicating both species identification and quantification. Therefore, the "DeepVision" stereo camera equipment was developed and mounted in the trawl, and tested during the BESS (Jørgensen and Rosen, 2012). The "DeepVision" keeps a continuous record of all organisms passing through the extension of the trawl (Rosen *et al.* 2013). Individuals ranging from macro plankton including krill, amphipods and jellyfish to 0-group and adult fish could be identified and measured in the images. Fine-scale patchiness and species distributions and overlap can be documented both vertically and horizontally along the cruise

track (Underwood et al., 2014). However, currently the images need to be processed manually, as automatic species identification of some fish is difficult due to e.g. similar body shapes. For routine use of DeepVision in ecosystem monitoring of the Barents Sea these limitations are crucial. Thus, the further development of "DeepVision" and software for automated image analyses (species identification, length measurement and object counting) should be prioritized in the future.

Additionally, it should be a high priority to improve the quantification of krill, since reliable estimates of krill are crucial in studies of predator-prey dynamics and pathways of energy transfer in the Barents Sea ecosystem. Improvements of sampling gears combined with more and better use of acoustic and optical technology offer great promise in this regard. The ship-borne echo sounders are able to observe krill, including large swarms in the water column and concentrations near the bottom. There is a challenge of acoustically determining the krill abundance in mixed swarms with e.g. fish larvae (Ressler et al. 2015). The echo sounders have been in use during these surveys since 1972 and data storage since 1990s, and a long term historic acoustic data from these surveys should be scrutinised using pelagic trawl and MOCNESS data to obtain an acoustic krill index.

# 3 The status and trends of the pelagic compartment

To understand ecosystem functioning long, consistent and uninterrupted time series of biological and environmental data are needed. Two types of time series were established for longer (abundance estimates, 1980- ) and shorter (biomass estimates (1993- ) periods based on data from long term monitoring of the Barents Sea (Section 1.2.1). The biomass time series were limited to 1990s-2000s due to lack of species weight at some stations and areas in 1980-1992.

## 3.1 A new time series reflects changes in the pelagic compartment

Data from only ordinary fishing station with pelagic trawl hauls of satisfactory quality (Sections 1.2) were used to establish new time series of krill, jellyfish, 0-group fish and lumpfish back to 1980, small non-commercial fishes back to 1990 (not part of the thesis), and new time series of 0-group fish biomass and spatially resolved for six areas time series for both macro plankton, 0-group fish, pelagic fish and small fishes back to 1993 (Table 1). These new time series established in this work (1980- or 1993- ) give new insight to spatio-temporal dynamics of species/groups in late summer-autumn and provide improved opportunities to study interspecies interaction, interactions between species and environmental conditions and their role in the ecosystem (Paper VIII).

Table 1. New time series for diverse ecosystem component in the Barents Sea pelagic compartment.

| Time series | Period | Species/ group | Paper |
|---|---|---|---|
| 0-group fish abundance | 1980- | Capelin (*Mallotus villosus* ), Barents Sea population<br>Herring (*Clupea harengus*), Norwegian spring spawning population<br>Cod (*Gadus morhua*), Northeast Arctic population<br>Haddock (*Melanogrammus aeglefinus*), Northeast Arctic population<br>Polar cod (*Boreogadus saida*)<br> Beaked redfish (*Sebastes mentella*)<br>Saithe (*Pollachius virens*), Northeast Arctic population<br>Blue whiting (*Micromesistius poutassou*)<br>Greenland halibut (*Reinhardtius hippoglossoides*)<br>Long rough dab (*Hippoglossoides platessoides*)<br>Wolffishes *Anarhichas spp.* | Paper 1 |
| 0-group fish biomass | 1993- | Capelin, herring cod and haddock | Paper IV |
| Macro plankton | 1980- | Jellyfish, mostly lion's mane jelly *Cyanea capillata*<br>Krill, not identified to species level | Paper III<br>Paper II |
| Lumpfish | 1980- | Lumpfish (*Cyclopterus lumpus*) (age 1+) | Paper VII |
| Small fishes abundance and biomass | 1990- | Ammodytidae (mainly *Ammodytes marinus*)<br>Agonidae (*Agonus cataphractus, Leptagonus decagonus, Ulcina olriki*)<br>Cottidae (*Artediellus atlanticus, Artediellus scaber, Icelus bicornis, Icelus spatula, Gymnocanthus tricuspis, Myoxocephalus quadricornis, Myoxocephalus scorpius, Taurulus bubalis, Triglops murrayi, Triglops nybelini, Triglops pingelii*)<br>Liparidae<br>Stichaeidae (*Anisarchus medius, Leptoclinus maculatus, Lumpenus lampraetaeformis*) | Eriksen *et al.* 2012 |
| Spatially resolved time series for the  pelagic compartment | 1993- | All species and group listed above for six region in the Barents Sea | Paper VIII |

The 0-group capelin is the most abundant 0-group fish in the Barents Sea, however, its abundance fluctuated dramatically from 952 million (1993) to 988 600 million individuals (2012) and were relatively high during 1980s and recent two decades (Figure 2 and Appendix). Abundant year classes were observed in 1980-83, 1989, 1999, 2006-2009 and record high year class in 2012. The 0-group cod makes a bulk of 0-group fish biomass in the Barents Sea. During 1980s middles and poor year classes were observed only, several strong year classes were observed in 1990s and only strong year classes were observed in period 2008-2014 with record high year class in 2011 (Figure 2). Abundance of 0-group herring fluctuated dramatically and was relative low in 1980s and last decade: one strong year classes of herring occurred in 1980s, six in 1990 and four in 2000s with record high in 2004. Abundance of 0-grpoup haddock was generally low during 1980s and 1990s and increased in 2000s. Record high year classes of haddock were observed in 2005. The variation in 0-group cod, herring and haddock biomass was positively correlated with spawning stock biomass (Paper IV), indicating that high recruitment tends to occur when spawner's stock biomass is high. Ponomarenko (1973) studied

recruitment of commercial important fish stocks in the Barents Sea and concluded that spawning stock biomass and age-structure of the spawners are a fundamental factor to the formation of year class strength. Marshall *et al.* (1998) pointed that spawner's condition are also important for the quality and of eggs and later survival of larvae.

Overfishing in 1970-1980s led to a rapid decline of slow-growing redfish stock, *Sebastes mentella*, and thus to recruitment failure in 1990s (Drevetnyak and Nedreaas 2009, ICES 2010). This was reflected with weak year classes strength during 1990 and beginning of 2000s (Paper VI). The polar cod stock has undergone large changes during the last three decades, with stock size decreasing to 0.1 million tonnes in 1988, increasing to 1.8 million tonnes in 2005, and falling to 0.1 million tonnes in 2015 (ICES 2016). Strong year classes of polar cod occurred in 1990s only, and thus low recruitment in 1980 may most likely limited by low stock size, while 2000s by other factors (see below).

The distribution and survival of juvenile fish are also influenced by environmental factors, and warmer temperature conditions associated with increased inflow of Atlantic water are commonly considered as driving forces for higher survival (Sætersdal and Loeng 1987; Loeng and Gjøsæter 1990; Ottersen and Loeng 2000). The synchrony found in year class strength of cod, haddock and herring and early growth is a result of a mutual response to temperature fluctuations (Ottersen and Loeng 2000), however this synchrony was altered in recent 2000s (Paper IV). During 2000s strong year classes of cod, haddock, herring and capelin with record high abundance in 2004 (herring), 2005 (haddock), 2011 (cod) and 2012 (capelin) occurred (Figure 2A), and these strong drive fluctuations in the stocks (Paper VIII). It seems that haddock and herring respond similar to the recent warming than cod and capelin, most likely due to similar thermal habitat and increased area of suitable temperature (Section 3.3).
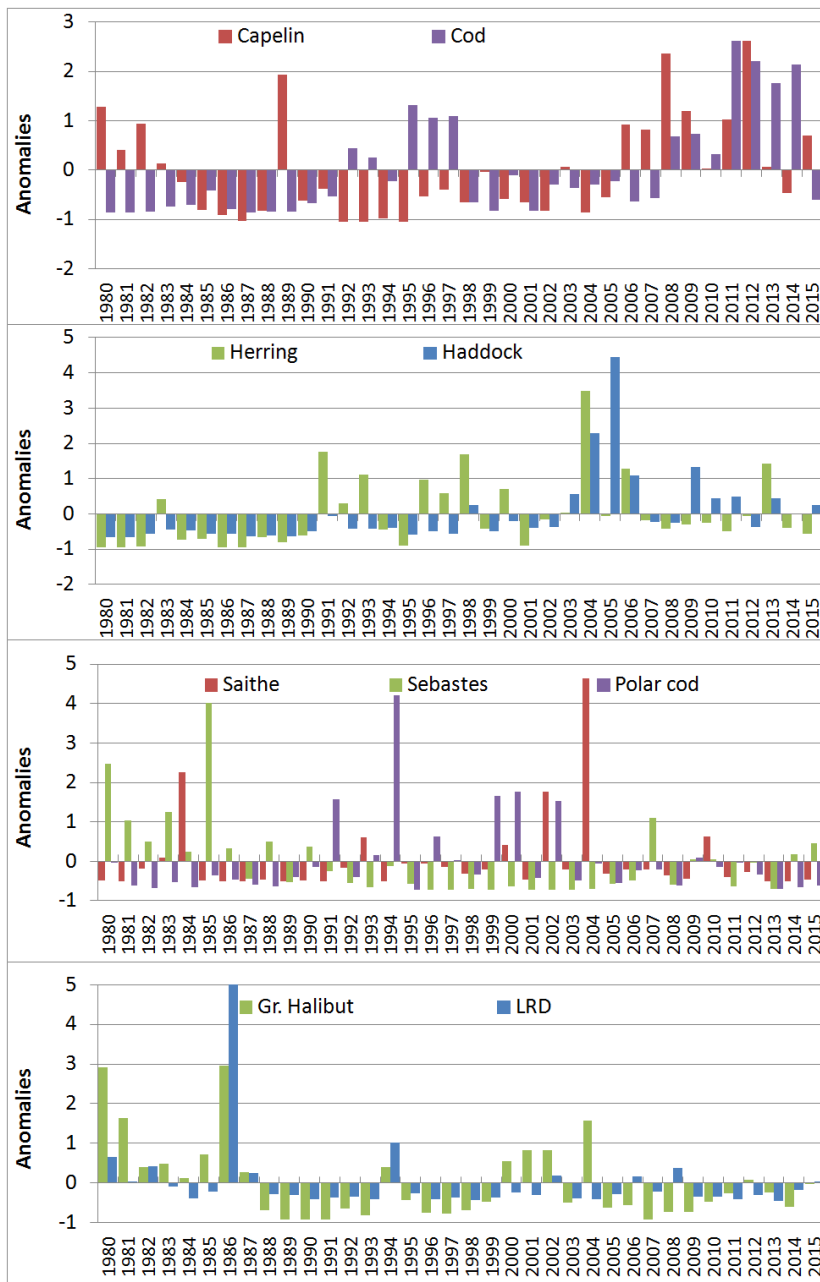
Figure 2A. 0-group fish (capelin, herring, haddock, cod, saithe, redfishes, polar cod, Greenland halinut and long rough dab) abundunce anomalies for the period 1980-2015. All data were standartized (value *x*-mean/SdDev) before anomalies were created. The time series were updated annually, and thus recent years were taken from the survey report http://www.imr.no/tokt/okosystemtokt_i_barentshavet/survey_reports/survey_report_2015/nb-no

During the last three decades, the autumn krill biomass fluctuated considerably in the Barents Sea (Paper II). Krill biomasses were generally low during 1980 and 1990s, and high in 2000s, especially in 2008-2011 (Figure 2B). Capelin is the largest pelagic stock and may impose high predation pressure on krill (Hassel *et al.* 1991; Dalpadado and Skjoldal 1996; Gjøsæter *et al.* 2002). However, during the last decade, the krill biomass has increased despite heavy predation from capelin in some years (Paper II) coincided with a general warming trend presumably with larger influx of euphausiids with Atlantic water, notably of *Meganyctiphanes norvegica* (Paper IX).

Jellyfish biomasses were low during 1980s, increased during 1990s, and were highest in 2000s (Figure 2B). Jellyfish biomass (wet weight) varied from 19 thousand tonnes in 1997 to ca. 5 million tonnes in 2001and 2014, with a long term mean of around ca. 900 thousand tonnes (Paper III).  Higher biomasses were generally found during average and warm years, and these findings are in agreement with Lynam *et al.* (2005) and Brodeur (2008), who found a warming trend favouring many species of jellyfish in other seas, and, within certain limits, the warming trend seems also to be favourable for Barents Sea jellyfish (Paper III).

A new time series of the abundance and biomass of lumpfish (*Cyclopterus lumpus*) has been established for the period 1980–2012 (Paper VII). The annual biomass ranged from 212 tonnes to 143 thousand tonnes, corresponding to 36 to132 million individuals. The proportion of juveniles (fish length <20 cm) have been generally higher than the adults in the Barents Sea. The biomass of lumpfish varied considerably during the last three decades, and was lowest during the 1980s, increasing in the 1990s, and highest in the 2000s (Paper VII, Figure 2B). Higher densities and occupied the largest areas observed during warm years with a larger inflow of Atlantic warm plankton-rich water which brings more larvae and small fish into the Barents Sea, and thus offering a wider suitable habitat for lumpfish (Paper VII). This is supported by earlier findings (Ignashev and Rusyaev 1999, Nikiforov and Rusyaev 2004), in which the amount of lumpfish in the Barents Sea depended on oceanographic conditions and was higher during warmer years.

The small fishes have been poorly studied and their role in the Barents Sea ecosystem is largely unknown. A new time series of abundance and biomass indices for pelagically distributed *Agonidae, Ammodytidae, Cottidae, Liparidae, Myctophidae* and *Stichaeidae,* has been established for the period 1980 to 2009 (Eriksen *et al.* 2012), but these time series are not a part of this thesis (Figure 2B). However, spatially resolved data of small fishes were used in estimation of pelagic biomass in the Barents Sea (Paper VIII), and thus spatially resolved time series were also established. Abundance of Ammodytidae, Myctophidae and Stichaeidae were generally low in 1990s and increased in 2000s, Agonidae, Cottidae varied between years, while Liparidae were abundant in 2005-2012 only.
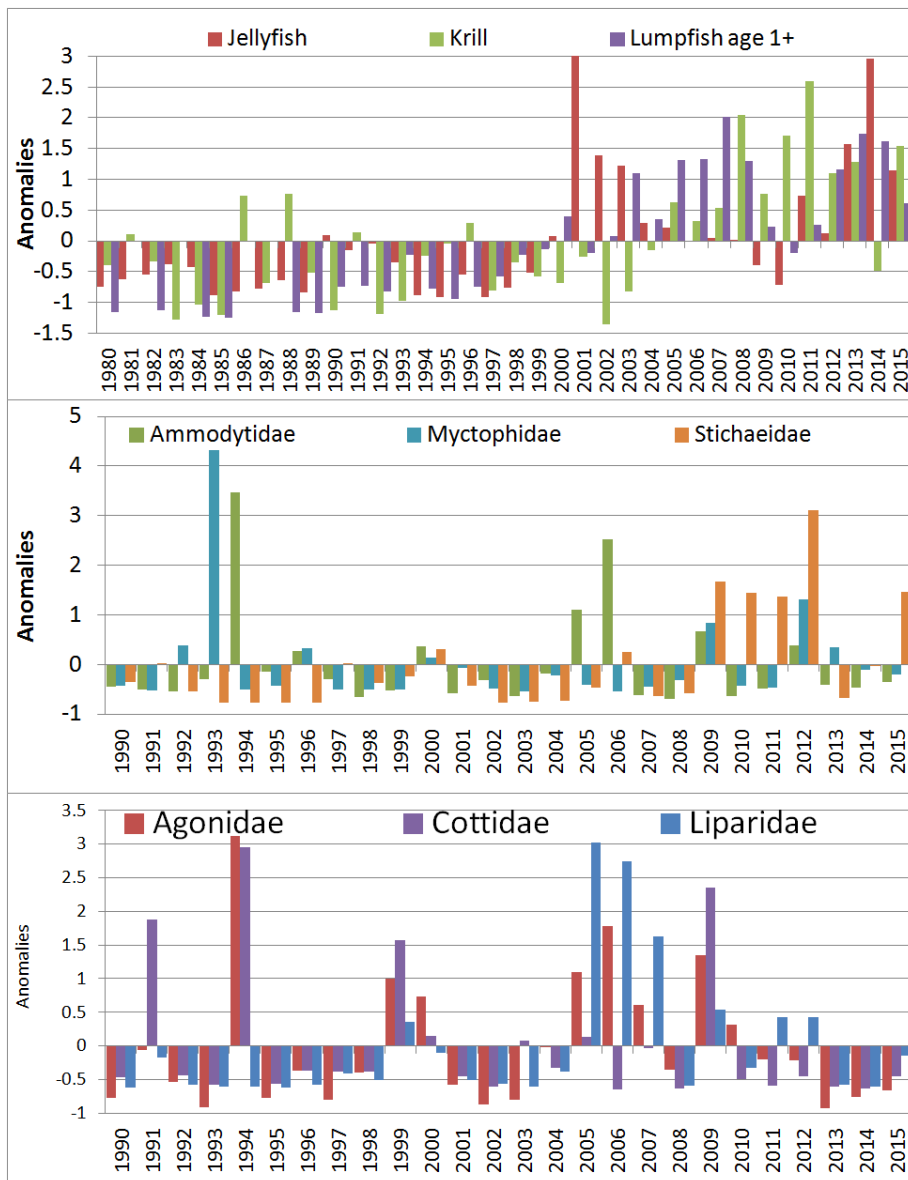
Figure 2B. Biomass of macro plankton (krill and jellyfish) and lumpfish age 1+ for anomalies for the period 1980-2015, and abundance anomalies for small non-commercieal fishes (poachers (family Agonidae), sculpins (Cottidae), pricklebacks (Stichaeidae), and snailfishes (Liparidae), sandells (Ammodytidae) and lanterfishes (Myctophidae) for the period 1990-2015. All data were standartized (value *x*-mean/SdDev) before anomalies were created. The time series were updated annually, and thus recent years were taken from the survey report http://www.imr.no/tokt/okosystemtokt_i_barentshavet/survey_reports/survey_report_2015/nb-no

## 3.2    Oceanographic and biological fluctuations in the pelagic comportment

The Barents Sea ecosystem is dynamic and has been shown to undergo large fluctuations in response to climate variability at different time scales including annual, decadal and multidecadal scales (Helland-Hansen and Nansen 1909, Hjort 1914, Sætersdal and Loeng 1987, Skjoldal and Rey 1989, Loeng and Drinkwater 2007, Drinkwater 2011, Johannesen *et al.* 2012). The most recent decade has been the warmest on record (Prokhorova *et al.* 2013). The pelagic compartment is directly and intimately connected to the ocean climate system and is expected to respond more rapidly to climate variability than for instance the benthic compartment due to shorter generation times, and thus arctic species may have favourable condition during the cold period, while boreal species during the warm period (Rijnsdorp *et al.* 2009, Perry *et al.* 2010, Ottersen *et al.* 2010, Fossheim *et al.* 2015).

The climate of the Barents Sea has shown long-term fluctuations with a warm period from the 1920s - 1960s followed by a cold period in the 1970s - 80s (Ingvaldsen *et al.* 2003, 2009, Ozhigin *et al.* 2011). In this thesis data from a 35-years period (1980-2015) were used to explore what changes have taken place in the pelagic part of the ecosystem of the Barents Sea associated with the recent warming. The period 1980-2015,which is the period of time series considered here, is characterized by warming from coldest period around 1980 to a record warm conditions observed in the 2000s (Figure 3).
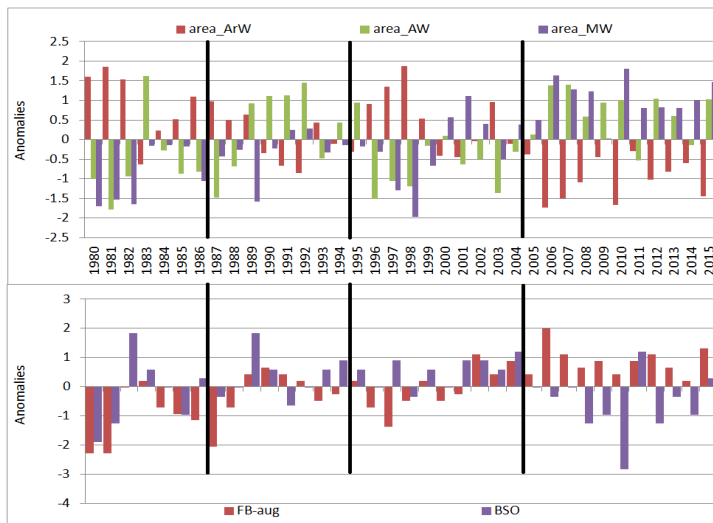


Figure 3. Climate variability in the Barents Sea. Anomalies of area of water Arctic (ArW), Atlantic (AW) and mixed (MW) masses, water temperature (50-200 m) at the Fugløya-Bjørnøya (FB-aug) section and the annual modelled net eastward volume transport between Norway and Bear Island (positive BSO (the Barents Sea Opening) into the Barents Sea).

Stratigraphically constrained clustering (using UPGMA algorithm) of years based on oceanographic (BSO flux, seawater temperatures and areas of water masses) and biological (biomass of krill and

jellyfish, and abundance 0-group fish and lumpfish) variables for the period 1980-2015 were used to identify different periods within the studied period. The period of 1980-2015 can be broadly divided into four segments based on differences in oceanographic and biological variables with break point in 1986, 1994, and 2004 as shown by a hierarchical clustering (Figure 4). The oceanographic condition in the Barents Sea during the first period (1980-1986) can be characterized as cold conditions with low water temperature and a large area of Arctic water masses, during the second period (1987-1994) as slightly warming with increased eastward volume transport, temperature and area of Atlantic Water masses, during the third period (1995-2003) as weak reverse situation with slightly increased area of Arctic and mixed water masses, varied temperature and stronger eastward Atlantic water transport, and during the fourth period (2004-2015) as warmest recorded with record high temperatures and largest areas of warm waters (Atlantic and Mixed) and a correspondingly lowest area of cold Arctic water after 2004 (Figure 3). The biological condition in the Barents Sea during the first period can be characterized by low biomass of macro plankton and good recruitment for wide distributed species (Greenland halibut, long rough dab, saithe and redfish) and capelin, the second period by low biomass of macro plankton and generally low fish recruitment, except herring and polar cod, the third period by record high biomass of jellyfish, good cod, herring and polar cod recruitment and increased abundance of lumpfish, and the fourth period by high biomass of macro plankton and good recruitment of boreal species and capelin.
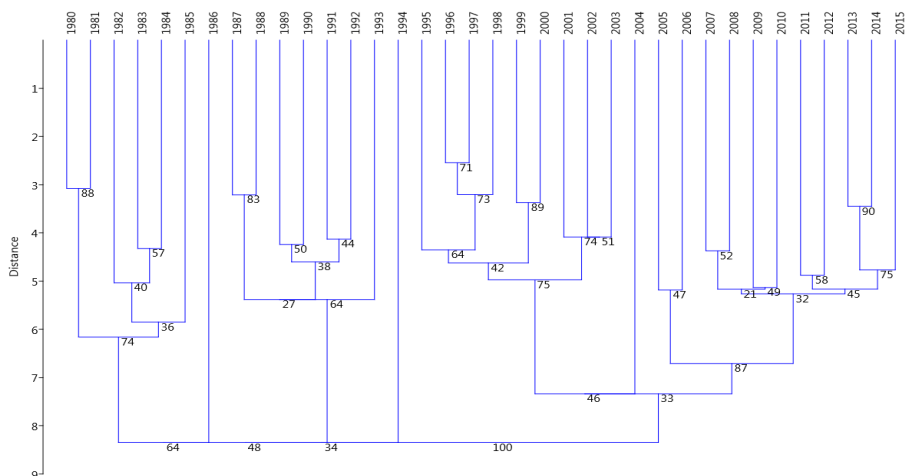


Figure 4. Stratigraphically constrained clustering of years based on abiotic (area of water masses: Arctic (ArW), Mixed (MW) and Atlantic (AW)) and biological (krill, jellyfish, 0-group fish abundance, lumpfish and small non-commercial fishes) variables for the period 1980-2015. Lines show linkages of groups of years based on similarity from constrained cluster analysis (using UPGMA algorithm). All values were standardized (value *x*-mean/StDev).

The environmental variables (BSO flux, seawater temperatures and areas of water masses) were used to investigate possible abiotic sources of pelagic abundance variability (time series of krill, jellyfish, 0-group (9 species) and 5 families of small fishes) in different years by Non-metric Multidimensional Scaling (NMDS). The arrangement of the data points in the NMDS plot suggested that the two axes separated warming (coordinate 1) and abundance (coordinate 2) gradients (Figure 5). The physical variables were strongly correlated with coordinate 1, suggesting that this can be interpreted as a "warming trend" axis. The variation along coordinate 2 (Figure 5) appears to reflect increased abundance of krill, jellyfish, 0-group fish (capelin, cod, herring, haddock) and small fishes, notable Stichaeidae, Ammodytidae and Agonidae during the period 1980-2015 (Figure 2AB and 5).
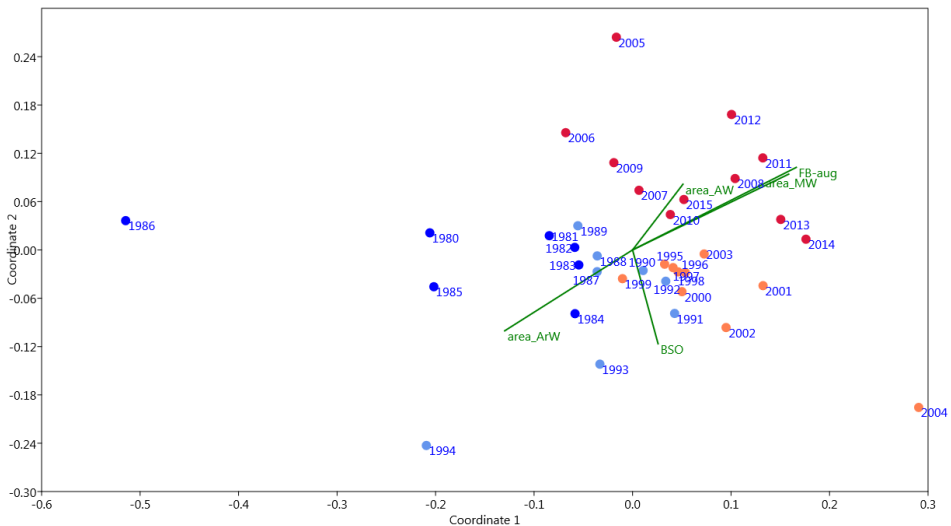


Figure 5. Plot from non-metric multidimensional scaling of annual variation (1980-2015) of oceanographic conditions and abundance values of 18 species or groups. The data points (years) for the different periods (see Figure 3) are shown with different colours. The horizontal coordinate (1) is interpreted as warming gradient; while vertical coordinate (2) as abundance gradient.

Large changes in the pelagic part of the Barents Sea ecosystem associated with the recent warming event over the last 35 years: from low productive cold system to high productive warm system. There was an overall increasing trend of pelagic biomass/abundance during the studied period, and this was driven primarily by an increase in the amount of krill and jellyfish, and also several strong year classes of cod and capelin. It is possible that the increase in the amount of krill, jellyfish and 0-group fish reflects stronger advection of these organisms with the inflowing Atlantic water and suitable living condition in the Barents Sea (Orlova *et al.* 2015, ICES 2016, and Papers II-IV). However, to understand how climate variability (reflected in fluxes, properties and distribution of water masses) effect on macro plankton

and species recruitment variability, which affects the pelagic system, needs detail knowledge about species thermal habitat and changes in the environmental condition.

## 3.3    Species thermal habitat and variation of area of suitable temperature

The pelagic organisms drifting with ocean currents into the Barents Sea directly and intimately respond to stronger flux, increased temperature and increased area of warmer water masses (Rijnsdorp *et al.* 2009). To study species response to varied temperature condition in the Barents Sea the thermal interval, where the majority of fish/jellyfish were observed, was defined as Core Thermal Habitat (CTH), and the area, where the majority of fish were observed, as core area (CO, Paper V). CTH were defined for jellyfish, 0-group fish (cod, haddock, herring, capelin, redfish and polar cod) and lumpfish (Paper V-VII).

The 0-group fish were observed in a wide thermal interval -1 °C < T < 10.5 °C, which indicates that they can stay in water with wide temperature range (1980-2008, Paper V). However, the thermal window differed between the different species: 2 - 5.5 °C (polar cod), 2.2 - 6.3°C (capelin), 4.4 - 8.0 °C (cod), 5.2 - 8.7°C (herring), 4.1 - 10.5 °C (haddock), and 5.5 - 8.5°C (redfish), Paper V. Thus, 0-group cod, haddock, redfish and herring were mostly found in the Atlantic Water masses (>3°C), while capelin and polar cod were found in Atlantic Waters and Mixed Water masses (0°C<T<3°C). The area with CTH for cod, haddock and herring increased north-eastwards when going from cold to warm years, and the species abundance increased (Figure 5 in Paper V). However, the southern warm boundary of the core area varied considerably between years (except for haddock) and decreased in warm years, as did the abundance of the species. The highest densities of capelin were observed within the core area only during cold years, while they showed a shift towards north-east in warm years (Figure 5 in Paper V), which was correlated with increased temperature and areas of Atlantic and mixed waters (Paper V and VIII). Thus for the cod, redfish and capelin any further increase in temperature within the core area is likely to alter the distribution of the core area, and could impact the year class development with regards to growth and/or survival. Particularly for the polar cod, an arctic fish species, further increase of temperature may decrease the area of suitable thermal habitat, although this may be counteracted by improved feeding condition (due to larger advection of plankton, Boitsov *et al.* 2013).

The largest 0-group fish are found within smaller thermal windows compared to core areas, e.g 5.5 - 7.7 °C (cod),  5.5- 7.7 °C (cod), 7.0 – 8.0 (redfish) and  3.0 – 3.5°C (capelin), while the fish length increased with temperature up to ~ 4.0 - 5.0 °C (herring and haddock, Paper V)). Paper V showed abrupt changes in fish densities and length (cod and capelin) with increasing temperature. Asymmetric distribution of fish densities with a stronger decline towards higher temperature has also been found for the response of growth (i.e. the difference between consumption needed for tissue maintenance and maximum

consumption; Peck *et al.* 2003) and may be linked to a bioenergetic limit for the distribution (Pörtner and Peck 2001). This complex coupling of multiple factors makes it difficult to unravel the total effects (both direct and indirect) of climate variability and trophic interactions on fish. Additionally, fish growth is not only affected by temperature during late summer-early autumn, but also by spawners conditions, spawning time and placement, access to food, and the temperature during the growing period.

In the Barents Sea, jellyfish (*C. capillata*) were found in the temperature interval $1°C < T < 10°C$, with most jellyfish occurring between 3 - 7 °C (Paper III). The occupation area and catches increased from the cold 1980s, to moderate 1990s and were largest in warm 2000s (Paper III). During the short summer months jellyfish biomass may reach extremely high levels, e.g. 3-5 million tonnes (2001-2003 and 2013-14, Paper III, Prokhorova *et al.* 2013, Eriksen *et al.* 2014), resulting in jellyfish in most regions in the system (Eriksen 2015). Thus, the ongoing warming trend seems to be favourable for Barents Sea jellyfish medusae (Paper III).

The majority of lumpfish were found in the temperature ranges of 5 - 7 °C (60% of juveniles) and 4 - 7 °C (70% of adults), indicating a strong association with Atlantic water masses in the Barents Sea (Paper VII). It seems that the recent warming conditions had favourable impacts on lumpfish by increasing area of suitable habitats (thermal and feeding) and the abundance may increase with further warming in the Barents Sea.

## 3.4 Species spatial distribution and their shift

A crucial aspect of monitoring of dynamic marine ecosystems is to obtain information on temporal and spatial trends in species abundances. To investigate the large scale spatial organization of the pelagic compartment and biomass fluctuations the monitoring data were aggregated into larger geographic strata. However, different stratifications were used in Paper IV, V and VIII, due to different approaches and focuses of the papers.

In paper IV the traditional 0-group survey strata was used, while in Paper V so-called 'Core areas' with high 0-group densities were established. These core areas broadly corresponded to topographic and oceanographic sub regions (Paper VIII, Figure 6), where banks and basins steers the currents and governs the distribution of water masses, primary production and the drift of egg/larvae and plankton (Loeng 1991, Skjoldal and Rey 1989, Sakshaug 2004).
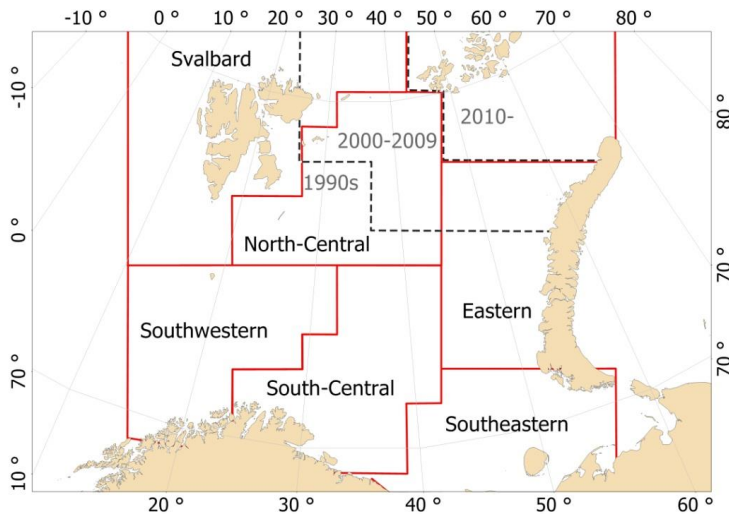
Figure 6. Division of the Barents Sea into six subareas (Southwestern, South-Central, Southeastern, Eastern, North-Central and Svalbard areas). Schematic northern boundaries for surveyed areas in the 1990s and 2000s are shown as dashed lines.

The pelagic fish stocks taken together occupied more or less the whole Barents Sea but with clear differences among the species. The highest concentrations of capelin were found mainly in the northern area, those of polar cod in the eastern area, while herring and blue whiting were found mainly in the southwestern and southern parts of the Barents Sea.

Capelin was widely distributed in the central and northern Barents Sea with a high degree of overlap between high concentrations of juvenile (1-2 years) and older (3-5 years) capelin (Figure 7 A, D). Using data only for the area south of 77 °N, both young and older capelin (1-2 and 3-5 years) showed a northern shift of center of gravity (CoG) between the 1990s and 2000s (Figure 8), that was correlated with area of AW (capelin 3+), however no significant trend was found (Appendix: Trend test).

Young (1-2 years) and older (3+) polar cod were found mainly in the Eastern area with a high degree of overlap between the two age groups (Figure 7 B, E). Young and older polar cod showed an eastern significant shift and older polar cod showed also weak southern shift in CoG between the 1990s and 2000s (Figure 8, Appendix: Trend test), which was correlated with increased water temperature and area of AW and decreased area of ArW.

Juvenile herring and blue whiting were found mainly in the southwestern and southern parts of the Barents Sea during the warm years in the 2000s (Figure 7 C, F). Herring showed variation of CoG in northeast direction and blue whiting showed some western shift of CoG (Figure 8, Appendix: Trend test), which were positively correlated with higher temperature and larger area of AW and MW.

Lumpfish was widely distributed in Barents Sea with high catches in the Southwestern, South-central and the southern part of the North-Central subareas (Figure 7 G). Lumpfish showed variation of CoG in eastern direction between the 1990s and 2000s (Figure 8, Appendix: Trend test), which was correlated with higher flux in second-third quarter of the year.

The groups of krill and jellyfish were widely distributed in the western and southern Barents Sea. The highest concentrations of krill were mainly found in the South-Central, the Southern part of the North-Central, and the Svalbard subareas (Figure 7H). The highest concentrations of jellyfish were mainly found in the Southeastern and Eastern subareas (Figure 7 I). Krill and jellyfish showed association between shifts of CoGs and environmental conditions: jellyfish showed a significant northern shift, which was positively correlated with increased temperature and areas of AW and MW, while krill showed a weak eastern shift, which was correlated with water temperature (but not significant, Appendix: Trend test).
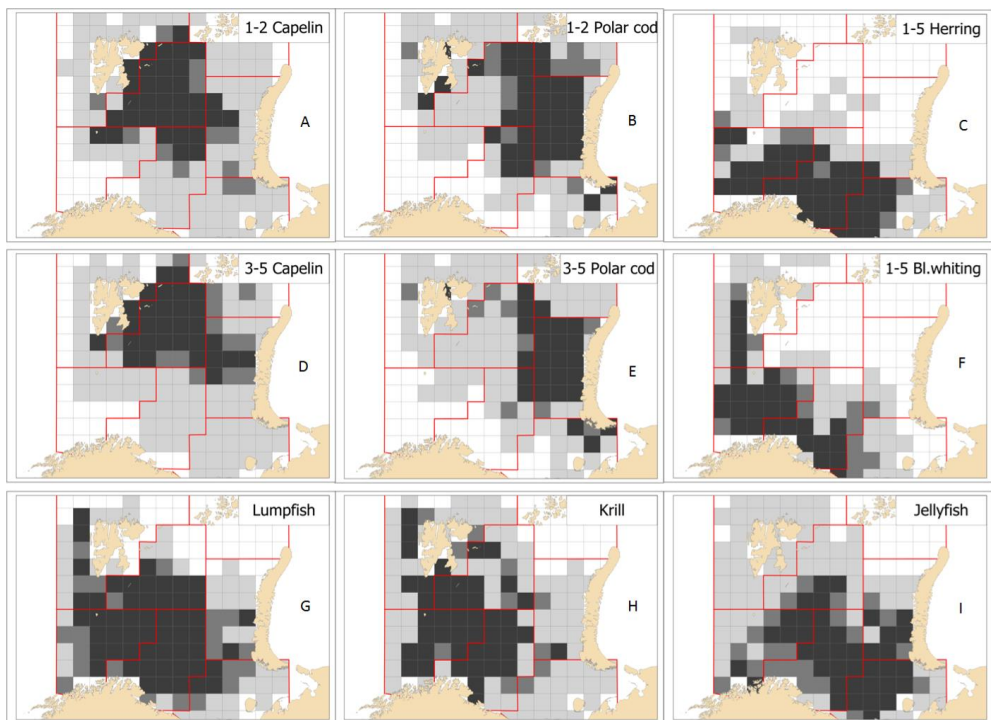


Figure 7 A-I. Spatial distribution of low, average and high densities of pelagic fish stock and macro plankton in the Barents Sea for the period 1993-2013. Definition of low, average and high densities and studied components are presented in Table 2, Paper VIII. Red lines indicate sub-areas reflecting different oceanographic regions (Paper VIII).

High catches of jellyfish and krill overlapped only to a limited extent and mainly in the South-Central subarea. High catches of lumpfish overlapped to a high degree with high catches of krill and jellyfish

and also with high catches of some of the 0-group fish, notably cod, haddock, capelin and herring. About one third of high catches of young (1-2) and older (3-4) capelin were found in areas with high krill catches.
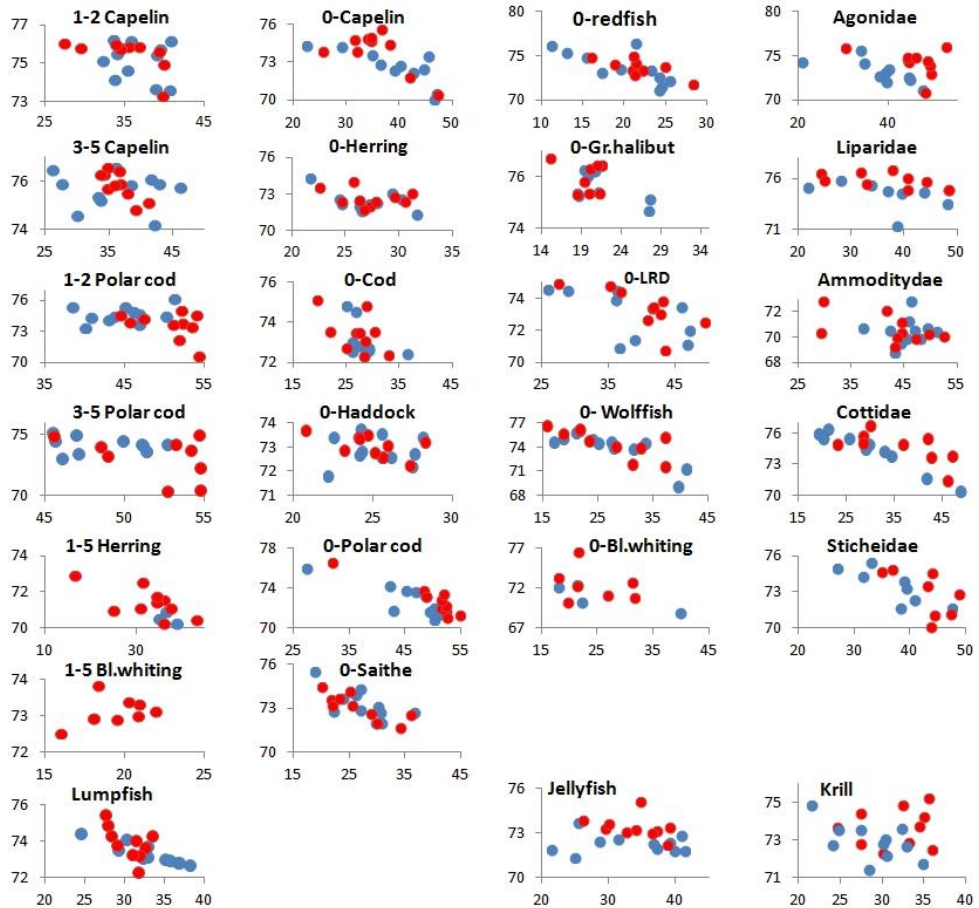


Figure 8. Annual centers of gravity for 0-group, pelagic and small fish and for macro plankton for the period 1993-2013. Blue dots are data points for the colder period 1993-2003, while red dots show data point for the warmer period 2004-2013.

0-group fish occupied more or less the whole Barents Sea (Figure 9 A-J). 0-group fish of the commercial species cod, haddock, herring, capelin, polar cod, and redfish were common and abundant. 0-group cod, haddock, saithe, capelin and herring had wide distributions in the Southwestern and South-Central areas, although a more western distribution was observed for cod and haddock, northern distribution for capelin and southern distribution for herring and saithe (Figure 9 A-D, J). 0-group polar cod was found mainly in the Eastern and Southeastern areas as were also 0-group long rough dab (Figure 9 E, G). 0-group

redfish was found in the western part of the Barents Sea in the Southwestern and Svalbard areas, whereas wolffishes and Greenland halibut were found mainly in the Svalbard area (Figure 9 F, I, J).



Figure 9 A-O. Spatial distribution of biomass of 0-group and other small fishes in the Barents Sea given as average values by grid cells for the period 1993-2013. Low, average and high values for the various species or groups are given in Table 2 (Paper VIII) and are shown with light, medium and dark grey shading, respectively. Red lines show the division of the Barents Sea into six subareas.

0-group fish showed no clear north-south or east-west shifts, except Greenland halibut, between the 1990s and the 2000s although the data points tended to spread in a northwest-southeast direction (Figure 8, Appendix: Trend test). Variation of CoG in northern direction was significantly correlated with decreased flux (herring), increased temperature (herring, capelin, Greenland halibut and wolfishes) and areas of AW, MW (wolffishes). Variation of CoG in eastern direction was correlated with increased temperature (Greenland halibut) and areas of AW (haddock). For 0-group polar cod there was a significant eastern shift of CoG, however no significant correlation with abiotic variables was found.

Small fishes of various families showed different patterns in their distributions in the Barents Sea, with high catches typically found within limited areas. Sandeels were found with high concentrations mainly in the shallow Southeastern area, sculpins and pricklebacks in the Southeastern and Svalbard areas,

whereas poachers and snailfishes were observed mostly in the North-Central, Eastern and Southeastern areas (Figure 7 K-O). Agonidae and Liparidae only showed significant northern shifts between the 1990s and the 2000s only (Appendix: Trend test).

Over the 21-year study period there were shifts in the positions of center of gravity along a northwest-southeast axis. In addition, there were also northwards or eastwards shifts between the cold 1990s and the warmer 2000s for several species (Figure 8). Spatial variation in centers of gravities (CoG) of main species or groups (25 variables) from 21 years (1993-3013) was analysed by Principal Components analyses (PCA). Positive values of CoG in the years 2004-2013, indicating north- and eastward displacement of CoG were associated with higher temperature and larger area of Atlantic and mixed water masses. Negative values of CoG (i.e., south- and westwards displacement) in the years 1993-2003 were associated with area of cold Arctic water masses. The oceanographic condition in these two periods explains almost 71% of the variation in the distribution of CoG of 25 species and groups.
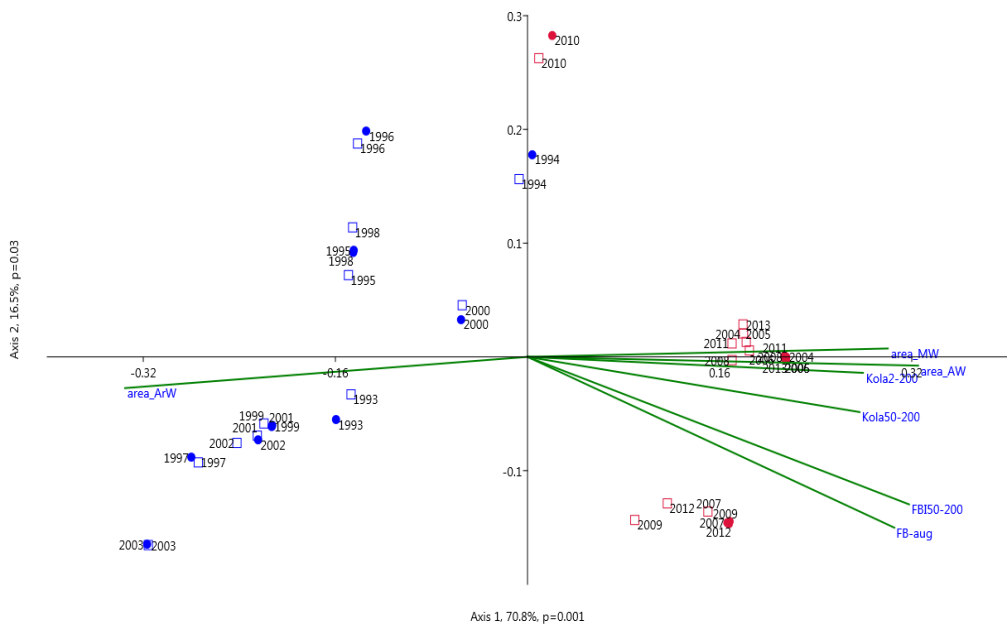


Figure 10 . Plot from PCA on spatial shift in center of gravity (GoC) of 25 species or groups in during the 1993-2013, where squares indicates longitudinal, while dots-latitudinal location of GoC. The data points for each year are shown also for the periods 1993-2003 (blue) and 2004-2013 (red). Abiotic variables: area of Atlantic waters (area_AW), Mixed waters (area_MW), temperature at 0-200m (Kola2-200), at 50-200 (Kola-50-200) at Kola section and the temperature from 50 to 200 m depth at FB in August-September (FB-aug) and annually (FB50-200) at Fugløya-Bjørnøya (FB).

## 3.5 Biomass fluctuation in the pelagic compartment during the recent warming

To study biomass fluctuation of studied ecosystem components (outlined in Table 1) the biomass data (kg wet weight per sq nm) from the survey stations and/or the acoustic recordings was gridded as average values for 60*60 nm$^2$ grid cells covering the whole Barents Sea for the period 1993-2013. In order to investigate spatial fluctuation of the pelagic biomasses at large scale the average values for grid cells were aggregated into larger six areas (Figure 6) and in order to investigate temporal fluctuation of the pelagic biomass the data were aggregated for whole Barents Sea.

The estimated total biomass of the pelagic compartment ranged between 6.6 million tonnes in 2003 to a maximum of about 30 million tonnes in 2008 and 2011 (Figure 11). On average the pelagic fish species made up about 26 %, krill 63 %, and 0-group fish 11% of the total estimated biomass. Pelagic occurrence of small fishes of the various families of mainly demersal groups (sculpins, poachers, pricklebacks, snailfishes and sandeels) made up a small fraction (0.02 %) of the total biomass of the pelagic community. Jellyfish (mainly lion's mane jelly) made up a relatively small average contribution to the pelagic biomass (about 0.3 million tonnes) when converted to unit equivalent to fish biomass (with factor of 0.04).

The study period 1993-2013 can be broadly divided into two segments based on differences in abiotic variables before and after 2004 (Figure 6), and similar to deviation the longer period (1980-2015, Figure 4). The first period from 1993 to 2003 was characterized by rapid changes in the pelagic community with shifts in dominance between pelagic fish stocks and krill. The biomass values tended to be relatively low with an average total biomass of 11.3 million tonnes (Figure 11). During the first period, capelin was the main component among pelagic fish, except in 1993 when herring was abundant (Figure 12A). The apparent stability of the total biomass reflected an increase in the amount of krill when the capelin stock collapsed in the mid 1990s, and a subsequent decline in krill as the capelin stock recovered (Figure 11).
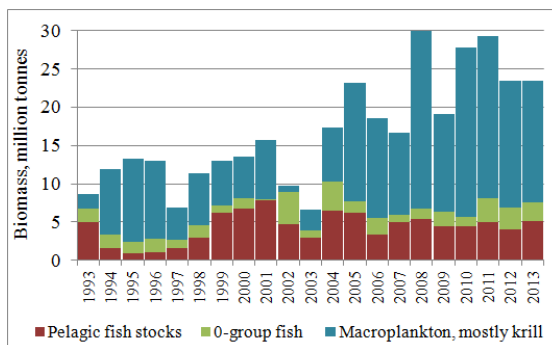


Figure 11.  Estimated biomass (million tonnes wet weight) of the pelagic compartment in the Barents Sea from 1993 to 2013.

After 2003 (2004-2013) the biomass values were generally higher with an average of 23.1 million tonnes, and there was a more stable situation with less pronounced shifts in the biomass contributions by the major pelagic groups (Figure 11). There was an overall shift-up in the level of pelagic biomass after 2003, and this was driven primarily by an increase in the amount of krill (Figures 11 and 13). The biomass of 0-group fish also tended to be higher in the second period than in the first, driven by strong year-classes of herring (2004, 2006, 2012-13) and cod (2008-2013) (Figure 12B). In contrast, 0-group biomass of polar cod tended to be higher in the first period than in the second and occurred with maximum biomass of over 2 million tonnes in 2002.
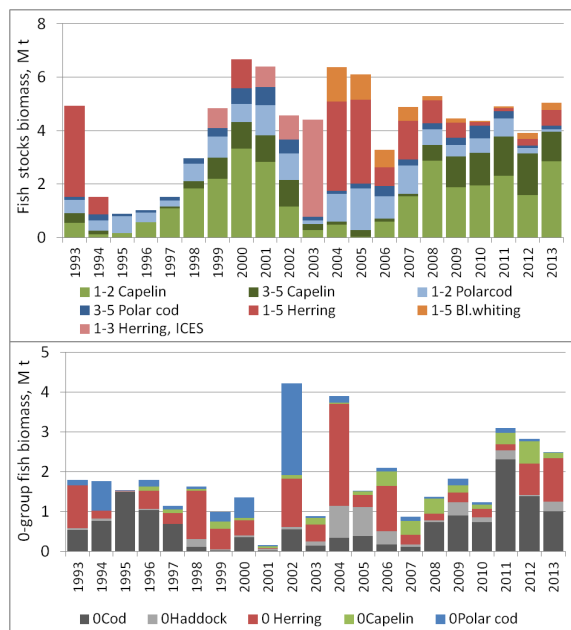


Figure 12. Temporal development of biomass (in million tonnes) of pelagic fish species (above) and 0-group fish (below) in the Barents Sea from 1993 to 2013.

The biomass distribution of the pelagic components differed among the six areas (Figures 13). The highest average biomass values were found in the Southwestern and South-Central areas with about 4.3 - 4.4 million tonnes in each, and in the North-Central areas with about 3.1 million tonnes. Krill was the major biomass component in the Southwestern and South-Central area (around 3 million tonnes), whereas pelagic fish (mainly capelin) was the predominant component along with krill in the North-Central area (Figures 13). 0-group fish contributed roughly the same amount of biomass (0.5 - 0.8 million tonnes) as pelagic fish (0.4 - 0.7 million tonnes) in the Southwestern and South-Central areas (Figure 13). The total biomass in the Southeastern and Eastern areas was lower with about 0.9 and 1.0 million tonnes, respectively, dominated by pelagic fish (mainly herring and polar cod). The total biomass

39

in the Svalbard area was 2.5 million tonnes on average, with krill as the dominant component (Figures 13).
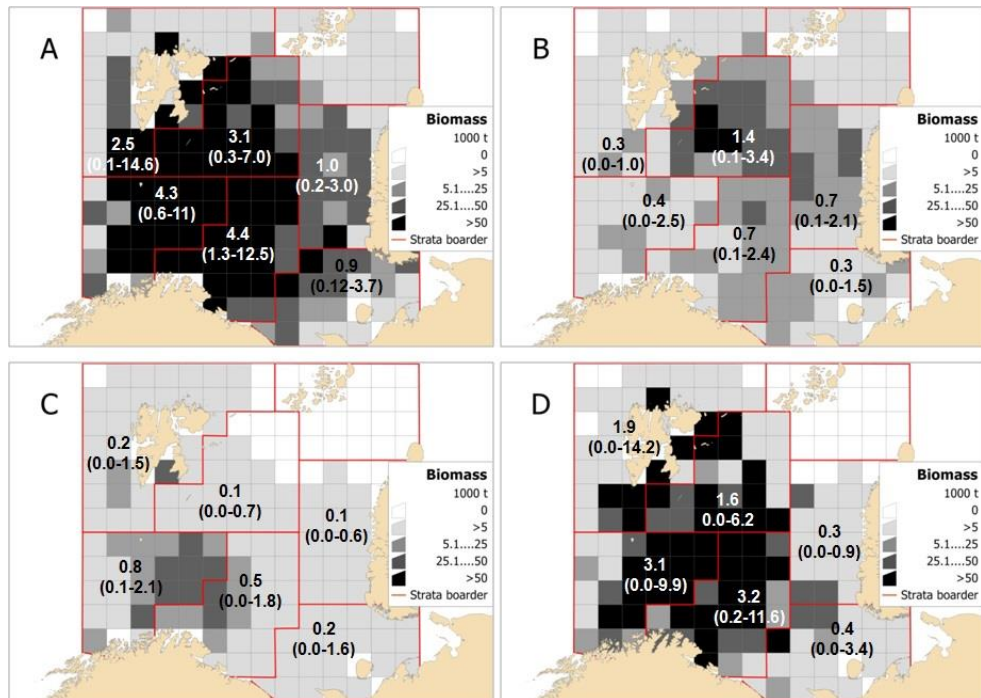


Figure 13. Spatial distribution of mean biomass densities ($10^3$ tonnes wet weight per 60*60 nm$^2$ grid cell; light/dark grey, more intensive coloring indicates denser concentrations) and total average biomass values (million tonnes) for the six subareas (red lines). A- Total biomass for all components of the pelagic compartment, B- Biomass of pelagic fishes, C- Biomass of 0-group fishes, and D- biomass of macrozooplankton, mostly krill. The mean biomass values are for the period 1993-2013 with the range of annual estimates for the subareas shown in parentheses.

The significant spatial structure is consistent with spatial life cycle closure and the advection of fish larvae, juveniles and zooplankton with the Atlantic inflow, in addition to relatively consistent geographic patterns in primary production within the Barents Sea. The Southwestern, South-Central and North-Central areas are the most productive areas and pelagically distributed biomasses increased at least twice during the warming period and the role of advection is important in supplying plankton, fish larvae with the inflowing Atlantic water.

Finally, biomass time series which were established in Paper VIII, basing on gridded data of pelagic catches and acoustic measurements for the period 1993-2013, were included in study of the overall state and trends of the pelagic compartment of the Barents Sea ecosystem. The results shown as an anomaly trend plot in Figure 14, indicates increasing trends for a little over half of the variables (shifting from

green to red in the upper part of the plot, including five abiotic variables), while another about 1/3 of the variables show the opposite trend (shifting from red to green in the lower part of the plot).

**Barents Sea time series**
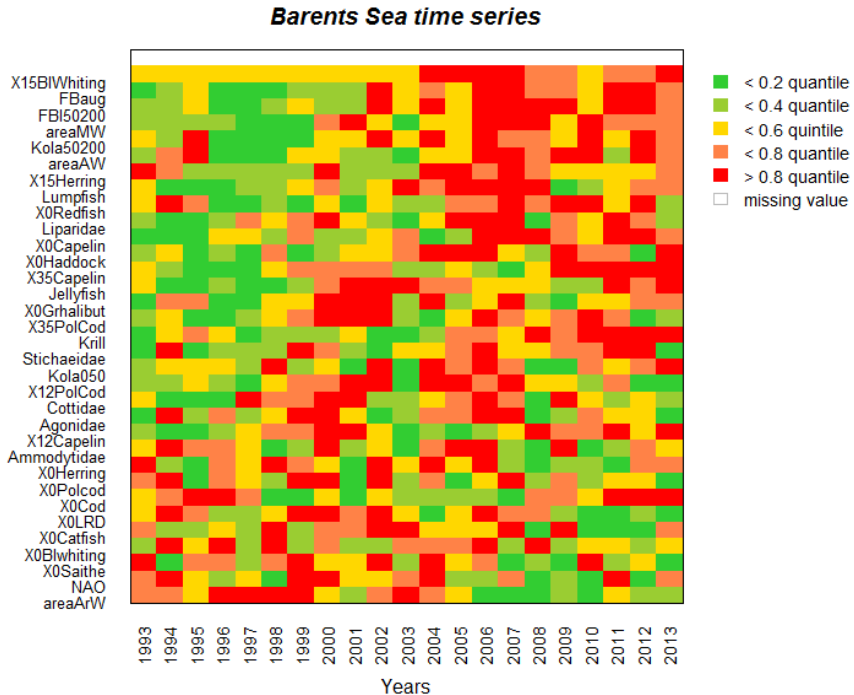


Figure 14. Temporal trend plots of 25 biological variables (biomass of macrozooplankton, pelagic fish and 0-group fish) and 8 physical variables (NAO index, modelled water fluxes, area of water masses and water temperatures) used in PCA analysis for the period 1993-2013. The variables are standardised as anomalies (zero mean and unit SD) and shown with red (positive deviations) and green (negative) deviations.

## 3.6 Species interactions and response to the warming

The Barents Sea pelagic system is relatively simple, in the sense that there are a limited number of species that play dominant roles as actors in the drama that unfolds on the ecosystem scene (Paper VIII). Yet, it is sufficiently complex, due to the many interactions and time-delayed species responses, and therefore difficult to unravel direct and indirect effects, propagating through the system through trophic interactions, of climate variability in this ecosystem.

Euphausiids play a significant role in the Barents Sea ecosystem, being a major prey to many species of fish, marine mammals and seabirds, thus constituting a crucial link in energy transport between lower and top trophic levels (Skjoldal and Rey 1989; Folkow *et al.* 2000; Haug *et al.* 2002, Dalpadado and Bogstad 2004; Orlova *et al.* 2001; Orlova *et al.* 2006; Dolgov *et al.* 2011a, b; Dalpadado and Mowbray 2013; Bogstad *et al.* 2015). Capelin has, at least in some periods, a great impact on the krill population in the Barents Sea, demonstrated by the inverse relationship between capelin and krill abundances

(Drobysheva 1994, Drobysheva and Nesterova 1996, Dalpadado and Skjoldal 1996, Dolgov *et al*. 2011b, Dalpadado and Mowbray 2013, ICES 2016). This inverse relationship was also evident in the analysed time series in Papers II and VIII. However, the strong impact by capelin has weakened in recent years, possibly due to a larger inflow of Atlantic water with more krill into the Barents Sea (Orlova *et al*. 2013, 2015, Paper VIII). Also 0-group cod may have a large predatory effect on the krill population due to its wide distribution and high abundance, at least in some years. In recent years, overlap between high densities of 0-group cod and krill increased, and estimated euphausiid consumption by 0-group cod increased from 7 from 2008  to 13 million tonnes in 2012 (Dolgov *et al*. 2015). As krill have been abundant and widely distributed in the Barents Sea in the recent years it has been available and ensuring good feeding conditions for many predator species (Figure 7H, Paper VIII, IX). Also jellyfish increased from 1980 to 2013, although the fluctuations in abundance were large throughout this period (Paper III, Prokhorova *et al*. 2013, and Eriksen *et al*. 2014). Jellyfish populations share the pelagic environment with many small planktivorous fishes, such as pelagic fish and 0-group fish (Brodeur *et al*. 2008; Paper III). The co-locations of high biomasses of fish, krill and jellyfish indicate highly productive areas in the Barents Sea, most likely defined by ocean currents (Eriksen 2015). However, catches of some species appeared to level off or decrease when catches of jellyfish were exceptionally high (Paper III, Eriksen 2015), which could indicate negative impact by jellyfish through trophic interactions. However, their role and place in the food web in the Barents Sea is still uncertain, and should be studied further.

Variable recruitment of fish stocks is a major source of variability in stock development and thus for the dynamics of the Barents Sea ecosystem. The biomass of 0-group fish contributes directly to the pelagic biomass when they are present as a plankton-feeding component in the water column (Paper VIII) and subsequently as juveniles and adults over the next years. The wide geographical distribution of 0-group fish (Paper IV, V and VIII, Figure 9 A- J) and their high abundances makes them important contributors to energy transfer between trophic levels and also between different geographic areas, thus playing an important role in the Barents Sea ecosystem (Paper V and VIII). Distribution of 0-group cod, haddock, herring and capelin generally increased from 1980s to 2000s, while only capelin showed a north-eastern shift of centre of gravity (Paper V). Young herring may have a strong predatory impact on capelin larvae, possibly causing recruitment failure and stock collapses of capelin (Gjøsæter and Bogstad 1998, Huse and Toresen 2000, Gjøsæter *et al*. 2009, Hallfredsson and Pedersen, 2007, Gjøsæter *et al*. 2015). The northward shift in the 0-group capelin distribution may have reduced the overlap with young herring (age 1+), which in turn can have a positive effect on capelin recruitment. Higher temperatures in summer-autumn could lead to worse conditions (less area of core thermal habitat) for 0-group polar cod, and decreased ice cover in winter provides less suitable habitat for spawners and eggs. The eggs are floating near the surface, may be exposed to unstable temperatures and increased water mixing when the ice cover is poor, which may have already resulted in reduced abundance (Paper VI and VIII).

The pelagic species capelin, herring and polar cod, mainly plankton-feeders, constitute important links between lower and higher trophic levels in the Barents Sea ecosystem (Skjoldal and Rey 1989, Dolgov *et al.* 2011b). The capelin stock dominated among the pelagic fish in most years. The Barents Sea capelin stock has undergone drastic changes in size during the last three decades. Three stock collapses were caused by poor recruitment, most likely in combination with low growth and increased predation pressure (the first two) and high natural mortality (the third collapse, Gjøsæter *et al.* 2009). The occurrence of strong year classes (2006-2013) and ability of juveniles to track a redistribution of thermal habitat (see above) indicated that the capelin stock development is adjusting to the warmer climate (Paper VIII) and sustain the heavy predation from the current large cod stock (ICES 2016). However, significant decrease in the polar cod stock may increase the predation pressure on capelin. Furthermore, reduced food availability due to downgrazing of the largest plankton organisms in the capelin area, reduced abundances of arctic zooplankton species (ICES 2016) and longer feeding and spawning migrations to southern coastal areas may all challenge the capelin stock development in the coming years.

Polar cod biomasses decreased from 1980s to 2000s (Paper VIII). Decrease of ice cover in winter provides less suitable habitat for spawners (Paper VI). While polar cod shifted eastwards over the sampling period, no significant changes in the condition of adults were observed, indicating a high degree of adaptability of *Gadidae* to changes in the environment and enough available food resources (ICES 2016). However, the polar cod experienced increased overlap with cod in recent years, increasing the predation pressure (ICES 2016). These factors may very well contribute to the negative trends in polar cod abundance in the latter years, in addition to the loss of suitable spawning habitat (Paper VI, VIII, ICES 2016). As a key species in the Arctic, the polar cod stock decline could cause structural reorganization of the Arctic food chain/web (Hop and Gjøsæter 2013, Paper VIII).

Juvenile herring of the Norwegian spring spawning stock grow up and spend the first 3-4 years of their life in the southern Barents Sea before they leave to join the adult stock in the Norwegian Sea (Marty 1956, Krysov and Røttingen 2011). Blue whiting is a widely distributed stock and occasionally come into the south western Barents Sea as in 2004 when the conditions were warm and the stock was large (Heino *et al.* 2008, Belikov *et al.* 2011). Both juvenile herring and blue whiting contributed significantly to the high pelagic fish biomass in 1993, 2000 and 2004-2005, and mostly in the Southwestern and South-Central subareas. At the same time the biomass of krill decreased in the Southwestern subarea (Paper VIII). As both herring and blue whiting prey on krill, and as summer-early autumn is a period of intensive feeding (reviewed by Dolgov *et al.* 2011b), the inverse relationship (Pearson $r = -0.43$ (herring), $r = -0.38$ (blue whiting) and $r = -0.49$ (combined herring and blue whiting) between these two pelagic stocks and krill indicate that they may reduce the krill biomass in the southwestern Barents Sea.

# 4   Conclusions

Even with modern research vessels, equipment and methods, monitoring limitations remain, and further development of survey equipment and observation methods, and testing new equipment and methods is needed for proper (effective, optimal for the main components, synoptic, and covering key ecosystem components) monitoring, and therefore should be prioritized.

Huge amounts of data have been collected during the autumn surveys and are available from IMR and PINRO databases. The databases have been updated, and quality checked data are available for the scientific community. The data are unique due to the long, uninterrupted and standardized monitoring approach, and useful for studies of species, communities and ecosystem responses to climate change, including changes in species distributions, recruitment and production, species overlaps and trophic interactions. The long-term data sets and time series give new insights to the dynamics of the pelagic compartment and contribute significantly to our understanding of ecosystem structure and functionality and responses to climate change, thereby supporting an ecosystem-based management of this system.

The recent warming affected the pelagic compartment in different ways. First: changes in oceanographic conditions, including increased temperature and area of Atlantic and mixed water, decreased area of Arctic water and possibly a redistribution of Atlantic water between the two branches, led to a redistribution of some 0-group fish and other pelagic components. Second, the biomass of different components of the pelagic compartment increased over the period, which can partly be explained by the warming. If the warming continues, the arctic species, including polar cod, is likely to decline due to decreasing suitable habitats within the Barents Sea, while the boreal species is likely to track the expansion of the warmer Atlantic water masses, pushing the northern limit of their distribution range. Thus, overlap between boreal and arctic species increase in the northern parts, possibly increasing the food competition between the species. Similar changes have also been reported for the demersal fish compartment (Fossheim *et al.* 2015). In conclusion, it is evident that the pelagic compartment has undergone large changes in two last decades in going from a colder to a warmer temperature regime and from a low to high productive pelagic compartment. The results presented support the general expectations under a climate change; increased production in the northern marine systems, and contraction and decline of arctic species while boreal species expand their distributions.

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# 6    Appendix

## 6.1    The Barents Sea 0-group strata system
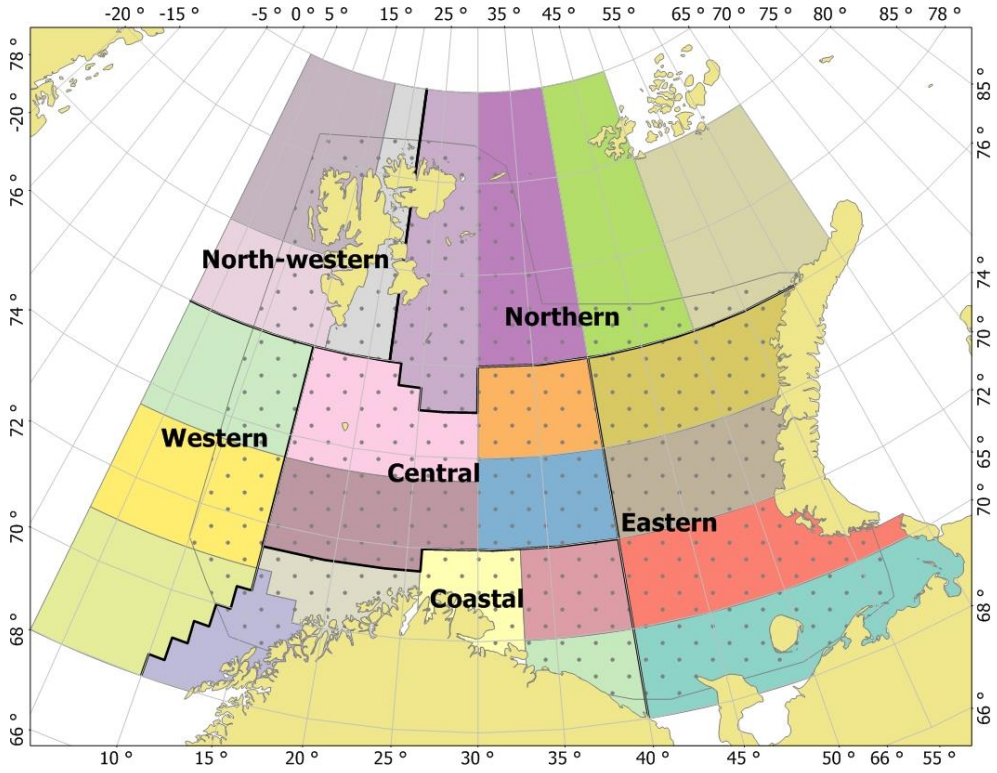


Figure 6.1.1. The Barents Sea 0-group strata system, which consists of 23 strata shown in different colours. Some strata were combined into the larger the north-western, northern, western, central, eastern and coastal areas and used in Paper III and IV. 0-group survey coverage area is shown by dots.

## 6.2 Plankton biomass variation in the Barents Sea
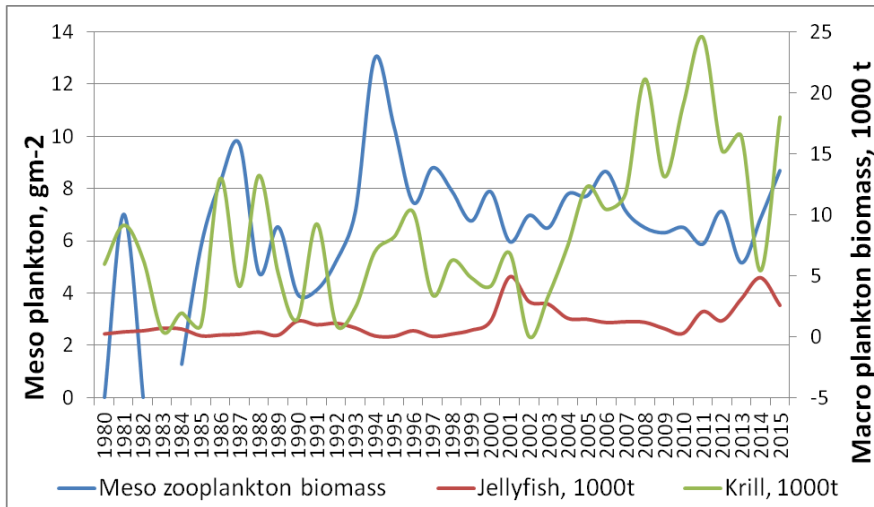


Figure 2. Biomass of meso plankton (<2000 my) in gm$^{-2}$ and macro plankton (krill and jellyfish (mostly *Cyanea capillata*) in 1000 tonnes in the Barents in August, 1980-2015.

## 6.3    0-group fish abundance indices
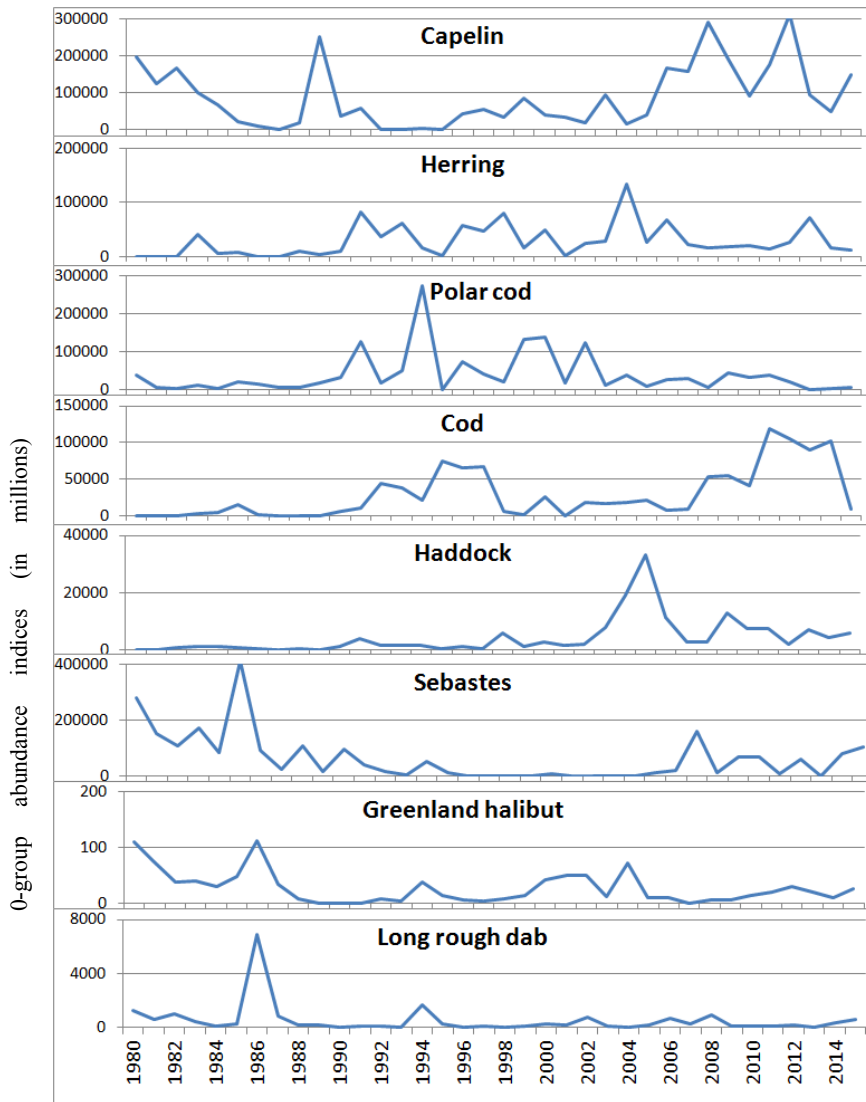


Figure 3. 0-group abundance indices (in millions), not corrected for capture efficiency. Indices taken from the survey reports 2015 (http://www.imr.no/filarkiv/2015/11/5_1_monitoring_the_pelagic_fish_community-fish_recruitment-final.pdf/nb-no)

## 6.4 Small non-commercial fish abundance indices
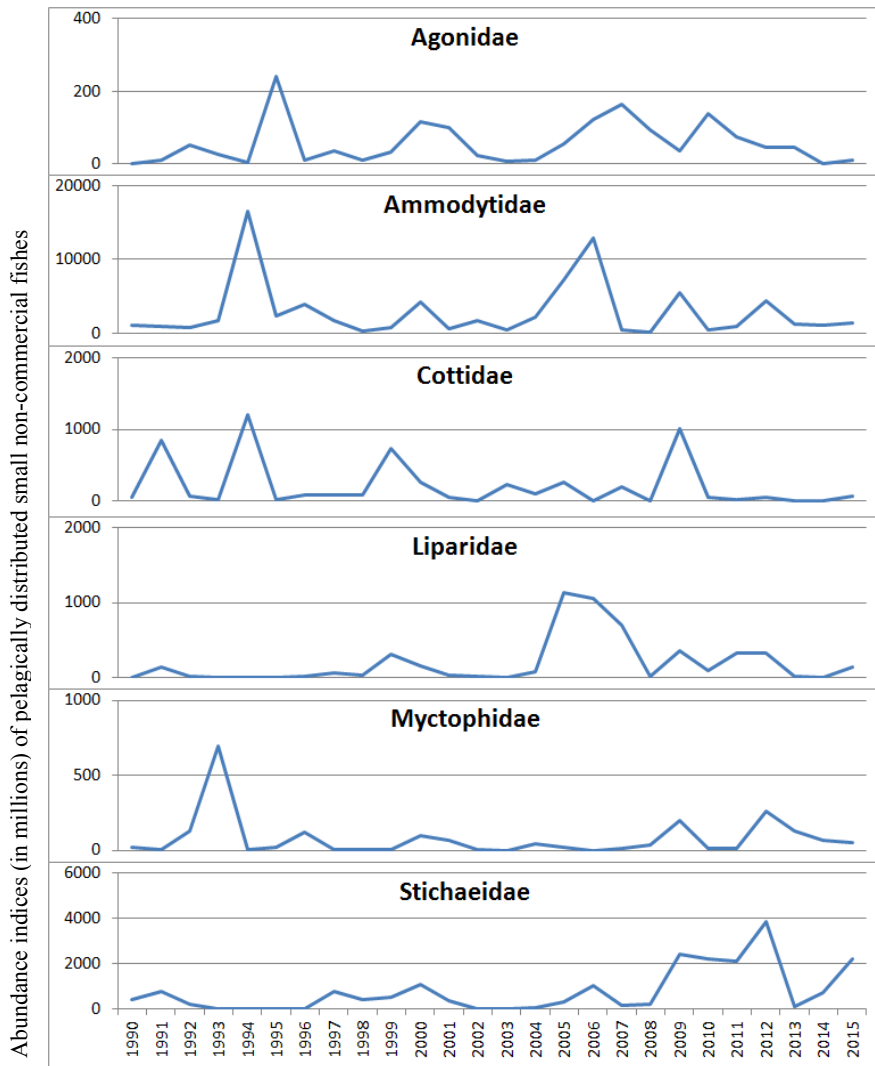


Figure 5. Abundance indices (in millions) of pelagically distributed Agonidae, Ammotydae, Liparidae, Cottidae, Myctophidae and Stichaeidae in August-September 1990-2015. Indices taken from the survey reports 2015 (http://www.imr.no/filarkiv/2015/11/8_3_small_non-target_fish_species.pdf/nb-no)

# 6.5 Trend test

**Mann-Kendall test**   There is a statistically significant increasing trend (<0.05)   Sigificance level of 0.1

**Enviromental parameters**

| | Kola050 | Kola50200 | FBI50200 | NAO | FBaug | areaAW | areaMW | areaArW | BSO-Q2-3 | BS-SH-Q2- | KS-Q2-3 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| S : | 29 | 72 | 101 | -52 | 106 | 75 | 94 | -94 | -21 | -3 | -39 |
| Z : | 0.85005 | 2.1591 | 3.0576 | 1.5433 | 3.1707 | 2.2356 | 2.8083 | 2.8083 | 0.60421 | 0.060421 | 1.148 |
| p trend): | 0.3953 | 0.03084 | 0.002231 | 0.12275 | 0.001521 | 0.025379 | 0.00498 | 0.00498 | 0.5457 | 0.95182 | 0.25097 |

**Biological parameters**

| | 0Herring | 0Capelin | 0Cod | 0Haddock | 0Polcod | 0Redfish | 0Grhalibut | 0LRD | 0Catfish | 0Blwhiting | 0Saithe | Jellyfish | Krill | Agonidae | Liparidae | Ammodyti | Cottidae | Stichaeida | Lumpfish | 1-2Capelin | 3-5Capelin | 1-2PolCod | 3-5PolCod | 1-5Blwhiti | 1-5Herring |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S : | -18 | 102 | 16 | 64 | -30 | 52 | 25 | -60 | -18 | -22 | -46 | 58 | 86 | -9 | 56 | -20 | 12 | 77 | 80 | 78 | 96 | 6 | 40 | | -44 |
| Z : | 0.51335 | 3.0499 | 0.45295 | 1.9024 | 0.87571 | 1.54 | 0.72727 | 1.7832 | 0.51444 | 0.80256 | 1.3589 | 1.7212 | 2.5667 | 0.24242 | 1.6623 | 0.57374 | 0.33349 | 2.296 | 2.3856 | 2.3252 | 2.8687 | 0.15098 | 1.1777 | | 2.62E+00 |
| p trend): | 0.60771 | 0.002289 | 0.65058 | 0.057118 | 0.38119 | 0.12355 | 0.46706 | 0.074546 | 0.60694 | 0.42223 | 0.17419 | 0.08521 | 0.010266 | 0.80845 | 0.096443 | 0.56614 | 0.73877 | 0.021675 | 0.017053 | 0.020063 | 0.004122 | 0.87999 | 0.23892 | | 0.008706 |

**CoG west-estern direction**

| | 0Herring | 0Capelin | 0Cod | 0Haddock | 0Polcod | 0Redfish | 0Grhalibut | 0LRD | 0Catfish | 0Blwhiting | 0Saithe | Jellyfish | Krill | Agonidae | Liparidae | Ammodyti | Cottidae | Stichaeida | Lumpfish | 1-2Capelin | 3-5Capelin | 1-2PolCod | 3-5PolCod | 1-5Blwhiti | 1-5Herring |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S : | 26 | -46 | -2 | -2 | 80 | 30 | 9 | 40 | -34 | 17 | -12 | 46 | 62 | 48 | 7 | 20 | 29 | 51 | -50 | -4 | -26 | 92 | 82 | -8 | 48 |
| Z : | 0.75492 | 1.3589 | 0.030197 | 0.030197 | 2.3856 | 0.87571 | 0.24198 | 1.1777 | 0.9965 | 0.51329 | 0.33217 | 1.3589 | 1.842 | 1.4193 | 0.18126 | 0.57374 | 0.8459 | 1.5105 | 1.4796 | 0.090591 | 0.75492 | 2.7479 | 2.446 | | 1.4635 |
| p trend): | 0.4503 | 0.17419 | 0.97591 | 0.97591 | 0.017053 | 0.38119 | 0.8088 | 0.23892 | 0.31901 | 0.60775 | 0.73976 | 0.17419 | 0.065473 | 0.15582 | 0.85616 | 0.56614 | 0.39761 | 0.13091 | 0.13897 | 0.92782 | 0.4503 | 0.005998 | 0.014447 | -0.31509 | 0.14333 |

**CoG north-south direction**

| | 0Herring | 0Capelin | 0Cod | 0Haddock | 0Polcod | 0Redfish | 0Grhalibut | 0LRD | 0Catfish | 0Blwhiting | 0Saithe | Jellyfish | Krill | Agonidae | Liparidae | Ammodyti | Cottidae | Stichaeida | Lumpfish | 1-2Capelin | 3-5Capelin | 1-2PolCod | 3-5PolCod | 1-5Blwhiti | 1-5Herring |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S : | 30 | 64 | 28 | 28 | -16 | 12 | 73 | -12 | 50 | 21 | -6 | 66 | 16 | 78 | 80 | -16 | 15 | -10 | 46 | 18 | 52 | -50 | -62 | 2 | -13 |
| Z : | 0.87571 | 1.9024 | 0.81532 | 0.81532 | 0.45295 | 0.33217 | 2.3372 | 0.33217 | 1.4796 | 0.64161 | 0.15098 | 2.1089 | 0.48666 | 2.4982 | 2.5631 | 0.45295 | 0.42295 | 0.292 | 1.3589 | 0.51335 | 1.54 | 1.4796 | 1.842 | | |
| p trend): | 0.38119 | 0.057061 | 0.41489 | 0.41489 | 0.65058 | 0.73976 | 0.019428 | 0.73976 | 0.13897 | 0.52113 | 0.87999 | 0.034955 | 0.6265 | 0.012482 | 0.010374 | 0.65058 | 0.67233 | 0.77029 | 0.17419 | 0.60771 | 0.12355 | 0.13897 | 0.065473 | 0.431 | 0.92802 |

**I**

# Paper I

*An evaluation of 0-group abundance indices of Barents Sea fish stocks*

# An Evaluation of 0-Group Abundance Indices of Barents Sea Fish Stocks

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**Abstract:** The International 0-group fish survey in the Barents Sea (1965-2002) aimed to give initial indication of the recruiting year class strengths. Since 2003 the 0-group survey has been a part of a Joint Norwegian-Russian ecosystem survey of the Barents Sea, conducted by IMR (Norway) and PINRO (Russian Federation). The electronic 0-group databases were missing some data and contained errors, therefore the databases have been quality checked and corrected for the period 1980-2006. Two separate sets of 0- group indices were re-estimated, both with and without correction for capture efficiency, using a stratified sample mean approach, and 0-group indices were correlated with other appropriate abundance indices. The exclusion of errors from the database has improved our confidence in the indices and analysis. In general, the 0-group indices seem to be reliable predictors of year class strengths and are adequate to use as input in stock assessment-models and recruitment studies.

**Key Words:** 0-group fish, abundance, Barents Sea, recruitment.

## INTRODUCTION

The knowledge of the size of the recruiting year classes is an important contribution for a successful assessment. The main goal with the Joint International 0-group fish survey has been to give an initial indication of year class strength of the commercially important fish stocks in the Barents Sea. The survey has been conducted since 1965 by the Institute of Marine Research, (IMR), Norway, the Polar Research Institute of Marine Fisheries and Oceanography (PINRO), Russia, and the United Kingdom (up until 1976). Since 2003 the 0-group survey has been a part of a Joint Norwegian-Russian ecosystem survey of the Barents Sea [1].

The 0-group survey has been carried out annually during August-September. In 1980 a standard trawling procedure was recommended by ICES [2, 3] and has since been used on Norwegian and Russian vessels. The standard procedure consists of predetermined tows at three or more depths, each of 0.5 nautical mile, with the head-line at 0, 20 m, 40 m and so on.

Developing methods for estimating year class strength/abundance has been an urgent task during the whole investigation period 1965-2006. The possibility of estimating abundance of 0-group fish, using echo-sounder was presented by Dragesund and Olsen [4]. Nakken and Raknes [5], improved the "area index" method [6], and this method is still in use. The "logarithmic index" method, developed by

Randa [7], was used until 2004. Dingsør [3] applied the "stratified sample mean" method and calculated the 0-group indices, this procedure was further developed [8] and is now the standard method for establishing the 0-group indices in the Barents Sea. In 2005 two separate sets of indices were estimated, both with and without correction for capture efficiency (called as old indices here).

The biological data collected during the survey is the basis for estimation of fish abundances. Thus, the quality of the collected data will influence the results and conclusions. After the survey, the collected data were exchanged between the Institutes. Before computer techniques were common, hand-written data were exchanged. In later years, data have been exchanged in electronic form. IMR and PINRO were responsible for punching of the historical hand-written data, from which two databases were established. The first aim for this work is to recalculate the 0-group abundance indices using a scrutinized and corrected database.

Several studies have compared the 0-group abundance indices with other abundance indices of early and later life stages. Gundersen and Gjøsæter [9] found significant correlation between 0-group and 1-group indices of capelin, but no correlation between larval indices and 0-group nor 1-group indices. The suggested explanation to this was a high mortality during the first months of capelins life. Helle *et al.* [10] found significant correlation between 0-group indices of cod and spawning-stock biomass (SSB) and acoustic survey abundance indices (WA). The second aim of this work is to compare the new indices with other year class estimates of the most important commercial species.

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## MATERIALS AND METHODS

### Recalculation of 0-Group Indices

Information in the databases was compared with the hand-written data and between the databases. The database was updated and errors were corrected. The corrected datasets (1980-2006) were used to re-estimate the 0-group indices of Barents Sea capelin *Mallotus villosus*, Norwegian spring spawning herring *Clupea harengus*, Northeast Arctic cod *Gadus morhua*, Northeast Arctic haddock *Melanogrammus aeglefinus*, Northeast Arctic saithe *Pollachius virens*, redfish *Sebastes* spp., Greenland halibut *Reinhardtius hippoglossoides*, long rough dab *Hippoglossoides platessoides*, and two populations (western and eastern) of polar cod *Boreogadus saida*. These indices, which are given both with and without correction for capture efficiency, are calculated by the method of stratified sample mean.

The number of fish per square nautical mile, $\rho_{s,l}$, of length, $l$ (in 1cm groups), at each station, $s$, are estimated by the following equation

$$\rho_{s,l} = \frac{f_{s,l} \cdot Keff}{a_s} \qquad (1)$$

where $f_{s,l}$ is the observed number of fish in lengthgroup $l$ at station $s$, $Keff$ is the correction functions defined below ($Keff=1$ when not correcting for capture efficiency), and $a_s$ is the swept area found by

$$a_s = \frac{d_s \cdot ws}{1852} \qquad (2)$$

where $ws/1852$ is the wingspread of the trawl converted into nautical mile and $d_s$ is the effective trawl distance found by total distance trawled divided by the number of depth layers [11].

The stratified swept area estimate, is given by

$$\bar{y}_{st} = \sum_{i=1}^{N} A_i \bar{y}_i \qquad (3)$$

where $N$ is the number of area-strata, $A_i$ is the covered area in the $i$-th stratum, and $\bar{y}_i$ is the average density in stratum $i$ given by

$$\bar{y}_i = \sum_s \sum_l \rho_{s,l} / n_i \qquad (4)$$

where $n_i$ is the number of stations in stratum $i$. The full description of the stratified sample mean method was published in volume 2 of the 2004 survey report [8].

Capture efficiency of pelagic trawl is highly selective for 0-group fish [12, 13], and the selectivity depends on species and fish length. Length correction functions, $Keff$, for trawl capture efficiency have been estimated by regressions between fish densities from simultaneous trawl and acoustic estimates of relatively "pure" concentrations [14]. By "pure" concentrations, we mean that only one species dominates the catches. Correction functions for three species types are:

$$Keff_{gadoids} = 17.065*\exp(-0.1932*l) \qquad (5)$$

$$Keff_{capelin} = 7.2075*\exp(-0.1688*l) \qquad (6)$$

$$Keff_{herring} = 357.23*\exp(-0.6007*l) \qquad (7)$$

where $l$ is the observed length in cm. Unfortunately, because of the requirement of "pure" concentrations, there are no correction functions available for other species.

### Comparing 0-Group Indices

A comparison of abundance estimates of Barents Sea fish at larval, 0-group, 1-group stages and recruitment for the year classes 1980-2005 will give an indication of abundance variation through the different life stages. The indices included in the analysis and general information about the surveys and the periods in which they were conducted are given in Table **1**.

Pearson's correlation was estimated to determine if the relative abundance of 0-group fish is proportional to its relative abundance at an earlier or later life stage. Pearson's r reflects the degree of linear relationship between two variables. It ranges from +1 to -1, a correlation of +1 means that there is a perfect positive linear relationship between variables. However, it is important to keep in mind that biases in the surveys will influence the results [3, 12], i.e. variable biases will weaken the correlations. 0-group indices (0grI) were correlated with the "area index" (AI), capelin larval index (LI), 1-year old abundance indices or estimate (1grE), bottom trawl index (WBT), acoustic index (WA), age-3 recruits (3R), maturing biomass (MB) and spawning stock biomass (SSB) (Table **1**). In addition a regression analysis was performed to describe ability of 0-group indices to predict 1 and 3 years old fish abundance. The correlations between 0-group indices of capelin, herring, cod, haddock, and saithe were also analyzed.

## RESULTS

### Recalculation of 0-Group Indices

The Norwegian and Russian 0-group databases containing twenty-six years of survey-data were quality checked. The main reason for a mismatch between the databases was punching errors and lack of specific test-programs to detect errors before the data are entered into the database.

New indices with and without length correction of 0-group capelin, herring, cod, haddock, saithe, polar cod, redfish, Greenland halibut and long rough dab were calculated for the period 1980- 2006 (Table **2**).

The recalculated 0-group indices showed some differences (Table **3**) from the old indices [1], and these differences varied between species. 0-group indices of capelin, herring, redfishes and Greenland halibut had the largest changes, and four year classes (1980, 1982, 1995 and 2001) of the eastern population of polar cod were missing in the old indices.

### Comparison of 0-group Indices

The Fig. (**1**) shows time series of 0-group abundance (0grI and 0grIK) and abundance of older fish for capelin, herring, cod, haddock, and saithe.

**Table 1. Summary of the Datasets Included in the Study**

| Index | Species | Abbreviation | Age, Month | Time Series | Survey | Covered Area/Time | Sampling GEAR | Ref. |
|---|---|---|---|---|---|---|---|---|
| Capelin larval Index | Capelin | LI | 0-1 | 1981-2005 | Capelin larval survey up to 2002, later the Barents Sea Ecosystem Survey (spring) | Norwegian coast and up to 74°N- June | GULF-III | [15] |
| 0-group area index | Capelin, cod and haddock. Herring | AI | 5-6 | 1980-2005 1993-2005 | 0-group fish survey | Barents Sea -August- September | Midwater trawl | [5, 15] |
| New 0-group fish indices | All analyzed species | 0grI and 0grIK | 5-6 | 1980-2005 | 0-group fish survey up to 2003, later the Barents Sea Ecosystem Survey (autumn) | Barents Sea -August -September | Midwater trawl | |
| Age-1 abundance index | Capelin | 1grI | 16 | 1980-2005 | Autumn capelin survey up to 2003, later the Barents Sea Ecosystem Survey (autumn) | Barents Sea -August -September | Midwater, bottom trawls, acoustic | [17] |
| Age-1 abundance estimate | Herring | 1grE | 12 | 1980-2004 | | Barents Sea | | [15, 16] |
| Age-3 abundance, VPA | Cod, haddock and saithe | 3R | 36 | 1980-2003 | | Barents Sea | | [17] |
| Winter bottom trawl indices | Cod and haddock | WBT | 10 | 1980-2005 | The Barents Sea demersal fish survey | Barents Sea -February | Shrimp trawl (bottom trawl) | [17, 18] |
| Winter acoustic indices | Cod and haddock | WA | 10 | 1980-2005 | The Barents Sea demersal fish survey | Barents Sea -February | Shrimp trawl (bottom trawl) | [17, 18] |
| Spawning stock biomass (VPA) | Cod and saithe Herring | SSB | | 1980-2005 1980-2004 | | Barents Sea Norwegian Sea | | [15, 17] |
| Maturing biomass, in 1.October | Capelin | MB | | 1980-2005 | Autumn capelin survey up to 2003, later the Barents Sea Ecosystem Survey (autumn) | Barents Sea -August -September | Midwater trawl | [15] |

Indices of 0-group capelin, herring, cod, haddock, and saithe without length correction (0grI) were compared with length corrected indices (0grIK), using Pearson's correlation. There were significant linear correlations between 0grI and 0grIK, with high values of Pearson's r; 0.91 (herring), 0.95 (saithe), 0.98 (cod) and 0.99 (haddock and capelin).

Table **4** contains the estimated Pearson's correlation between 0-group indices and other available indices (Table **1**). Highly significant correlations were found between the new 0-group indices (0grI and 0grIK) and the area index (AI) for all species, with Pearson's r between 0.80 and 0.89.

**Capelin** The new capelin 0-group indices varied some from the old indices [1], and shows that the old indices underestimated the 1987, 1992, 1995, and 2001 year classes, while the 1988, 1994, and 2003 year classes were overestimated (Table **3**).

We found a significant linear correlation between capelin 0-group and 1-group indices, but weaker correlation with the larval index and the maturing biomass (Table **4**). The relationship between 0-group and 1 group (1grI) of capelin can be described by regressions

$$1grI = 40.697 + 0.0027*0grI \quad (R^2 = 0.668, p < 0.01)$$

$$1grI = 47.523 + 0.0008*0grIK \quad (R^2 = 0.652, p < 0.01)$$

**Herring** The new herring 0-group indices (0grI) varied some from the old indices [1]. The 1982, 1984, and 1990 year classes were underestimated, while 1980, 1986, 1994, and 1995 were slightly overestimated (Table **3**). The largest changes (in percentage) were observed in the years with low herring abundance. 0-group index without length correction (0grI) had stronger correlation with 1-group indices than 0grIK had. However, both 0grI and 0grIK had a significant linear correlation with 1grE and SSB (Fig. **1** and Table **4**).

The relationship between 0-group and 1 group (1grE) of herring can be described by regressions

$$1grE = 15.543 + 0.0015*0grI \quad (R^2 = 0.560, p < 0.01)$$
$$1grE_I = 29.959 + 0.0002*0grIK \quad (R^2 = 0.277, p = 0.01)$$

**Table 2. Abundance Indices (in Millions) of 0-Group Fish in the Barents Sea, without (0grI) and with (0grIK) Correction for Catching Efficiency**

| Species Year | Capelin | | Cod | | Haddock | | Herring | | Redfish | Saithe | | Gr. Halibut | LRD | Polar Cod (East) | | Polar Cod (Eest) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0grI | 0grIK | 0grI | 0grIK | 0grI | 0grIK | 0grI | 0grIK | 0grI | 0grI | 0grIK | 0grI | 0grI | 0grI | 0grIK | 0grI | 0grIK |
| 1980 | 197278 | 740289 | 72 | 276 | 59 | 265 | 4 | 77 | 277873 | 3 | 21 | 111 | 1273 | 28958 | 203226 | 9650 | 82871 |
| 1981 | 123870 | 477260 | 48 | 289 | 15 | 75 | 3 | 37 | 153279 | 0 | 0 | 74 | 556 | 595 | 4882 | 5150 | 46155 |
| 1982 | 168128 | 599596 | 651 | 3480 | 649 | 2927 | 202 | 2519 | 106140 | 143 | 296 | 39 | 1013 | 1435 | 1443 | 1187 | 10565 |
| 1983 | 100042 | 340200 | 3924 | 19299 | 1356 | 6217 | 40557 | 195446 | 172392 | 239 | 562 | 41 | 420 | 1246 | 1246 | 9693 | 87272 |
| 1984 | 68051 | 275233 | 5284 | 24326 | 1295 | 5512 | 6313 | 27354 | 83182 | 1339 | 2577 | 31 | 60 | 127 | 871 | 3182 | 26316 |
| 1985 | 21267 | 63771 | 15484 | 66630 | 695 | 2457 | 7237 | 20081 | 412777 | 12 | 30 | 48 | 265 | 19220 | 143257 | 809 | 6670 |
| 1986 | 11409 | 41814 | 2054 | 10509 | 592 | 2579 | 7 | 93 | 91621 | 1 | 4 | 112 | 6846 | 12938 | 102869 | 2130 | 18644 |
| 1987 | 1209 | 4032 | 167 | 1035 | 126 | 708 | 2 | 49 | 23747 | 1 | 4 | 35 | 804 | 7694 | 64171 | 74 | 631 |
| 1988 | 19624 | 65127 | 507 | 2570 | 387 | 1661 | 8686 | 60782 | 107027 | 17 | 32 | 8 | 205 | 383 | 2588 | 4634 | 41133 |
| 1989 | 251485 | 862394 | 717 | 2775 | 173 | 650 | 4196 | 17956 | 16092 | 1 | 10 | 1 | 180 | 199 | 1391 | 18056 | 164058 |
| 1990 | 36475 | 115636 | 6612 | 23593 | 1148 | 3122 | 9508 | 15172 | 94790 | 11 | 29 | 1 | 55 | 399 | 2862 | 31939 | 246819 |
| 1991 | 57390 | 169455 | 10874 | 40631 | 3857 | 13713 | 81175 | 267644 | 41499 | 4 | 9 | 1 | 90 | 88292 | 823828 | 38709 | 281434 |
| 1992 | 970 | 2337 | 44583 | 166276 | 1617 | 4739 | 37183 | 83909 | 13782 | 159 | 326 | 9 | 121 | 7539 | 49757 | 9978 | 80747 |
| 1993 | 330 | 952 | 38015 | 133046 | 1502 | 3785 | 61508 | 291468 | 5458 | 366 | 1033 | 4 | 56 | 41207 | 297397 | 8254 | 70019 |
| 1994 | 5386 | 13898 | 21677 | 70761 | 1695 | 4470 | 14884 | 103891 | 52258 | 2 | 7 | 39 | 1696 | 267997 | 2139223 | 5455 | 49237 |
| 1995 | 862 | 2869 | 74930 | 233885 | 472 | 1203 | 1308 | 11018 | 11816 | 148 | 415 | 15 | 229 | 1 | 6 | 25 | 195 |
| 1996 | 44268 | 136674 | 66047 | 280916 | 1049 | 2632 | 57169 | 549608 | 28 | 131 | 430 | 6 | 41 | 70134 | 588020 | 4902 | 46671 |
| 1997 | 54802 | 189372 | 67061 | 294607 | 600 | 1983 | 45808 | 463243 | 132 | 78 | 341 | 5 | 97 | 33580 | 297828 | 7593 | 62084 |
| 1998 | 33841 | 113390 | 7050 | 24951 | 5964 | 14116 | 79492 | 476065 | 755 | 86 | 182 | 8 | 27 | 11223 | 96874 | 10311 | 95609 |
| 1999 | 85306 | 287760 | 1289 | 4150 | 1137 | 2740 | 15931 | 35932 | 46 | 136 | 275 | 14 | 105 | 129980 | 1154149 | 2848 | 24015 |
| 2000 | 39813 | 140837 | 26177 | 108093 | 2907 | 10906 | 49614 | 469626 | 7530 | 206 | 851 | 43 | 233 | 116121 | 916625 | 22740 | 190661 |
| 2001 | 33646 | 90181 | 908 | 4150 | 1706 | 4649 | 844 | 10008 | 6 | 20 | 47 | 51 | 162 | 3697 | 29087 | 13490 | 119023 |
| 2002 | 19426 | 67130 | 19157 | 76146 | 1843 | 4381 | 23354 | 151514 | 130 | 553 | 2112 | 51 | 731 | 96954 | 829216 | 27753 | 215572 |
| 2003 | 94902 | 340877 | 17304 | 81977 | 7910 | 30792 | 28579 | 177676 | 216 | 65 | 286 | 13 | 78 | 11211 | 82315 | 1627 | 12998 |
| 2004 | 16701 | 53950 | 19157 | 65969 | 19144 | 39303 | 133350 | 773891 | 849 | 1395 | 4779 | 70 | 36 | 37156 | 290686 | 367 | 2892 |
| 2005 | 41808 | 148466 | 21532 | 72137 | 33283 | 91606 | 26332 | 125927 | 12332 | 55 | 176 | 9 | 200 | 6540 | 44663 | 3216 | 25970 |
| 2006 | 166400 | 515770 | 7860 | 25061 | 11421 | 28505 | 66819 | 294649 | 20864 | 142 | 280 | 11 | 710 | 26016 | 182713 | 2078 | 15965 |
| Mean | 62766 | 217010 | 17746 | 68057 | 3800 | 10581 | 29632 | 171320 | 63208 | 197 | 560 | 31 | 603 | 37809 | 309303 | 9106 | 74971 |
| Median | 38144 | 126155 | 9367 | 32846 | 1326 | 4083 | 19642 | 93900 | 14937 | 82 | 277 | 14 | 190 | 11217 | 89595 | 5026 | 46413 |

**Cod** The differences between new and old 0-group abundance indices were larger in 1982, 1986, 1993, 1994, and 2004 than in other years (Table **3**).

Cod 0-group indices were highly correlated with all analyzed indices, except age-3 recruits, and the variation in 0-group abundance was retained through the other indices (Fig. **1** and Table **4**). The regression analyses show no significant relationship between of 0-group and 3 years old cod (3R).

**Haddock** The old 0-group haddock indices was underestimated in 1982, 1986, and 1993 and overestimated in 1980, 1994, and 2001, but differences between old and new indices were small (Table **3**). Haddock 0-group indices were significantly correlated with all analyzed indices (Fig. **1** and Table **4**).

**Table 3. Differences (%) Between Old and New Abundance Indices of 0-Group Fish, without (0grI) and with (0grIK) Correction for Catching Efficiency. If New Indices are 100% Correct, Differences (Diff) Between Old (x) and New (y) can be Describes as Diff=100-((x*100)/y). Negative that the Old Index was Overestimated While Positive Numbers Means that Old Index was Underestimated**

| Species Year | Capelin | | Cod | | Haddock | | Herring | | Redfish | Saithe | | Gr. HALIBUT | LRD | Polar Cod (East) | | Polar Cod (West) | | Mean Year |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0grI | 0grIK | 0grI | 0grIK | 0grI | 0grIK | 0grI | 0grIK | 0grI | 0grI | 0grIK | 0grI | 0grI | 0grI | 0grIK | 0grI | 0grIK | |
| 1980 | -9 | -9 | 8 | -15 | -12 | -16 | -12 | -21 | -2 | 10 | 2 | 48 | 7 | 100 | 100 | -35 | -53 | 5 |
| 1981 | 11 | 10 | -1 | 4 | 3 | 6 | 3 | -1 | -2 | 0 | 0 | 7 | 7 | 49 | 49 | -5 | -5 | 8 |
| 1982 | -7 | -2 | 23 | 26 | 17 | 22 | 17 | 68 | -37 | 4 | 10 | -2 | 15 | 100 | 100 | 74 | 74 | 30 |
| 1983 | -1 | 2 | -1 | 18 | 0 | 28 | 0 | 38 | 69 | -2 | 25 | 5 | -3 | -11 | -13 | 36 | 36 | 13 |
| 1984 | -7 | 39 | -11 | 16 | 1 | 32 | 1 | 33 | 48 | 43 | 61 | 0 | 25 | 3 | 86 | -2 | -2 | 22 |
| 1985 | -12 | -15 | 2 | 5 | 0 | 0 | 0 | -50 | 23 | -13 | -14 | 6 | -6 | -6 | 41 | -4 | -4 | -3 |
| 1986 | -16 | -35 | 9 | 8 | 20 | 20 | 20 | -20 | -17 | -10 | -9 | -2 | -5 | 34 | 38 | 1 | 1 | 2 |
| 1987 | 50 | 43 | 0 | 0 | -2 | -6 | -2 | -1 | -4 | -1 | -1 | -6 | -4 | -1 | -1 | -4 | -3 | 3 |
| 1988 | -32 | -41 | -4 | -4 | -1 | -2 | -1 | -3 | 36 | 4 | 3 | 2 | 3 | -5 | -5 | -2 | -2 | -3 |
| 1989 | -3 | -2 | 0 | 0 | -1 | -2 | -1 | 2 | 0 | 1 | 0 | -20 | 3 | -13 | -15 | 4 | 4 | -3 |
| 1990 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 48 | 2 | 4 | 4 | -64 | 2 | 4 | 3 | -1 | -1 | 0 |
| 1991 | 3 | 3 | -2 | -2 | -3 | -4 | -3 | -1 | 7 | 4 | 2 | -66 | 7 | 29 | 30 | -4 | -4 | 0 |
| 1992 | 88 | 85 | -2 | -2 | -4 | -3 | -4 | -6 | 0 | -2 | -2 | -1 | -7 | 5 | 5 | -1 | -1 | 9 |
| 1993 | 22 | 19 | 29 | 28 | 19 | 18 | 19 | -13 | -5 | -2 | -2 | -3 | 9 | 68 | 67 | -2 | -2 | 16 |
| 1994 | -42 | -51 | -19 | -23 | -13 | -16 | -13 | -26 | -2 | 3 | 8 | 0 | -6 | 29 | 43 | -1 | -1 | -8 |
| 1995 | 29 | 28 | -16 | -19 | -13 | -14 | -13 | -30 | -28 | -14 | -14 | -22 | -12 | 100 | 100 | -10 | -12 | 2 |
| 1996 | -6 | -5 | -7 | 1 | -2 | 1 | -2 | -3 | 1 | -10 | -10 | 0 | -5 | -6 | -4 | 0 | 0 | -3 |
| 1997 | -5 | -4 | -1 | -1 | -4 | -4 | -4 | -1 | -10 | -3 | -3 | -1 | 0 | 3 | 3 | -2 | -2 | -2 |
| 1998 | -6 | 22 | 4 | 4 | 0 | 0 | 0 | 0 | 1 | 9 | 10 | 1 | -1 | -10 | 82 | 0 | 0 | 7 |
| 1999 | -4 | -3 | -5 | -6 | -1 | -2 | -1 | -3 | 13 | 1 | 1 | -14 | -1 | -1 | -1 | -9 | -11 | -3 |
| 2000 | 1 | 1 | 0 | -1 | -1 | -1 | -1 | 0 | 0 | -1 | -1 | 9 | 7 | 3 | 3 | -7 | -8 | 0 |
| 2001 | 85 | 78 | -8 | -10 | -15 | -17 | -15 | -2 | -7 | -2 | -2 | -1 | 52 | 100 | 100 | -18 | -22 | 17 |
| 2002 | -6 | 67 | 0 | 55 | 0 | 0 | 0 | 38 | -1 | 42 | 76 | -17 | -3 | 0 | 88 | -8 | -9 | 19 |
| 2003 | -27 | -35 | -9 | -10 | -8 | -7 | -8 | -8 | 11 | -81 | -100 | -11 | -36 | 3 | 0 | -41 | -12 | -22 |
| 2004 | -19 | -28 | -15 | -18 | -5 | -6 | -5 | -3 | -17 | -2 | -2 | -14 | -4 | 10 | 11 | 14 | 16 | -5 |
| 2005 | -12 | -4 | 0 | 0 | -1 | -1 | -1 | 0 | 0 | 1 | 2 | 4 | 6 | 11 | 11 | -4 | -6 | 0 |
| 2006 | -11 | -10 | -2 | -3 | -1 | -3 | -1 | -4 | -20 | -1 | -1 | -41 | -12 | 8 | 7 | -19 | -23 | -8 |

The regression analyses shows that relationship between 0-group and abundance of 3 years old haddock (3R) can be described by

$3R = 1.1134 + 0.5548*ln(0grI)$   ($R^2 = 0.552$, $p < 0.01$)
$3R_I = 47.523 + 0.0008*ln(0grIK)$  ($R^2 = 0.511$, $p < 0.01$)

**Saithe** 0-group index without length correction (0grI) had weaker correlation with age-3 recruits (3R) and SSB than 0grIK had. However, the correlations were poor with 3R and SSB for both 0grI and 0grIK (Fig. **1** and Table **4**).
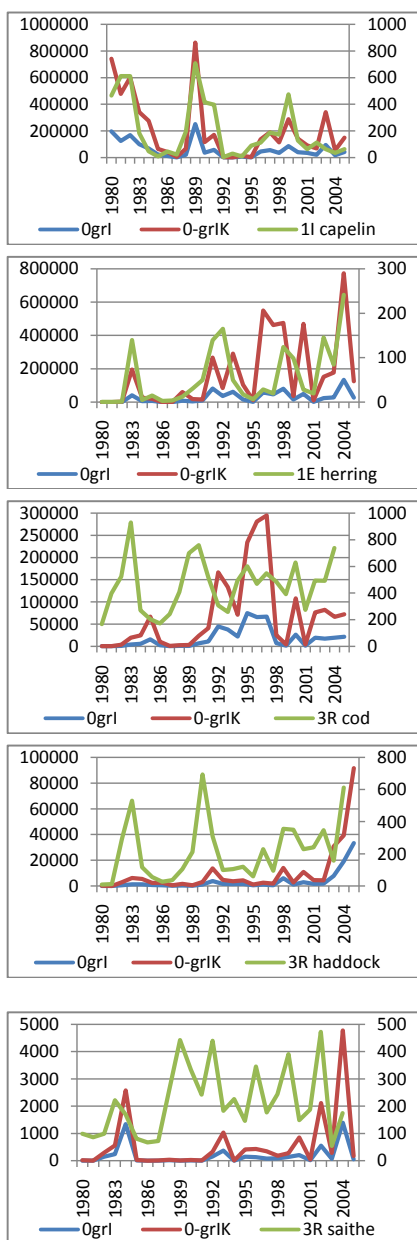
**Fig. (1).** Time series of 0-group (0grI in blue and 0grIK in red) and abundance for capelin (1grI), herring (1grE), cod (3R), haddock (3R) and saithe (3R). Abundance of older fish shows as a green line.

The regression analyses show no significant relationship between of 0-group and abundance of 3 years old saithe (3R).

**Table 4. Pearson's Correlation Between Other Recruitment Indices and the New 0-Group Indices (0grI and 0grIK). N is Number of Years in the Analysis and Index is Abbreviations of Analyzed Abundance Andices. Correlations Significantly Different from Zero (p≤0.05) are Shown in Bold**

|  | Index | N | $r_{0grI}$ | $r_{0grIK}$ |
|---|---|---|---|---|
| Capelin | LI | 26 | 0.23 | 0.23 |
|  | AI | 26 | **0.83** | **0.80** |
|  | 1grI | 26 | **0.82** | **0.81** |
|  | MB | 26 | 0.15 | 0.16 |
| Herring | AI | 13 | **0.87** | **0.84** |
|  | 1grE | 26 | **0.60** | **0.69** |
|  | SSB | 25 | **0.75** | **0.53** |
| Cod | AI | 26 | **0.81** | **0.80** |
|  | 3R | 25 | 0.02 | 0.01 |
|  | WBT | 26 | **0.70** | **0.66** |
|  | WA | 26 | **0.81** | **0.80** |
|  | SSB | 26 | **0.64** | **0.61** |
| Haddock | AI | 26 | **0.89** | **0.88** |
|  | 3R | 25 | **0.49** | **0.43** |
|  | WBT | 26 | **0.70** | **0.66** |
|  | WA | 26 | **0.64** | **0.59** |
|  | SSB | 26 | **0.63** | **0.61** |
| Saithe | 3R | 24 | 0.04 | 0.07 |
|  | SSB | 26 | 0.28 | **0.43** |

### Interaction Between 0-group Fishes

Correlations between 0-group indices of capelin, herring, cod, haddock and saithe are shown in Table **5**.

Capelin was negatively correlated with cod, haddock, herring, and saithe. However, only the correlation with cod was significant. Herring was positively correlated with cod, haddock, and saithe. Saithe was positively, but not significantly correlated with haddock.

**Table 5. Pearson's Correlation Between Indices (0grI and 0grIK) of 0-Group Capelin (A), Herring (B), Cod (C) and Haddock (D). Correlations Significantly Different from Zero (p≤0.05) are Shown in Bold**

|  | 0grI | | | | 0grIK | | | |
|---|---|---|---|---|---|---|---|---|
| r | A | B | C | D | A | B | C | D |
| Herring | -0.18 |  |  |  | -0.22 |  |  |  |
| Cod | **-0.39** | 0.25 |  |  | -0.36 | **0.46** |  |  |
| Haddock | -0.06 | **0.43** | 0.01 |  | -0.05 | 0.28 | -0.02 |  |
| Saithe | -0.15 | **0.42** | 0.03 | 0.24 | -0.18 | **0.52** | 0.08 | 0.21 |

**DISCUSSION**

**Recalculation of 0-Group Indices**

The quality of the database is fundamental for the estimated results. The joint Norwegian-Russian database was corrected and updated for the period 1980-2006. The increased quality of the database makes us more confident in the indices and hence in analyses based on these data. Indices were estimated both with and without correction for capture efficiency.

The 0-group indices estimated in this work showed some differences from the old indices and the differences vary between years. The differences are mainly due to errors in punching of historical data. Therefore, to avoid these faults in later recording of historical data or during later surveys, collected biological data must be tested by specific test-programs, which detect errors before the data are entered into the database.

The corrections to the indices due to errors in the database are severe in some years. E.g. the years 1987-88, 1992-95, 2001 and 2003 for capelin, 1986 for herring, 1982, 1993-94 for cod, and 1986 for haddock. During this work we also found mistakes in punching of fish lengths, which influence the length corrected indices (0grIK). 0-group survey data was also used to study fish growth, errors may have influenced results if studies were based on data from years 1984-88, 1992-95, 2001-04 for capelin, 1982-86, 1994-95 and 2002 for herring, 1982-83 and 1993-94 for cod, and 1982-84 for haddock. Although we call attention to changes, the general trends have not changed much, and we do not know how the errors have influenced the results of earlier recruitment and fish growth studies.

**Comparison of 0-group Indices**

**Capelin** Our results showed that capelin 0grI and 0grIK had no significant correlation with the maturing capelin biomass (MB). Capelin is the main prey species for larger predatory fish such as cod, as well as for marine mammals [20, 21]. Estimated MB, based on the autumn survey, will therefore differ from the spawners' abundance in following winter-spring due to predation and harvesting. In addition, variable survival of larvae and post-larvae will weaken the correlation between MB and 0-group of capelin.

Gundersen and Gjøsæter [9] found no correlation between larval index and 0-group index nor between larval index and 1-group index. Our results showed that capelin 0grI and 0grIK had a no significant correlation between the larval index (Table **4**), while strong correlation with 1grI. Egg and larvae are the most vulnerable stages of the fish life cycle due to suitable food availability and predation pressure in areas they are transported through. Therefore, variable survival of capelin during its first months of life, as demonstrated for other species in the area [19], may cause the weak correlation between larvae and 0-group.

The 0grI and 0grIK were proportional to the estimates 1-group and the 0-group "area index", and more than 60% of 1-group abundance variation was explained (Table **4**) by the variation in 0-group abundance. Therefore new indices of 0-group abundance appear to be a better predictor of year class strength than the estimates of maturing biomass or the larval index. Hence, it is adequate and recommended to use the 0-group index in management and recruitment analyses as an early predictor of capelin recruitment.

**Herring** Our results showed that 0-group herring abundance indices (0grI and 0grIK) were significant correlated with the age-1 estimate (Table **4**). Regression analyses showed that 0grI explained a large part (56%) of the variation in age-1, while 0grIK explain only (28%). Weaker correlation between 0grIK and age-1 estimate may be influenced by uncertainties in length correction function for herring. Our results showed that the variation in 0-group herring abundance in the Barents Sea is strongly correlated with SSB (Table **4**). SSB have commonly been used in herring assessment and management as a predictor of recruitment [15]. Therefore, we can recommend using the 0-group index as input in SeaStar (herring assessment model) [15] and as predictor of year class strength in herring recruitment studies and analyses.

**Cod** The 0-group indices were significantly correlated with all analyzed indices, except age-3 recruits. The variation in 0-group abundance can be explained by the variation in SSB (Table **4**), and higher SSB level will in most years give a higher level of 0-group abundance. The 0-group abundance of cod is highly correlated with abundance at age-1. It seems that age-1 estimate from the acoustic winter survey (WA) is better correlated with 0grI than age-1 estimates from the bottom trawl winter survey (WBT). This may be caused by a better detection, by the acoustic gear, of age-1 cod distributed in the pelagic. Our results showed that 0-group indices (0grI and 0grIK) were not significantly correlated with recruitment at age-3, this may be related to a high variability in survival at age-1 and age-2. Nevertheless, 0-group indices for cod appear to be reliable predictors of year class strengths; this is useful to study cannibalism and survival, and thus can be applied in to assessment models.

**Haddock** 0-group indices of haddock were significantly correlated with all analyzed indices, and level of 0-group indices explained most of age-1 estimate from the bottom trawl winter survey (WBT), and the variation in age-3 abundance (Table **4**). Haddock 0-group is also highly correlated to SSB. Higher number of spawners increases the abundance of 0-group, and only 0-group indices, without environmental condition and predation pressure, can explain about 50% of variation of abundance at age-3.

In conclusion, the 0-group abundance of haddock is highly correlated with abundance at older ages and the 0-group indices appear to be reliable predictors of year class strengths and can be useful as input in to assessment model.

**Saithe** Correlations and regression analyses showed that saithe 0-group indices were poorly correlated with both age-3 abundance and SSB (Table **4**). During the first years of life, a large proportion of this saithe stock is distributed in the fjords along the Norwegian coast [22], and is therefore not available to be covered by the 0-group survey. Consequently, saithe 0-group indices are underestimates and representative only for the surveyed area. Thus, the saithe 0-group indices can not be recommended as year class

strengths indicators. However, 0-group data is useful in spatial and temporal multispecies analyses.

### Interaction Between 0-group Fishes

The transport of egg and larvae along the Norwegian and Murman coast and into the Barents Sea is largely determined by currents. Inter-annual variation in currents and climate will therefore influence the distribution and survival of 0-group fish [23, 24]. Distribution varied between years and between species. In the western, central and southern parts of the Barents Sea more or less all of the analyzed species have been observed, while in the northern part mostly capelin, polar cod, and cod have been observed. Therefore, the positive correlation between cod, herring, haddock, and saithe (Table **5**) indicate a possible spatial overlap during the first summer and a homogenous response to the environment. We found negative correlations between 0-group capelin and 0-group of cod, herring, and saithe (Table **5**), species that overlap both spatially and temporally. Capelin and cod, herring and saithe presents different biogeographic groups, with different responses to temperature and environmental conditions. In addition, our results are in agreement with an earlier study [25] showing that 0-group of cod, herring, and saithe are potential predators of capelin. Therefore, variation in 0-group fish abundance indices depends on oceanographic conditions as well as interactions between 0-group fishes and their spatial and temporal overlap during the first crucial months of their life.

### CONCLUSIONS

The goal with this work has been to improve the joint Norwegian and Russian 0-group database and estimate new sets of abundance indices of Barents Sea capelin, Norwegian spring spawning herring, Northeast Arctic cod, Northeast Arctic haddock, Northeast Arctic saithe, redfish, Greenland halibut, long rough dab and two populations of polar cod. 0-group indices have been used in recruitment studies and in stock assessment, therefore it was necessary to correct both database and indices. The updated database has improved the abundance estimates and we have larger confidence in the new indices. We call attention to the errors that have been present in the database and old indices. The general abundance trends have not changed much, and we do not know how the errors have influenced the results of earlier studies of fish growth and recruitment. In general, the 0-group indices seem to be reliable predictors of year class strengths. Capelin, herring and haddock 0-group indices are able to predict numbers of older fish and may be used in stock assessment. While cod and saithe 0-group indices seem to be incapable to predict recruitment at age-3. Nevertheless, indices for cod appear to be reliable predictors of year class strengths, and can be useful as input in to assessment models. 0-group saithe data is useful in spatial and temporal multispecies analyses.

### ABBREVIATIONS

LI      =    capelin larval Index

AI      =    0-group area index

0grI    =    new 0-group fish indices without correction for catching efficiency

0grIK   =    new 0-group fish indices with correction for catching efficiency

1grI    =    age-1 abundance index

1grE    =    age-1 abundance estimate

VPA    =    Virtual Population Analyse

3R      =    age-3 abundance, VPA

WBT    =    winter bottom trawl indices

WA     =    winter acoustic indices

SSB    =    spawning stock biomass (VPA)

MB     =    Maturing biomass, in 1.October

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**III**

# Paper III

*Biomass of scyphozoan jellyfish, and its spatial association with 0-group fish in the Barents Sea*

PLoS one

# Biomass of Scyphozoan Jellyfish, and Its Spatial Association with 0-Group Fish in the Barents Sea

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## Abstract

An 0-group fish survey is conducted annually in the Barents Sea in order to estimate fish population abundance. Data on jellyfish by-catch have been recorded since 1980, although this dataset has never been analysed. In recent years, however, the ecological importance of jellyfish medusae has become widely recognized. In this paper the biomass of jellyfish (medusae) in 0–60 m depths is calculated for the period 1980–2010. During this period the climate changed from cold to warm, and changes in zooplankton and fish distribution and abundance were observed. This paper discusses the less well known ecosystem component; jellyfish medusae within the Phylum Cnidaria, and their spatial and temporal variation. The long term average was ca. $9 \times 10^8$ kg, with some years showing biomasses in excess of $5 \times 10^9$ kg. The biomasses were low during 1980s, increased during 1990s, and were highest in early 2000s with a subsequent decline. The bulk of the jellyfish were observed in the central parts of the Barents Sea, which is a core area for most 0-group fishes. Jellyfish were associated with haddock in the western area, with haddock and herring in the central and coastal area, and with capelin in the northern area of the Barents Sea. The jellyfish were present in the temperature interval $1°C < T < 10°C$, with peak densities at ca. $5.5°C$, and the greatest proportion of the jellyfish occurring between $4.0–7.0°C$. It seems that the ongoing warming trend may be favourable for Barents Sea jellyfish medusae; however their biomass has showed a recent moderate decline during years with record high temperatures in the Barents Sea. Jellyfish are undoubtedly an important component of the Barents Sea ecosystem, and the data presented here represent the best summary of jellyfish biomass and distribution yet published for the region.

## Introduction

It has been suggested that the abundance of gelatinous zooplankton varies considerably in many marine ecosystems around the globe and that the abundance fluctuates with climate [1,2,3]. Kogosek et al. [4] investigated 200 years of jellyfish data, and showed periodic jellyfish blooms in the northern Adriatic. Several anthropogenic changes capable of promoting increased jellyfish biomass have been identified, including e.g. climate change, eutrophication, pollution, overfishing, and species introductions [1,2,5–7]. One of the main concerns is that the affected ecosystems may switch to an alternative, jellyfish dominated regime, from which it may be difficult to revert [3,8]. Such regime shifts seem to have taken place in the Benguela current [5,9], the Black and Caspian Seas [10,11], and some fjords in western Norway, such as Lurefjord (e.g. [12]). However, due to the scarcity of long time series on jellyfish abundance, quantitative data verifying global increases remain scarce [2,13,14].

Many jellyfish are generalist predators, and often exhibit large year-to-year variations in abundance [5,8,15]. Major fluctuations in abundance can be linked to climatic oscillations [5,8,16], global warming [5] and overfishing [8,14]. However, few long time-series from complex marine ecosystems exist. Climatic (sea surface temperature, salinity and atmospheric variability) and biological

factors (e.g. density dependence, prey availability) were found to be important for the fluctuation of the abundance and distribution of scyphozoan jellyfish in the North Sea [5,6,8,17], in the Irish Sea [18] and in the Bering Sea [19].

Abundant jellyfish can significantly impact the pelagic community through direct predation and competition for food (reviewed by [15,20–22]), as well as through cascading effects [23–25]. Fish can be negatively affected through predation on fish eggs and larvae, as well as through competition for zooplankton prey (reviewed by [7,20,26]). Conversely, young gadoid fish (cod, haddock, Pollock, saithe and whiting) shelter among the jellyfish tentacles to avoid predation [17,19,27].

The Barents Sea is a high-latitude, arctoboreal shallow shelf sea, where the circulation is dominated by the Norwegian Atlantic Current entering through the Bear Island Trench in the centre of the Barents Sea (Figure 1). South of the Atlantic inflow, the extension of the Norwegian Coastal Current flows along the northern Norwegian coast and becomes the Murman Coastal Current [28]. In the northern Barents Sea, cold Arctic water generally flows south-westward [29].

The climate of the Barents Sea can be characterised as being relatively cold during the period 1900–1920 to generally warm in 1930–1950, and cold again in the late 1970s and early 1980s. The water temperature has generally increased from the late 1980s,
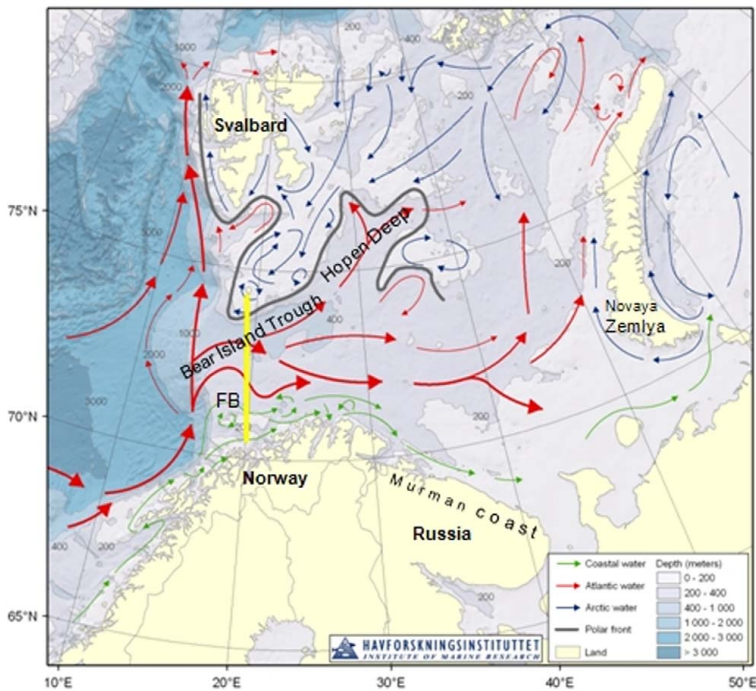
**Figure 1. Map of the Barents Sea** (www.imr.no)**, showing oceanographic and topographic features.** The Fugløya-Bear Island (FB) section is shown by yellow line.
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with a peak in 2006. The inflow of Atlantic Water is of crucial importance for the physical and ecological conditions of the Barents Sea [29]. The Fugløya-Bear Island (FB) section across the western entrance to the Barents Sea is representative of the climatic variations in the Atlantic inflow [30]. The annual water temperature at 50–200 m depth from 1980 to 2008 varied between 4.6°C and 6.4°C (http://www.imr.no/sjomil). Due to the importance of the Barents Sea as a commercial fishery area and a foraging area for fish, numerous studies have been published on the fish species [31–36], 0-group fish [37] and mesozooplankton stocks [38,39,40]. Recruitment (5–8 month old fish) of commercially and ecologically important fish species, such as including Barents Sea capelin (*Mallotus villosus*), Norwegian spring spawning herring (*Clupea harengus*), Northeast Arctic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) have varied considerably between years, depending on a combination of many factors, both physical and biological [41]. In contrast, jellyfish in the Barents Sea remain poorly studied, and the overlap with 0-group fish is unknown.

In this paper, we use data from thousands of survey stations in August-September over the period 1980–2010 in the Barents Sea to explore the following questions: What is the jellyfish biomass, and how has it varied spatially and temporally? What is thermal habitat for jellyfish medusae in the Barents Sea? Furthermore, we investigate how variation in the distributions and biomasses of jellyfish medusae are related to variation in 0-group fish of capelin, haddock, cod and herring and temperature.

## Materials and Methods

### Study species

Two species of scyphozoan jellyfish commonly occur in the Barents Sea: the lion's mane jelly *Cyanea capillata* and the moon jelly *Aurelia aurita* [42–44]. *Cyanea capillata* is a northern boreal species [44–45], while *Aurelia* is a cosmopolitan genus, particularly abundant in the coastal waters, although occurring also in the open ocean [44]. Both *C. capillata* and *A. aurita* typically exhibit large year-to-year variations in abundance [43,46,47]. In the Barents Sea during summer and autumn, both *C. capillata* and *A. aurita* abundance varies greatly, and their biomass or abundance indicators give early warning signals with respect to climate change [43]. In the Northeast Atlantic strobilation (asexual budding of jellyfish ephyrae from benthic polyps) of *C. capillata* takes place in the late winter and spring [46,48], although there seems to be differences in the timing of reproductive events between populations [7,47,49]. The timing of reproductive events in the Barents Sea area is currently not known.

### Survey

A Joint Norwegian-Russian 0-group survey has been carried out annually in August-September in 1965–2003. Since 2004 the 0-group investigations have continued as part of a Joint Norwegian-Russian ecosystem survey (here referred to as O-group survey). The survey provides data for the estimation of 0-group fish
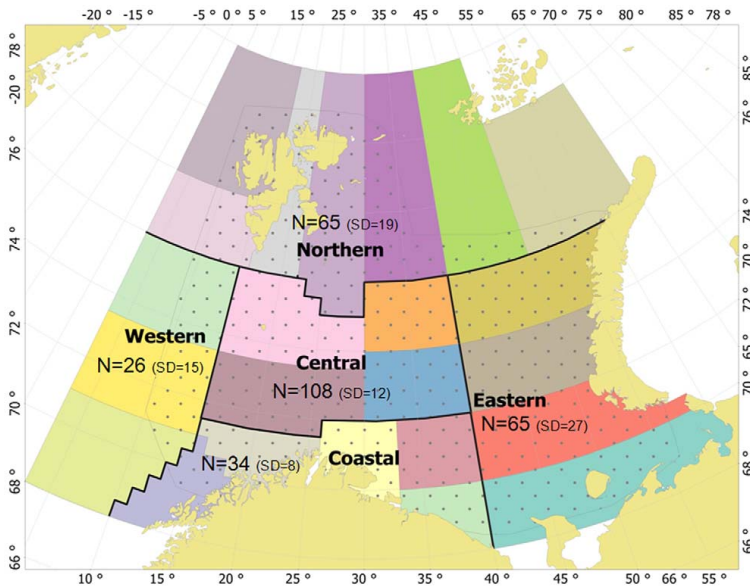
**Figure 2. The strata system used in the jellyfish biomass calculation.** The strata system is taken from that used in the 0-group fish abundance and biomass calculation [37,50], and stratas were combined into the larger the northern, western, central, eastern and coastal areas. The 0-group survey coverage area is shown by dots. In addition, mean number of stations (N) with standard deviation (SD) per each area are shown.
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abundance indices for the most important commercial fish species. By-catch, including jellyfish medusae within the Phylum Cnidaria, (hereafter call jellyfish), has only been weighed and not identified to species level. The trawling procedure consists of tows on predetermined positions 46–65 km apart along the survey track. At each station a pelagic "Harstad" trawl is towed at 3 or more depths, with the head-line at 0 m, 20 m and 40 m depths and each depth tow of ca 900 m with a trawling speed of 5.56 km/h. Additional tows at 60 and 80 m, also of ca 900 m, were made when dense fish concentrations were recorded deeper than 40 m depth on the echo-sounder, but the number of such deeper stations is low. The pelagic "Harstad trawl" has a 20 m×20 m mouth opening, and consists of 7 panels and a cod end. The mesh size varied from 100 mm in the first panel to 30 mm in the last. The cod end consisted of a 30 m long capelin net with 20 mm meshes for catching pelagic fish, and a 14 m long inner net with 7 mm meshes for catching 0-group fish. Therefore, we believe that larger *C. capillata* may be captured by all panels, while smaller and less robust species, such as *A. aurita* are also probably sieved through trawl meshes. It is likely they are only reliably captured by the last panel, and probably partially or totally destroyed in the cod end.

The joint Norwegian-Russian fish database has recently been corrected and updated for the period 1980–2006 [50]. The data for jellyfish were missing from the electronic database; therefore, the first task of the present study was to update the database for the period 1980–2010 to include jellyfish data. These data have not been previously analysed and published.

### Biotic data

**Jellyfish.**   Data for scyphozoan jellyfish were collected from pelagic trawl catches during the 0-group survey in the Barents Sea. Over the study period (1980–2010) 9529 pelagic trawl stations,

each with 3 trawl depths or more, were sampled. We used these data to estimate biomass indices of jellyfish in the Barents Sea for the period 1980–2010, and to examine spatial overlap with 0-group fish for the shorter period (1980–2008) due to missing temperature data in the database.

**0-group fish (cod, haddock, herring and capelin).**   Fish data were collected from pelagic catches during the 0-group survey in the Barents Sea (1980–2008). We used these data to calculate fish density (individuals per $m^2$) for each trawl haul with regard to catch and trawl haul data (depth interval, effective opening and distance trawled). The method is described by Dingsør [51] and Eriksen et al. [50]. Eriksen et al. [41] described several areas in the Barents Sea (the coastal, central, eastern, western, north-western and northern), based mostly on bathymetric and water features. To make our results comparable with this early study we use a similar spatial division (Figure 1), except for the north-western and northern areas, which we combined due to limited fish and jellyfish catches there. This combined area we hereafter call the northern area.

### Abiotic data

The water temperature data are from CTD (Conductivity, Temperature and Depth sensors) samples taken at each 0-group trawl station. The CTD profiles were taken either before or after trawling, and in this study we used the temperatures aggregated to standard depths (5 m, 10 m, 20 m, 30 m, 40 m). Over the study period (1980–2008), 7089 CTD stations were conducted. We used these data to define temperature ranges for jellyfish.

Temperature (and since 1997, volume inflow) of Atlantic Water to the Barents Sea has been measured monthly at the standard oceanographic section Fugløya-Bear Island ($70°30'$ and $20°00'$ to $74°15'$ and $19°10'$, Figure 1) by the Institute of Marine Research (IMR, Norway,). The water temperature was measured by CTD

**Table 1.** Estimates of Barents Sea jellyfish biomass ($10^6$ kg) with 95% confidence interval for the period 1980–2010.

| Year | Surveyed area, $10^9$ km$^2$ | Number of stations | Mean biomass, g/m$^2$ | Annual biomass, $10^6$ kg | Confidence limit (min) | Confidence limit (max) |
|------|------|------|------|------|------|------|
| 1980 | 1222 | 327 | 0.23 | 227 | 178 | 277 |
| 1981 | 1146 | 298 | 0.39 | 392 | 307 | 477 |
| 1982 | 1004 | 280 | 0.51 | 485 | 359 | 610 |
| 1983 | 1105 | 279 | 0.74 | 688 | 532 | 844 |
| 1984 | 1119 | 324 | 0.57 | 623 | 459 | 788 |
| 1985 | 1179 | 292 | 0.05 | 68 | 37 | 100 |
| 1986 | 1088 | 305 | 0.13 | 136 | 97 | 176 |
| 1987 | 1077 | 285 | 0.20 | 195 | 97 | 294 |
| 1988 | 1114 | 288 | 0.38 | 371 | 97 | 645 |
| 1989 | 1394 | 424 | 0.09 | 123 | 64 | 182 |
| 1990 | 1213 | 398 | 1.07 | 1279 | 1067 | 1492 |
| 1991 | 1312 | 403 | 0.78 | 973 | 784 | 1161 |
| 1992 | 1077 | 306 | 0.98 | 1096 | 804 | 1388 |
| 1993 | 1071 | 273 | 0.70 | 716 | 529 | 902 |
| 1994 | 952 | 250 | 0.07 | 63 | 39 | 87 |
| 1995 | 893 | 247 | 0.03 | 30 | 16 | 43 |
| 1996 | 1095 | 400 | 0.36 | 485 | 383 | 587 |
| 1997 | 948 | 269 | 0.02 | 19 | 9 | 28 |
| 1998 | 1099 | 361 | 0.21 | 212 | 169 | 255 |
| 1999 | 1040 | 230 | 0.52 | 524 | 384 | 664 |
| 2000 | 1162 | 269 | 1.07 | 1260 | 1009 | 1511 |
| 2001 | 1184 | 278 | 4.11 | 4906 | 4191 | 5620 |
| 2002 | 1129 | 255 | 2.60 | 2870 | 2436 | 3303 |
| 2003 | 1176 | 277 | 2.44 | 2663 | 2202 | 3125 |
| 2004 | 1144 | 309 | 1.33 | 1510 | 1260 | 1759 |
| 2005 | 1360 | 318 | 1.08 | 1423 | 1040 | 1806 |
| 2006 | 1078 | 304 | 1.02 | 1157 | 715 | 1599 |
| 2007 | 1297 | 305 | 1.08 | 1221 | 725 | 1716 |
| 2008 | 1246 | 316 | 0.85 | 1174 | 864 | 1483 |
| 2009 | 1274 | 331 | 0.48 | 664 | 499 | 828 |
| 2010 | 1272 | 304 | 0.23 | 279 | 359 | 43 |
| **Mean** | **1144** | **307** | **0.78** | **898** | | |

In addition, the surveyed area (km$^2$), number of stations and annual mean biomass (g/m$^2$) are presented.

at standard depths at predetermined stations along the FB. Here we use a time series of annual temperature at 50–200 m depth taken from the path of Atlantic inflow. The annual mean temperature from 1980 to 2008 was 5.5°C, and years were categorized into three similar groups: average (long term mean temperature ±16% of the long term mean value), cold (below average) and warm (above average).

### Data treatment

We calculated the following:

**Biomass indices.** Biomass indices for the period 1980–2010 using the stratified sample mean method of swept area estimates [51]. For jellyfish biomass estimation, the Barents Sea 0-group strata system, which consists of 23 strata, was used (Figure 2). The biomass (g/m$^2$), $b_s$, at each station, $s$, was estimated by the equation

$$b_s = \frac{w_s}{wsp * (td_s/dl_s)} \quad (1)$$

where $w_s$ is the catch (g) at station $s$, $wsp$ is the effective wingspread of the trawl (20 m), $td_s$(m) the total distance trawled at station $s$, and $dl_s$ is the number of depth layers at station $s$. If the number of depth layers at station, $s$, is 1, it means that the trawl was towed for ca 900 m at the surface (0 meter depth) covering the water layer between 0 and 20 m. If the number of depth layers at station, $s$, is 2, it means that trawl was towed for ca 900 m covering 0–20 m and ca 900 m at 20–40 m, and so on.

For each of the strata the total biomass, $B$, was calculated by

$$B = \sum_{i=1}^{N} A_i \bar{y}_i \quad (2)$$
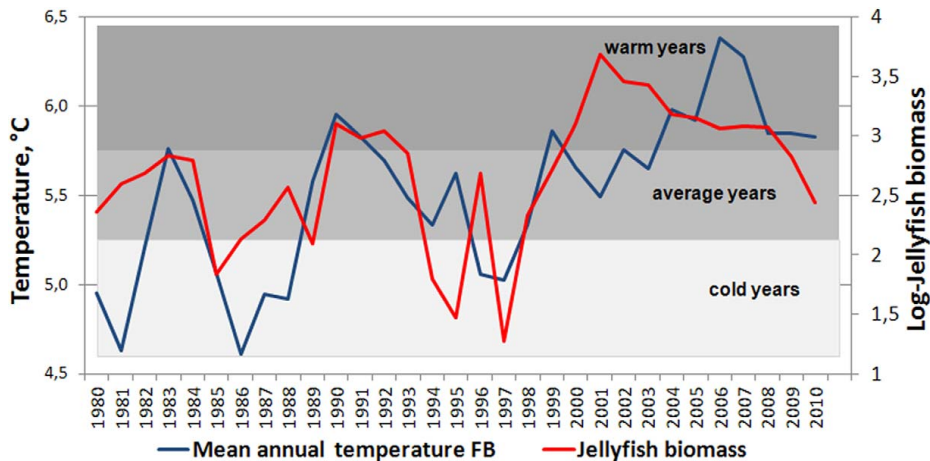
**Figure 3. The mean annual water temperature at the Fugløya-Bear Island section (left axis) and the log transformed jellyfish biomass indices (right axis).**
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where $N$ is the number of strata, $A_i$ is the area covered in the $i$-th stratum, and $\bar{y}_i$ is the average biomass in stratum $i$ given by

$$\bar{y}_i = \frac{1}{n_i} \sum_{s=1}^{n_i} b_s \qquad (3)$$

where $n_i$ is the number of stations in stratum $i$, and $b_s$ is biomass (g/m$^2$), at each station, $s$.

The estimated variance of the B is given by

$$\mathrm{var}(B) = \sum_{i=1}^{N} A_i^2 \frac{s_i^2}{n_i} \qquad (4)$$

where

$$s_i^2 = \left( \sum_{s=1}^{n_i} (y_{i,s} - \overline{y_i})^2 \right) / n_{i-1} \qquad (5)$$

A biomass estimate ($10^9$ kg) for each area (the coastal, central, eastern, western, and northern) was calculated as the sum of the stratified swept area biomass estimates ($B$) of all strata within the area (see Figure 2). Jellyfish biomasses were not interpolated to the whole strata/area, and represent only the covered area. The estimated jellyfish biomass is likely to be conservative, since smaller individuals may have passed through the larger mesh sizes, and some of jellyfish species distribute deeper than the sampled depths (0–60 m) or outside the covered area. Consequently, the estimated biomasses may be interpreted as minimum biomass.

**The fish density.** The fish density (individuals/m$^2$) for each trawl haul was calculated using catch and trawl data (depth intervals, effective opening and distance trawled). The method is further described by Dingsør [51] and Eriksen et al. [50].

**The jellyfish biomass.** The jellyfish biomass, wet mass (g/m$^2$), for each trawl haul was calculated with regard to catch and

trawl data (depths interval, effective opening and distance trawled). The method is further described by Dingsør [51] and Eriksen et al. [50].

**The mean temperature.** The mean temperature per station for the water layer 5–50 m calculated as the average of the temperatures from standard depths. Temperature was recorded at a total of 7089 CTD stations.

## Statistical modelling

We investigated relationships between jellyfish, 0-group fish of cod, haddock, herring and capelin, and temperature for the period 1980–2008. We used a GAM (Generalized Additive Model) in the R (version 2.12.2) package mgcv [52]. To study associations between the biomass of jellyfish (JF$_B$) and densities of 0-group capelin (Cap$_D$), haddock (Had$_D$), cod (Cod$_D$), herring (Her$_D$) and temperature in sample (i.e. station) $i$ were fitted to the covariate according to the following models:

$$\begin{aligned} \mathrm{JF_B} = {} & s(\mathrm{year}_i) + s(\mathrm{Cap_D}) + s(\mathrm{Had_D}) + s(\mathrm{Cod_D}) \\ & + s(\mathrm{Her_D}) + s(\mathrm{T}) + e_i \end{aligned} \qquad (6)$$

where the additive effect included the smoothed fits (s) of variables of sample i. Year was included as a factor in the model (Equation 6), $e_i$ denotes the error for sample $i$. Separate models were constructed for the coastal, central, eastern, western, and northern areas. We used backward selection to identify the best model based on Akaike information criterion (AIC) and genuine cross validation (GCV).

**Core Thermal Habitat (CTH).** A temperature range was estimated from the model as the temperatures corresponding to jellyfish biomasses larger than the mean modelled jellyfish biomass. This temperature range, including about ~60% of the observations we hereafter call the Core Thermal Habitat (CTH).

## Results

The estimated jellyfish biomass the Barents Sea varied considerably from year to year (Table 1 and Figure 3). Jellyfish
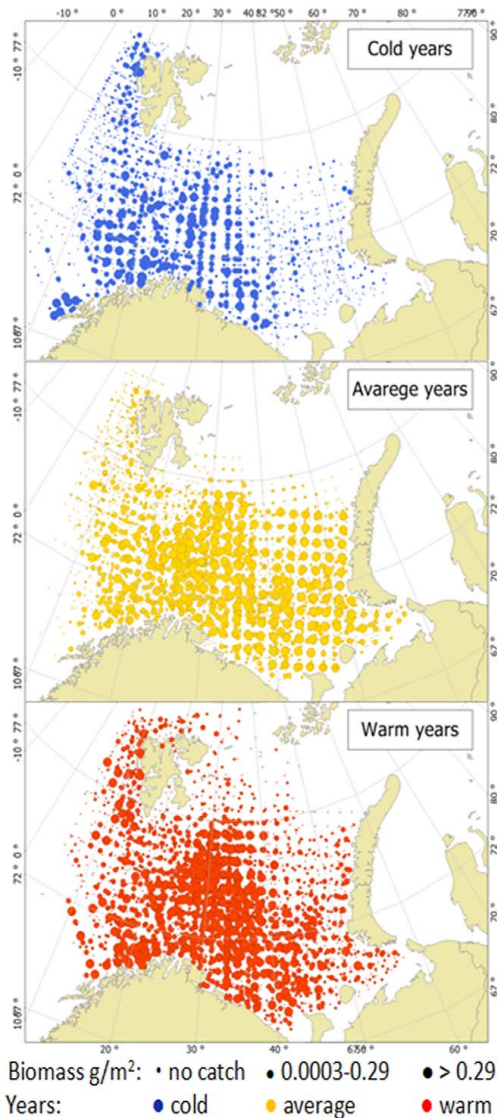
**Figure 4. Spatial distribution of jellyfish biomass (wet weight g/m²) during years with different temperature regimes in the Barents Sea (see Figure 3).** Cold years are shown in blue (up), average in yellow (middle) and warm years in red (bottom). Circle size indicates biomass; stations with no jellyfish are shown with the smallest circle size, 0.0003–0.29 g/m² with the medium circle, and with more than 0.29 g/m² jellyfish shown with the largest circle size.
doi:10.1371/journal.pone.0033050.g004

biomass was generally low during the 1980s, moderately high in the 1990s, and high in 2000s, and the mean biomass ($10^6$ kg) was about 330 *(SE = 68; SD = 216)*, 540 *(SE = 147; SD = 465)* and 1700 *(SE = 390; SD = 1295)* respectively. Estimated jellyfish

biomass varied from $19 \times 10^6$ in 1997 to ca. $5 \times 10^9$ kg in 2001, with a long term mean for the period 1980–2010 of around $1 \times 10^9$ kg *(SE = 184; SD = 1023)*. The long term mean biomass of jellyfish was approximately 0.78 g/m² *(SE = 0.16; SD = 0.87)*. The highest biomasses occurred during 2001–2003, when mean biomass was 2.4–4.1 g/m² and station specific biomass ranged as high as 44.3 g/m² (Figure 3). There has been a decrease in biomass since 2009 (Figure 3).
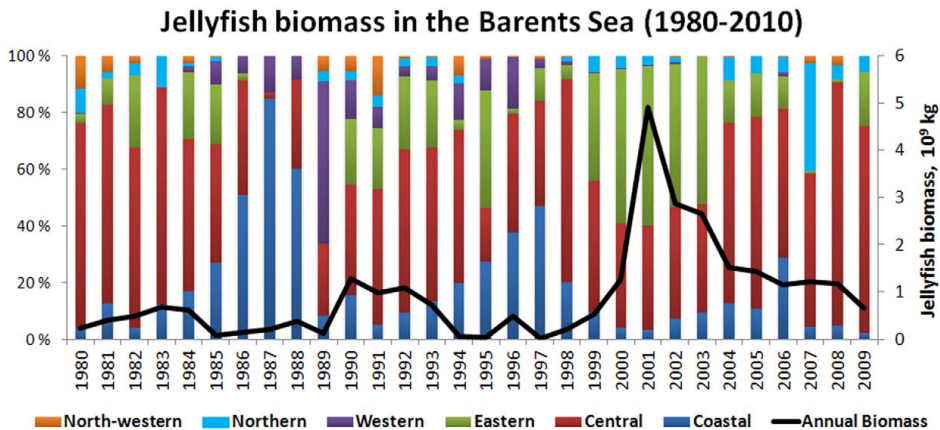
The spatial distribution of jellyfish biomass varied between years with different temperature conditions. The most restricted distribution and generally low catches were observed during cold years, while during average and warm years jellyfish occupied almost whole of the Barents Sea, and catches were very high (Figure 4). Jellyfish biomass also varied between different areas in the Barents Sea. The central and eastern areas contributed most of the total jellyfish biomass. Their average contribution over the study period was about 49% and 31% respectively (Figure 5), although the proportion of jellyfish in these areas showed considerable variability. The eastern area, in particular, showed highly varied levels of jellyfish biomass. A high proportion of the total biomass was found in the eastern area during years with unusually high total biomasses (1999–2003 and to a lesser extent 1990–1993), whereas in the lowest years (1986–1989) there was little or no jellyfish reported from the eastern area (Figure 5). In years with low estimated biomass the relative importance of the coastal area increased, although the average jellyfish density in the coastal area over the study period was approximately half of that in the central area, at 81.6 g/m² in the coastal region compared with 131.2 g/m² in the central area. Averaged over the whole period (1980–2010), the contribution from the coastal, western and northern areas were low, and these areas contribute only 11%, 2% and 7% of total jellyfish biomass, respectively. However, the coastal area contained a relatively stable population, in contrast to the marked variability in the other areas (Figure 5).

Jellyfish were associated with 0-group cod, haddock, herring and capelin in the areas where fish were abundant, and these relationships varied between areas (Table 2, Figure 6). Jellyfish biomass was positively correlated with haddock (coastal and western areas) and herring (central, eastern and coastal area) and cod (eastern area). In the central area we found no association between jellyfish and 0-group cod, and the association with haddock was non-linear. In the northern area, dominated by 0-goup capelin, jellyfish was associated only with capelin, and the association was non-linear.

The jellyfish were present in the temperature interval 1°C<T<10°C (Figure 6). The CTH, was bounded in a temperature band around the maximum between 4.0–7.0°C, indicating that jellyfish associated with Atlantic water masses. However, the jellyfish showed a dome shaped distribution with temperature in the central and coastal areas, with maximum biomass at ca. 5.5°C and 6.5°C, respectively (Figure 6). In the coastal and western area, jellyfish were positively correlated with temperature (Figure 6).

## Discussion

The Barents Sea is a productive ecosystem, with more than 200 fish species, thousands of benthic invertebrate species, and diverse communities of plankton, seabirds and marine mammals which inhabit or visit the area [53]. Only a few fish species, including cod, haddock, saithe, capelin, redfish, Greenland halibut, and polar cod are of commercial interest. Nonetheless, these form the basis of one of the largest fisheries in the world [54]. Historically, scientific surveys focused on monitoring commercially important

**Figure 5. Variation of jellyfish biomass indices in the Barents Sea ($10^9$ kg, black line) and the spatial distribution of jellyfish biomass (colored bars).**
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fish stocks, although after a strong decrease of the cod fishery in the Barents Sea, and a near collapse in herring fishery in the Norwegian Sea, an 0-group fish survey was started in order to give early signals of fish recruitment and further stock development. Gelatinous zooplankton have not been the focus of research until recent decades. Recent trends, including some of the old fish recruitment "rules of thumb" ceasing to apply, a strong increase of the temperature in the Barents Sea [41,50], and an increasing focus on the impacts of rising populations gelatinous zooplankton in other ecosystems [1,2,5–7] has changed this. Understanding jellyfish distributions and interactions with other species is increasingly seen as important in order to avoid having a "black box" in our understanding of the ecosystem. In order to gain an insight into jellyfish presence and especially their relationship with 0-group fish, we have used available trawl data from 0-group fish survey.

Sampling jellyfish is problematic, due to an extremely patchy distribution and fragile nature, making both standard fisheries gear and conventional plankton nets of limited value [55]. Several studies have used by-catch of jellyfish from fisheries surveys [14,56,57], but the large mesh size of the gear typically used in such surveys is not well suited to catching jellyfish. Our data were collected by small "Harstad" trawl with small mesh size (see above). This trawl is smaller than standard fisheries trawls gear used in previous studies, and therefore has increased catchability and decreased chance of damage to jellyfish within the trawl net. This sampling gear is also larger than conventional plankton nets and therefore i) better able catch larger jellyfish, *C. capillata,* due to larger effective opening and faster trawling speed, but ii) less able to catch smaller jellyfish, *A. aurita,* which is sieved through trawl meshes or partially or totally destroyed in the cod end [53]. Therefore, our results consist mostly of *C.capillata,* and the biomass presented must be interpreted as minimum for the total jellyfish biomass in the Barents Sea. Nonetheless, long term monitoring of the Barents Sea using this standard sampling procedure and standard regular station grid makes data comparable between vessels, areas and years.

The biomass of Barents Sea jellyfish varied considerable between years and higher jellyfish biomasses were generally found in the beginning of 1990s, and high or record high during the

2000s, with a moderate decrease in the end of 2000s (Table 1, Figure 5). In the Bering Sea an increase of jellyfish catches was observed during the 1990s, with a maximum in 2000, moderate amounts during period 2001–2007, and decreased amount in 2008 [57]. Both Lynam et al. [18] and Brodeur [57] found that a warming trend favouring many species of jellyfish in other seas. During the period studied here, temperature conditions changed from cold during the 1980s, to moderate in the 1990s, and to warm during the last decade. It seems that, at least up to a certain point, a warming trend is also favourable for the Barents Sea jellyfish. Warmer temperature conditions in the Barents Sea are associated with increased inflow of Atlantic water, bringing more zooplankton from the Norwegian Sea into the Barents Sea [58] and better feeding conditions for plankton feeders from larvae to adult [58,59,60]. The highest biomasses of jellyfish were found in the temperature range of $4$–$7.0^\circ$C, indicating that i) an increase of temperature may not lead to further increases in jellyfish biomass in the Barents Sea, and ii) the greater proportion of jellyfish are resident in water masses of Atlantic origin (i.e. waters having temperatures above $3^\circ$C, [61]), with a lesser proportion distributed in the mixed water masses (i.e. waters having temperatures between $0^\circ$C and $3^\circ$C [61]). Spatial distribution of jellyfish varied between years and was widest during the 2000s (Figure 4). The greater proportion of jellyfish occurred in the central area throughout the time series. The highest plankton biomass was observed during the summer at the entry of the Barents Sea due to the ocean currents, making this area the core nursery area for 0-group fish [41,62]. In the central area, jellyfish overlapped mostly with cod, haddock and herring, although a statistically significant relationship was only found with haddock. This relationship was dome-shaped, with low jellyfish biomasses where there was a low or high density of fish, while the highest jellyfish biomasses overlapped with averaged values of haddock. During the 2000s, a substantial increase in areas with mixed water has been observed in the Barents Sea [61], and such redistribution of water masses seems likely to impact the jellyfish distribution by extending of the area with suitable living conditions (Figure 4). A similar redistribution has been observed for 0-group capelin, suggesting sufficient feeding conditions in the eastern and northern areas

**Table 2.** Additive models for the relationship between jellyfish, temperature, haddock, cod herring and capelin in the different areas in the in the Barents Sea, adjusted $R^2$ (i.e. proportion of variance explained), and genuine cross validation (GCV).

| Models | s/F Mean Temp | s/F Haddock | s/F Herring | s/F Capelin | s/F Cod | $R^2$ | GCV score/Scale est. |
|---|---|---|---|---|---|---|---|
| Central | 4.95/4.45 | 5.06/3.46 | 1.03/11.84 | ns | | 0.37 (37.7) | 10.18 (10.02) |
| East | 6.36/8.34 | | 1.00/7.32 | 3.00/5.62 | 1.76/8.86 | 0.55 (56.2) | 6.84 (6.68) |
| Coastal | 1.98/4.05 | 1.3/11.00 | 1.87/3.51 | | | 0.24 (27.2) | 11.78 (11.25) |
| Western | 1.93/5.50 | 1.18/21.28 | | | | 0.32 (35.1) | 7.59 (7.17) |
| Northern | 4.09/5.02 | 3.03/2.13 | | 6.9/5.02 | | 0.25 (27.7) | 9.13 (8.82) |

The selected model includes both significant terms (i.e. p≤ 005) and not significant terms (i.e. p≤ 0.05).
doi:10.1371/journal.pone.0033050.t002
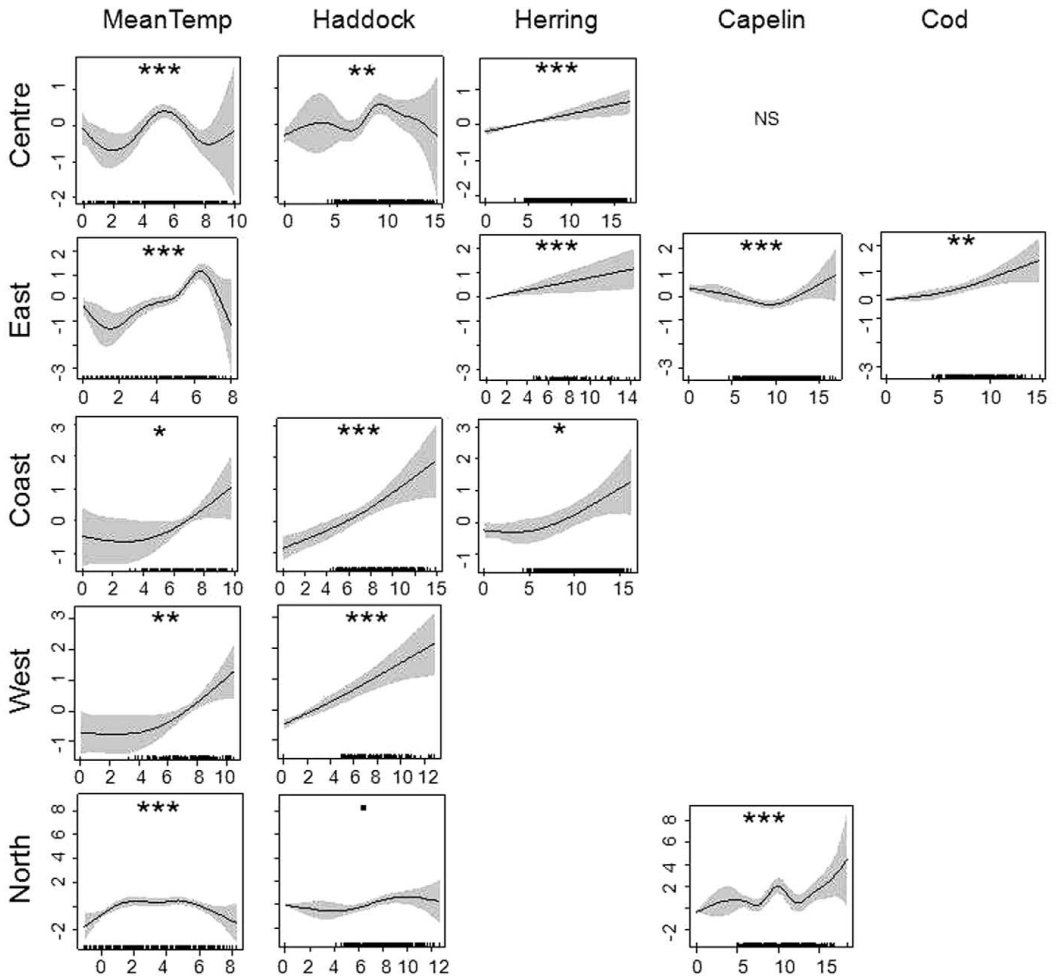


**Figure 6. Estimated functions for jellyfish and prognostic factors (mean temperature (MeanTemp) and 0-group fish (haddock, herring, capelin and cod) densities).** Jellyfish biomass shows at y-axis, while prognostic factors at x-axis. Separate models were performed for the coastal, central, eastern, western, and northern areas codes are shown: 0.001 as ''***'', 0.01 as ''**'', 0.05 as ''*'', 0.1 as''·'', and not significant means as Ns.
doi:10.1371/journal.pone.0033050.g006

[41]. Our results showed significant overlap between jellyfish and 0-group capelin in the eastern and northern areas, however jellyfish biomass and 0-group density were much lower than in the central area and varied considerable between years.

In contrast, the coastal areas acted as a reserve area for the jellyfish, with relatively constant biomasses over time. Scyphozoan jellyfish success in the coastal waters is determinate by morphological, behavioural and life history characteristics [63]. This rich coastal environment seems to have led to a stable jellyfish population in this area, resulting in it forming a significant fraction of the population during low biomass years. In the coastal area jellyfish significantly overlapped with 0-group of haddock and herring, and higher biomasses of jellyfish were observed with higher fish densities and increasing temperature. The complex physical structure of coast supports zooplankton productivity [64,65,66], and may impact positively on amount of jellyfish and 0-group fish there.

During years with extremely high amounts of jellyfish (2001–2003), no strong fish year classes occurred. These years were characterized by average or high spawning stock biomass of cod, haddock, herring and capelin (except cod, in 2001 SSB was lower than average) and warmer temperature conditions as proxy for better feeding conditions and successful recruitment of cod, haddock and herring. One might therefore expect the occurrence of average or strong year classes during this period. It seems that jellyfish was positively related with 0-group herring (the central and coastal areas), cod (eastern), and 0-group haddock (western), indicating that they inhabited similar water masses. It is possible, therefore, that the large stock of biomass played a role in preventing the occurrence of large year classes during this period. However, the relationship between jellyfish and 0-group fishes is complex and depends on many factors both physical and biological (reviewed by [15,20,21,22]), making it difficult to separate influence of different factors and combination of them. Thus, diet studies of both 0-group fish and jellyfish are needed to understand spatial overlap between them, and we recommend to prioritize species identification of jellyfishes onboard during this survey to minimize uncertainties surround the biomass indices calculation.

The Barents Sea is an important commercial fishery area, currently containing the largest cod and capelin stocks in the world, and in 2010 the fish and shrimp catches were reported to be close to $2.9 \times 10^9$ kg [67–69]. Marine mammals are also harvested, although on a smaller scale. Removal of top-predators such as demersal fish through fisheries might cause trophic cascades and abrupt changes in ecosystem state [70]. Despite a high level of exploitation of demersal and pelagic fish, high jellyfish biomass (such as $5 \times 10^9$ kg in 2001) and a trend of increasing temperatures, no dramatic shifts have been reported from the Barents Sea. However, many of the long established relationships and mechanisms in the Barents Sea seem to be changing.

This study provides i) basic information about the spatial and temporal distributions of jellyfish biomass in the Barents Sea, ii) indicates the complexity of an ecosystem including jellyfish, rather simple ecological effect on 0-group fish or whole system, and iii) suggests a possible jellyfish core temperature habitat in the Barents Sea. This study is based on long term (and ongoing) monitoring, and gives a insight into the Barents Sea ecosystem which may be useful for ecosystem modellers, researches within plankton, ecology and fisheries biology and fisheries managers around the world.

## Acknowledgments

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# Paper VI

*The effect of recent warming on polar cod and beaked redfish juveniles in the Barents Sea*

VI

CrossMark

# The effect of recent warming on polar cod and beaked redfish juveniles in the Barents Sea

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## ARTICLE INFO

## ABSTRACT

During 1980–2008, climatic conditions in the Barents Sea changed from cold to warm. This recent warming has led to a greater area of Atlantic water and a smaller area of Arctic water within the Barents Sea, which influences suitable habitats for arctic and boreal fish. Using extensive survey observations of temperature and the presence of juvenile polar cod (arctic) and beaked redfish (boreal), we defined a core thermal habitat for these species and studied how climate variability has influenced abundance indices, fish density and length, and geographical distribution. The distribution of polar cod has often been split into western (Svalbard) and eastern (Novaya Zemlya) components, which correspond to spawning sites. Most polar cod were found in a temperature band of 2–5.5 °C (core thermal habitat, CTH). Higher temperatures will lead to worse conditions (less CTH) for polar cod, which will result in decreased fish density and distribution for this species in the Barents Sea. Decreased ice cover provides less suitable spawning sites for polar cod, which may result in reduced abundance (0-group index). Redfish were primarily distributed in the western and central parts of the Barents Sea and were seldom observed east of 30°E. The majority of beaked redfish were found in a temperature band of a 5.5–8.5 °C. For redfish, higher temperatures resulted in better conditions (larger CTH), but redfish did not seem to utilise the increased habitat. The abundance of redfish (0-group index) seemed to depend more on exploitation than on CTH. Thus, recent warming negatively influenced polar cod recruitment due to a shrinking habitat, but it positively affected redfish recruitment.

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## 1. Introduction

The climate in the Barents Sea has varied from cold during the 1980s to intermediate during the 1990s to warm during the 2000s, and there has been an increasing trend in both oceanic and atmospheric temperatures over this time period (Ingvaldsen et al., 2003; Johannesen et al., 2012). The temperature increase has been particularly strong in the last two decades, which have been the warmest decades on record (Levitus et al., 2009; Boitsov et al., 2012). Strong inflow is associated with a wide area of Atlantic water and a push-back of sea-ice with a lower extent of sea-ice cover in the winter (Boitsov et al., 2012; Johannesen et al., 2012). The ice has retracted further north, decreasing the area influenced by Arctic water in the Barents Sea. These changes have influenced the distribution, abundance and trophic interactions of true arctic species (Fossheim et al., 2015). Most boreal species followed

the redistribution of warm Atlantic water, and thus, spatial distributions of zooplankton and several fish species have extended northwards in the last decade (Rass, 1968; Fossheim et al., 2015). Variable inflow of Atlantic water and changing temperature conditions have in turn been found to affect the recruitment variability of all the major fish stocks in the Barents Sea, including Atlantic cod, haddock, herring and capelin (Rass, 1968; Borkin, 1979; Monstad and Gjøsæter, 1987; Sundby, 2000; Korshunova, 2012; Eriksen et al., 2012). Water temperature influences larvae and juveniles directly through metabolism and indirectly through food availability and habitat conditions (Brett, 1979). Planktonic crustaceans (e.g., copepods) constitute the majority of the diet of polar cod and redfish juveniles (Dolgov and Drevetnyak, 1995; Orlova et al., 2008). In mid-summer, the biomass of *Calanus finmarchicus* in Atlantic water and *Calanus glacialis* in Arctic waters can reach 4.0 and 3.8 g dry weight per square meter respectively (Arashkevich et al., 2002). The biomass of *C. finmarchicus* has increased in recent years (Drobysheva, 1994; Skjoldal and Rey, 1989; Dalpadado et al., 2003; Orlova et al., 2005) due to increased advection of warm, plankton-rich Atlantic water into the Barents Sea

(e.g., Skjoldal and Rey, 1989; Sundby, 2000; Dalpadado et al., 2003; Orlova et al., 2005). A decrease in the area influenced by Arctic water and a reduction in the associated arctic plankton community (e.g., the calanoid copepods *C. glacialis* and *Calanus hyperboreus*) may result in some species of arctic plankton and fish "running out of shelf" (Ponomarenko, 1968; Wassmann, 2006).

In this study, we studied 0-group polar cod (*Boreogadus saida*) and redfish (*Sebastes mentella*) and their thermal habitats using pelagic trawl catches and temperature observations from the upper 50 m. All samples were collected during standard fishery-independent surveys from 1980–2010. We also examined how variation in the distribution and abundance of the 0-group were related to recent warming. If temperature is an important controlling factor for juvenile abundance, distribution and growth, then we expected that increasing temperatures would have positively influenced the abundance, fish length and distribution of redfish, which were associated with Atlantic water, and negatively influenced polar cod, which were associated with Arctic water.

## 2. Materials and methods

### 2.1. Study area

The Barents Sea is a high-latitude, arcto-boreal, shallow shelf sea. The water masses in the Barents Sea are dominated by warm water from the Atlantic Ocean flowing into and across the Barents Sea. The flow of Atlantic water into the Barents Sea is influenced by the atmospheric pressure and winds. Cold water from the Arctic Ocean is found overlying the Atlantic water in the northern Barents Sea. Some of the Arctic water of the northern Barents Sea may circulate around the Svalbard and Franz Josef Land archipelagos. The inflow of Atlantic water results in boreal conditions in the western, central and southern part of the Barents Sea, while the influence of water from the Arctic leads to sub-arctic and arctic conditions in the northern part of the sea (Boitsov et al., 2012). There is a biogeographical transition zone between the boreal and arctic communities.

### 2.2. Studied species

Polar cod is a small, relatively short-lived (5–7 years) circumpolar species that is widely distributed in cold waters. In the Barents Sea, this species occurs in the northern and eastern areas. Spawning of polar cod is associated with the ice in the southeastern Barents Sea during the winter (primarily from January–February) (Ponomarenko, 1968; Hop and Gjøsæter, 2013). Pre-spawners and fry have been observed in the northern and western parts of the Spitsbergen archipelago, indicating that spawning may occur in that region during February and March (Korshunova, 2012). Female polar cod are able to spawn more than once, whereas males (who have a high-energy investment in maturation and sex products) most likely suffer post-spawning mortality (Hop and Gjøsæter, 2013). Polar cod produce large, floating eggs (1.5–1.9 mm), which are widely distributed in the Pechora Sea and along the west coast of Novaya Zemlya (Rass, 1968; Ponomarenko, 1968). The incubation period of the eggs may last for 1.5–3 months, and both eggs and small larvae are found in high concentrations below the ice or in the upper water layers after ice melt (Rass, 1968; Ponomarenko, 1968; Hop and Gjøsæter, 2013). Young-of-the-year (hereafter referred to as 0-group) polar cod have been found in the autumn near Svalbard, in the northern Barents Sea and along the Novaya Zemlya (Hop and Gjøsæter, 2013). In some years, the distribution of polar cod is discontinuous, with western (around Svalbard) and eastern (along Novaya Zemlya) components (Hop and Gjøsæter, 2013).

Beaked redfish is a slow-growing, long-lived boreal species. While the species can live for more than 70 years, the maximum confirmed age in the Barents Sea is more than 40 years old (Drevetnyak and Nedreaas, 2009). Adult beaked redfish (hereafter referred to as redfish) are distributed in the northeastern Atlantic from approximately 62°N in the south to the Arctic ice in the north and from the east side of the Spitsbergen archipelago to 35°E. Redfish larvae are transported by currents from the spawning grounds along the continental slope to the Norwegian Sea and into the Barents Sea towards the Svalbard (Spitsbergen) archipelago region. 0-group redfish occupy the western and northwestern regions of the Barents Sea, while other year-classes occupy the central Barents Sea, particularly near the Hopen Deep (Drevetnyak and Nedreaas, 2009; Ajiad et al., 2011). When redfish reach 5–6 years of age, they migrate to sites along the continental slope, where mature individuals of the population aggregate (Ajiad et al., 2011).

### 2.3. Survey

The joint Norwegian–Russian 0-group fish survey (operated since 2004 as part of the joint Norwegian–Russian ecosystem survey; see below) has been annually conducted during August and September in the Barents Sea. The standard trawling procedure, used on both Norwegian and Russian vessels, consists of stepwise tows at three depths, with the head-line at 0 m, 20 m and 40 m. At each depth level, the trawl is towed for 10 min at a speed of 3 knots (corresponding to a tow length of 0.5 nm or 0.93 km). Additional tows with the head-line at 60 and 80 m are occasionally made if dense concentrations of fish are recorded at depths greater than 60 m on the echo-sounder. Further trawling details and procedures are provided in Anonymous (2004) and Eriksen and Prozorkevich (2011).

Since 2004, the 0-group fish survey has been part of a Joint Norwegian–Russian ecosystem survey, designed and jointly carried out by the Institute of Marine Research (IMR, Norway) and the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO, Russia) (Eriksen and Gjøsæter, 2013). The area covered by the survey has become larger over time due to reduced ice-coverage and has expanded into the northern and northeastern regions of the Barents Sea. Survey details are available at http://www.imr.no/tokt/okosystemtokt_i_barentshavet/sampling_manual/nb-no.

### 2.4. Biotic data

During the study period (1980–2008), approximately 8851 stations were sampled for 0-group fish. The 0-group fish were caught by pelagic trawling in the upper 50 m. 0-group fishes were identified to the species level. Body lengths were measured to a precision of 1 mm on Norwegian vessels and 0.5 mm on Russian vessels and were thereafter aggregated into length groups of 0.5 cm intervals. The data were obtained from the joint Norwegian–Russian 0-group database, which underwent a complete revision and quality check in 2006–2009 (Eriksen et al., 2009).

The surveyed area has increased in recent years due to reduced ice coverage in the north (Prokhorova, 2013; Eriksen and Gjøsæter, 2013); thus, to make our results comparable across all years, we excluded the areas east of Spitsbergen and north of 78°N and the areas east of 35°E and north of 76°N.

### 2.5. Abiotic data

Temperature data were acquired from CTD samples taken at each 0-group trawl station. The CTD profiles were collected either before or after trawling. Here, we used the temperatures averaged to standard depths (5, 10, 20, 30, 40, and 50 m), corresponding to

vertical trawl coverage, to identify the CTH for the 0-group polar cod and redfish. The temperature data were obtained from the Barents Sea Atlas, which contained data through 2008.

Ice coverage during spawning of polar cod (February) were taken from the Norwegian Meteorological Institute (http://met.no/ English/).

### 2.6. Data treatment

Fish density, presented as individuals per square nautical mile (sq nm), was calculated for each trawl haul using catch and trawl data (i.e., depth interval, effective opening and distance trawled). This method is described in detail in Eriksen et al. (2009) and Eriksen and Prozorkevich (2011). To investigate fish response to temperature, we only included sampling stations with fish observations.

The mean fish length for each species at each station was calculated based on the number of fish per length group and weighted by the total fish number. The stations without length measurements were removed from further analyses. The number of stations with length measurement data varied between species. Polar cod were measured at 2186 of the 2194 stations with polar cod observations, while redfish were measured at 2230 of the 2356 stations with redfish observations.

The mean temperature of the 5–50 m water layer at each station was calculated as the average of the temperatures at standard depths (see above). The temperature was measured at a total of 6115 of the 8851 trawl stations.

Ice coverage (sq nm) during spawning of polar cod (February) was calculated for two areas corresponding to the western and eastern components of the polar cod population. The western area was limited to 10–30°E and 76–80°N (hereafter referred to as the Svalbard area), and the eastern area was limited to 40–55°E and 68–72°N (hereafter referred to as the Pechora Sea).

### 2.7. Statistical modelling

The number of stations used for modelling differed from those mentioned above due to lack of temperature and length measurements at some stations and the area restrictions (see above). We expected non-linear associations between biological (fish density and length) and predictor variables (temperature, latitude and longitude), with years having random effects; therefore, we used a General Additive Effects Model (GAM, Wood and Augustin, 2002) approach, implemented in the *mgcv* package in R''. For polar cod, we further divided the reduced data set into two subsets, the western component (west of 35°E) and the eastern component (east of 35°E), and constructed separate models for each subset. The fish density ($D_i$) and fish length ($L_i$) of each species in a sample $i$ (i.e., station) were fitted to the covariate according to the following models:

$$D_i = s(T_i) + year_i + latitude_i + longitude_i + e_i$$
$$L_i = s(T_i) + year_i + latitude_i + longitude_i + e_i$$

where the predictors include the smoothed fits ($s$) of the mean temperature at 5–50 m (T) and the location (latitude and longitude) of sample $i$. The year was entered as a random variable, and $e_i$ denotes the error for sample $i$. The Akaike information criterion (AIC) and genuine cross validation (GCV) values were used to compare possible models.

The core thermal habitat (CTH) was estimated from the model as the temperature range corresponding to fish densities greater than the mean modelled fish density (72% for redfish and 75% for polar cod).

Polar cod spawn in association with ice and changes in spawning conditions will influence recruitment. Therefore, we tested the

similarity in 0-group abundance indices at two spawning sites, which had differing ice coverage, representing the eastern and western population components. 0-group indices were taken from Prokhorova (2013) and are available at http://www.imr.no/sjomil/ index.html.

### 3. Results

The western (west, north and southeast of Spitsbergen) and eastern (west, north and south of Novaya Zemlya) components of the 0-group polar cod population were clearly evident in the distribution maps (Fig. 1). During the 1980 s, polar cod densities were generally low (average of 23,000 fish per sq nm), and contributions from the western and eastern components were similar. Polar cod densities were highest in the 1990s (average of 196,000 fish per sq nm), and higher catches were taken along Novaya Zemlya. During the 2000s, no distinct spatial separation
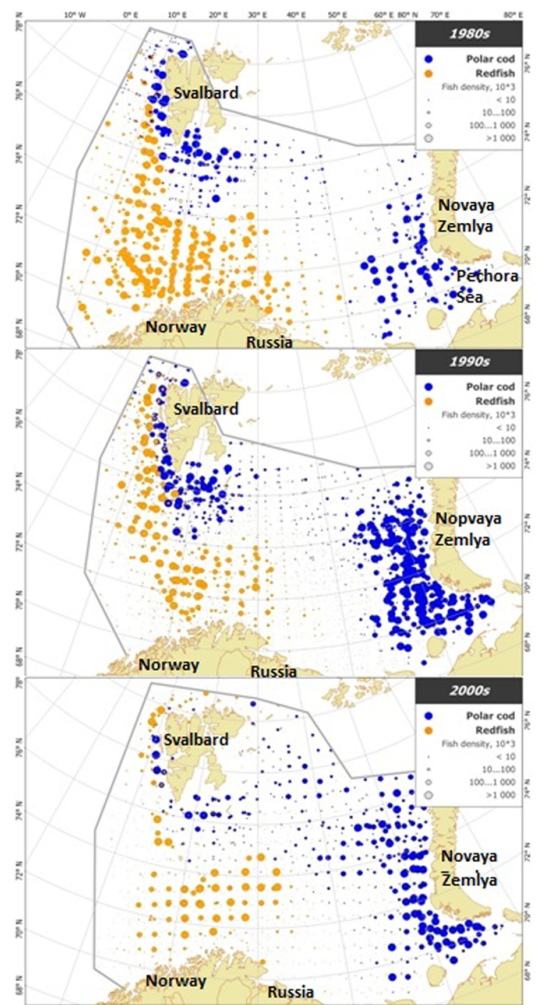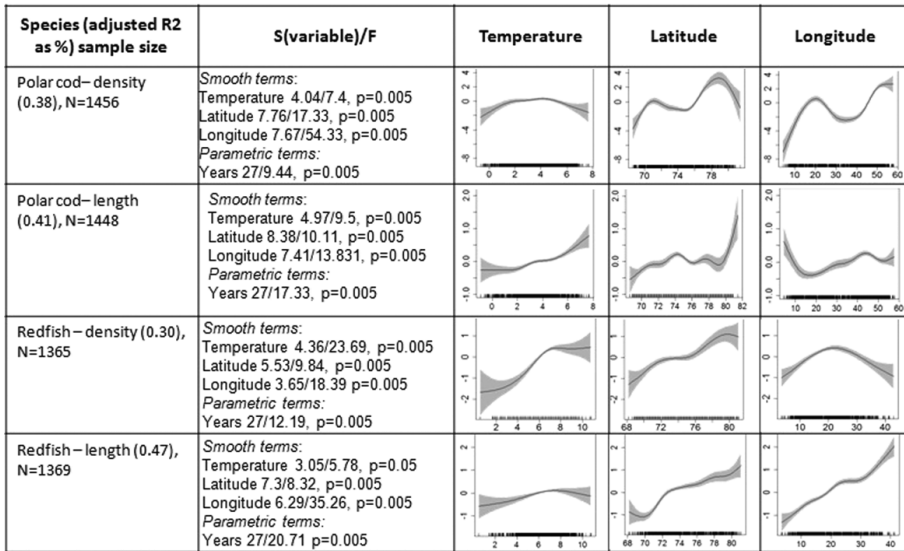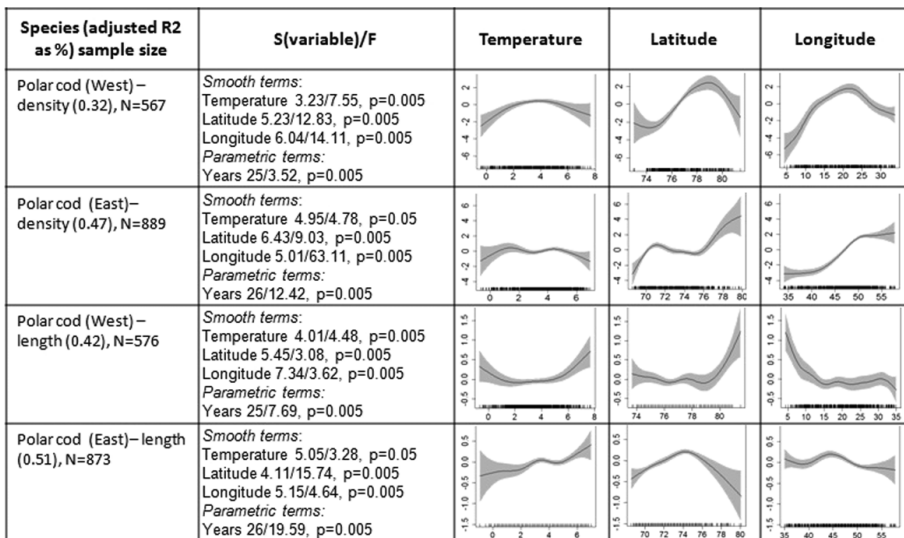


**Fig. 1.** Density distributions of polar cod and redfish by decade: the cold 1980s, the intermediate 1990s, and the warm 2000s.

| Species (adjusted R2 as %) sample size | S(variable)/F | Temperature | Latitude | Longitude |
|---|---|---|---|---|
| Polar cod– density (0.38), N=1456 | Smooth terms: Temperature 4.04/7.4, p=0.005 Latitude 7.76/17.33, p=0.005 Longitude 7.67/54.33, p=0.005 Parametric terms: Years 27/9.44, p=0.005 | | | |
| Polar cod– length (0.41), N=1448 | Smooth terms: Temperature 4.97/9.5, p=0.005 Latitude 8.38/10.11, p=0.005 Longitude 7.41/13.831, p=0.005 Parametric terms: Years 27/17.33, p=0.005 | | | |
| Redfish– density (0.30), N=1365 | Smooth terms: Temperature 4.36/23.69, p=0.005 Latitude 5.53/9.84, p=0.005 Longitude 3.65/18.39 p=0.005 Parametric terms: Years 27/12.19, p=0.005 | | | |
| Redfish– length (0.47), N=1369 | Smooth terms: Temperature 3.05/5.78, p=0.05 Latitude 7.3/8.32, p=0.005 Longitude 6.29/35.26, p=0.005 Parametric terms: Years 27/20.71 p=0.005 | | | |

**Fig. 2a.** Additive models for associations between temperature and spatial distribution (expressed as latitude and longitude) and the abundance and length of polar cod and redfish in the Barents Sea; only non-zero data were used. The adjusted R2 (i.e., proportion of variance explained) and genuine cross validation (GCV) for each model are also given. The shaded regions indicate the 95% point-wise confidence intervals.

| Species (adjusted R2 as %) sample size | S(variable)/F | Temperature | Latitude | Longitude |
|---|---|---|---|---|
| Polar cod (West)– density (0.32), N=567 | Smooth terms: Temperature 3.23/7.55, p=0.005 Latitude 5.23/12.83, p=0.005 Longitude 6.04/14.11, p=0.005 Parametric terms: Years 25/3.52, p=0.005 | | | |
| Polar cod (East)– density (0.47), N=889 | Smooth terms: Temperature 4.95/4.78, p=0.05 Latitude 6.43/9.03, p=0.005 Longitude 5.01/63.11, p=0.005 Parametric terms: Years 26/12.42, p=0.005 | | | |
| Polar cod (West)– length (0.42), N=576 | Smooth terms: Temperature 4.01/4.48, p=0.005 Latitude 5.45/3.08, p=0.005 Longitude 7.34/3.62, p=0.005 Parametric terms: Years 25/7.69, p=0.005 | | | |
| Polar cod (East)– length (0.51), N=873 | Smooth terms: Temperature 5.05/3.28, p=0.05 Latitude 4.11/15.74, p=0.005 Longitude 5.15/4.64, p=0.005 Parametric terms: Years 26/19.59, p=0.005 | | | |

**Fig. 2b.** Estimated smoothing curves for the temperature and spatial distribution (expressed as latitude and longitude) effect on polar cod from western and eastern components used in the model; only non-zero data were used. The adjusted R2 (i.e., proportion of variance explained) and genuine cross validation (GCV) for each model are also given. The shaded regions indicate the 95% point-wise confidence intervals.

between the western and eastern components was found, although higher catches were taken along Novaya Zemlya. The modelled densities for all years showed two peaks for polar cod distribution corresponding to the western (15–25°E and 77–80°N) and eastern components (45–55°E and 70–72°N, Fig. 2a).

The distribution of 0-group redfish was concentrated in the western and central areas, with only a few individuals found east of 30°E. The occupation area for redfish showed a gradual decrease over the three decades of the study (Fig. 1). However, the highest densities were observed during the 1990s (with an average of $0.8 \times 10^9$ fish per sq nm). The modelled redfish densities increased from 70°N to 80°N but with greater variability in the northern region. Most of the modelled densities were distributed between 15 and 30°E (Fig. 2a).

0-group polar cod and redfish were found in the temperature ranges −0.9–8.0 °C and 0–11.0 °C, respectively (Fig. 2a). The CTH (based on the models) that contained the majority of fish was in a temperature range of 2.0–5.5 °C for polar cod and 5.5–8.5 °C
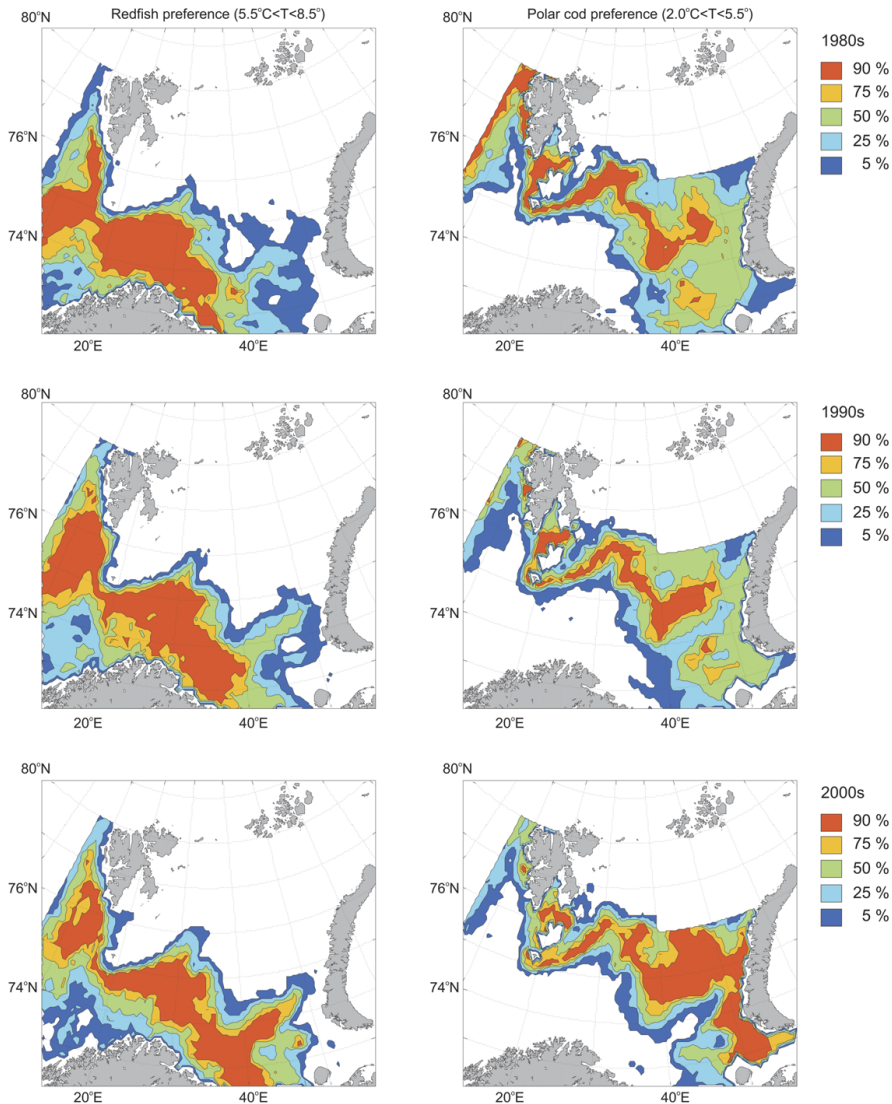
**Fig. 3.** Variation in the distribution of CTH for polar cod (right) and redfish (left) in 1980s (upper), 1990s (mid) and 2000s (below). The contoured values are the number of years (as a percentage of the total number of years, $N = 29$) when the water in each grid cell was within the CTH range.

for redfish (Fig. 2a). While the polar cod densities within this temperature range were similar, the redfish densities increased with increasing temperature. Only 5% of redfish were observed at temperatures higher than 8.5 °C.

The mean fish length was 4.0 cm for polar cod and 3.6 cm for redfish. The modelled and observed fish length distributions showed that polar cod length increased with increasing temperatures above 2 °C (Fig. 2a), but some larger individuals occurred at lower temperatures in the western region (Fig. 2b). The relationship between redfish length and temperature was not as pronounced as for polar cod. The smallest redfish were observed at the lowest temperatures, and the average length increased from 2 to 8 °C. At temperatures of 8 °C and above, the average length decreased (Fig. 2a).

During the cold 1980s, the area of polar cod CTH was larger than the long-term mean (920 thousand km², 1980–2010), while the area of CTH was smallest during the intermediate temperatures of the 1990s (Fig. 4). The area of the CTH decreased, especially west and south of Spitsbergen, in the last two decades of the study compared to the 1980s. However, the opposite trend was observed for the Novaya Zemlya region during the 2000s. Variations in the distribution of water with temperatures within the CTH range were thus more evident in the southeastern Barents Sea and west and south of Spitsbergen. For redfish, the area of CTH was smaller during the 1980s than the long-term mean (950 thousand km², 1980–2010, Fig. 3). The area of redfish CTH increased from the 1980s to the 1990s (Fig. 4); however, this increase occurred primarily in the southeast, outside of the main redfish occupation
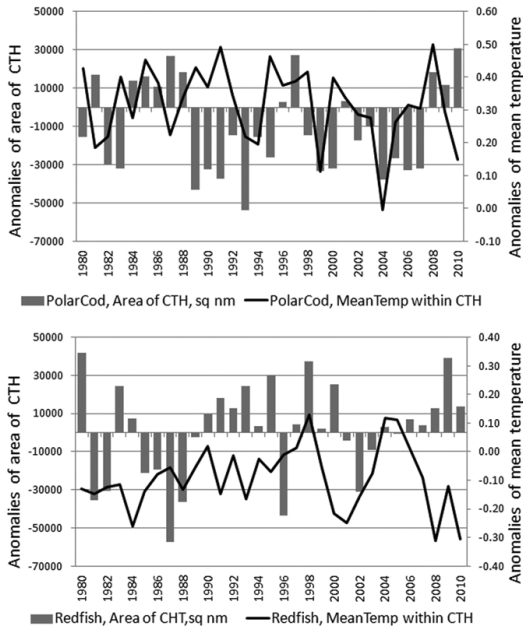
**Fig. 4.** The core thermal habitat (CTH) occurred from 2.0–5.5 °C for polar cod and 5.5–8.5 °C for beaked redfish. Annual variation in the area of the CTH (grey columns) and the mean temperature (solid black line) within the CTH for polar cod (upper panel) and redfish (lower panel) in 1980–2008.

area. Variations in the distribution of water with temperatures within the CTH were more evident along the southwestern border of the redfish occupation area.

Ice coverage varied between years and regions (see the Materials and Methods section). Annual ice coverage in the Pechora Sea showed high interannual variability in ice coverage (Fig. 5(A) (B)), while somewhat less variability was observed in the Svalbard region (Figure C, D). However, the Svalbard region had a significant decreasing trend in ice coverage (Fig. 5(E)). There was a positive significant correlation between ice coverage in the Pechora Sea and 0-group indices for the polar cod eastern ($r = 0.31$, $p < 0.05$) and western ($r = 0.27$, $p < 0.05$) component.

## 4. Discussion

The Barents Sea is a nursery area for several commercially and ecologically important fish stocks, including redfish and polar cod. The main goals of the 0-group investigations have been to give an early indication of year class strength for commercially important fish stocks and to map their spatial distribution in the Barents Sea (Eriksen and Gjøsæter, 2013). Since 1980, both abundance estimates and distribution of 0-group polar cod and redfish have been presented in the survey reports (Anonymous, 2004; Eriksen and Gjøsæter, 2013). However, 0-group polar cod are also distributed outside of the survey area, e.g., in the fjords of the Spitsbergen archipelago and northeast of Novaya Zemlya, and dense concentrations of 0-group redfish are also found beyond the western region of the survey area. The numbers of these two species that are distributed outside of the survey area are unknown due to lack of monitoring (Drevetnyak and Nedreaas, 2009; Ajiad et al., 2011; Prokhorova, 2013). Additionally, the survey coverage in the north has varied due to ice coverage, and thus an unknown part of the polar cod population has not been

sampled in some years. Therefore, we excluded the area in the north that was not surveyed in each year to make our results comparable across all years. This reduction in the amount of data (<5% in fish number) may have weakened the model with regards to accurate habitat boundaries. Despite these shortcomings, the long term monitoring, based on standard procedures, allowed us to explore how recent warming trends may be influencing the abundance, distribution and growth of polar cod and redfish in the Barents Sea. Polar cod is an arctic fish that prefers low temperatures (Borkin, 1979; Ponomarenko, 1968; Christiansen et al., 2012; Hop and Gjøsæter, 2013). The majority of 0-group polar cod in the Barents Sea were found at water temperatures between 2.0 and 5.5 °C. However, the lower range limit of thermal habitat is uncertain and should be interpreted with care. The results supplement earlier observations of adult polar cod, which showed that most of the fish were observed in the Barents Sea at temperatures below 5 °C (Ponomarenko, 1968; Ajiad et al., 2011). The majority of the western component of polar cod was found within a narrower temperature range (2–5.5 °C) compared to the eastern component (1–5.5 °C). This is due to general hydrographic conditions, i.e., water from the Atlantic water creates boreal conditions near the Spitsbergen archipelago, while coastal and Arctic waters from the Kara Sea result in arcto-boreal conditions in the Pechora Sea (Boitsov et al., 2012).

Additionally, the decrease in areas of CTH for polar cod and the high variability of temperature within these areas, especially west of Spitsbergen, may negatively influence the resulting year class strength. The polar cod stock has undergone large changes during the last three decades, with stock size decreasing to 0.1 million tonnes in 1988, increasing to 1.8 million tonnes in 2005, and falling to 0.3 million tonnes in 2013 Boitsov et al. (2013) and Eriksen et al. (0000). The occupation of adults in the eastern component has had an eastward and southward shift (ICES, 2014), and there was a reduction of ice coverage during the spawning period in both the Svalbard region and the Pechora Sea. The Pechora Sea had larger annual variation in ice coverage than did Svalbard (Fig. 5), and correlations between ice coverage and 0-group abundance indices were evident, indicating that reductions in ice coverage resulted in poorer recruitment. The eastern component contributed to 81% of total 0-group polar cod abundance; therefore, a reduction in suitable spawning habitat in the Pechora Sea may significantly influence the outcome of spawning. Earlier studies have shown that decreasing areas of Arctic water is associated with a redistribution of the occupation area of both juveniles and adults (Hop and Gjøsæter, 2013; ICES, 2014), and Hop and Gjøsæter (2013) concluded that the reduction of sea ice and increased temperatures had reduced the sympagic (ice-associated) part of the species' life cycle. This study supplements earlier findings and indicates that continued warming will lead to a further reduction of suitable spawning habitat during the winter and of 0-group habitat during the late summer–early autumn. Both adult and juvenile polar cod may lack suitable habitat within the Barents Sea. Furthermore, because polar cod are a key link in the Arctic food web (Ajiad et al., 2011; Christiansen et al., 2012; Boitsov et al., 2013), a further decline in abundance may lead to a restructuring of the Arctic community, which in turn will influence the Barents Sea ecosystem (Hop and Gjøsæter, 2013; Boitsov et al., 2013).

Redfish, in contrast, is a long-lived boreal species (Drevetnyak and Nedreaas, 2009; Ajiad et al., 2011). Redfish larvae are transported by warm currents into the Barents Sea, and 0-group redfish are usually found in the western and northwestern regions (core area). The majority of 0-group redfish were found within a CTH range of 5.5–8.5 °C. However, the upper bound of the CTH was not properly defined by the model, indicating that redfish may remain in water with higher temperatures than 8.5 °C. Additional sampling conducted at greater depths (>500 m) along
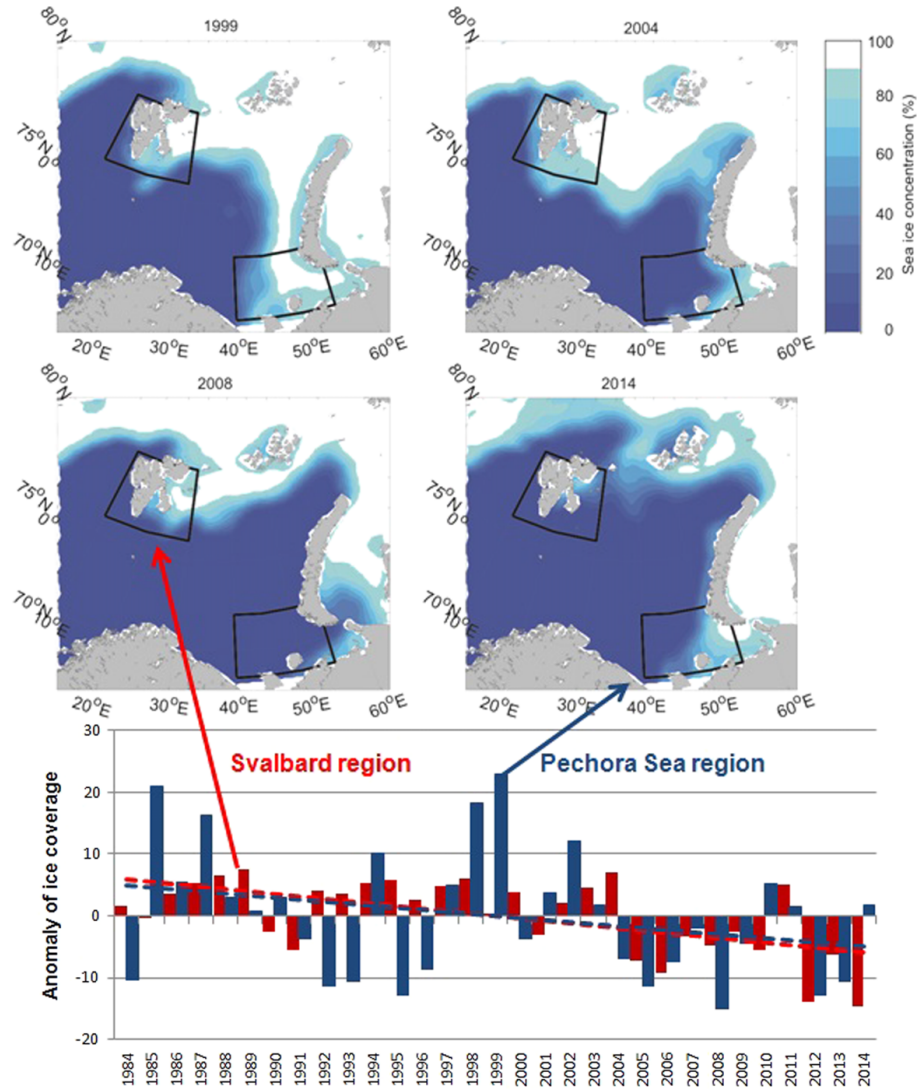
**Fig. 5.** Ice coverage for spawning sites in the Svalbard region (northwest) and Pechora Sea, where A–D show the minimum and maximum ice coverage within the boxed areas and *E* shows anomalies in February ice coverage (during the spawning period) in the Barents Sea from 1984–2014.

the continental shelf between 72°N and 79°N in 2014 showed dense concentrations of 0-group redfish between 25 and 120 m depth (Engås et al., 2013) within a temperature range of 5–8 °C (Trofimov and Ingvaldsen, 2013). Thus, 0-group redfish were not exclusively associated with the Barents Sea shelf and may have a wider distribution into the Norwegian Sea. Furthermore, few 0-group redfish were found in the eastern Barents Sea (east of 30°E), even though these eastern areas had temperatures within the CTH for redfish. These results indicate that westward and eastward extension of the redfish occupation area are more likely to be determined by the location of spawning sites, currents and the drift routes of larvae than by available CTH.

Variation in the distribution of waters with temperatures within the CTH was most evident along the southwestern border of the redfish occupation area. Here the redfish may be limited by

warmer water masses (above 8.5 °C), which may apply a thermal stress on the redfish (i.e., temperatures outside the CTH) and hence limit redfish abundance in the southwestern shelf region. Strong year classes of redfish, primarily beaked redfish, were recorded in the 1980s and then again in 2007. The fishery for beaked redfish was traditionally located south of Bear Island near Spitsbergen, and the years with the largest landings (269,000 tonnes in 1976 and 115,000 tonnes in 1982) were followed by a rapid decline (Drevet-nyak and Nedreaas, 2009; ICES, 2010). After the stock collapsed, beaked redfish was classified as a threatened species on the Nor-wegian red-list (ICES, 2010). Additionally, before the sorting grid was introduced to the commercial shrimp fishery in 1992, large numbers of redfish juveniles were caught as by-catch in the Bar-ents Sea shrimp fishery (Ajiad et al., 2007). It is indisputable that the remarkable decline of the beaked redfish stock was the main

reason for the low recruitment in the 1990s and 2000s. If the mature stock is sufficiently high and well composed demographically, the ongoing warming trend may be favourable for redfish recruitment. However, the present findings demonstrate that there seems to be an upper thermal limit for this species. Redfish may avoid suboptimal temperatures by changing depth, although the efficacy of this strategy depends on the swimming ability of 0-group redfish. The dense pelagic concentrations observed between 25 and 120 m depth along the continental shelf between 72°N and 79°N, where bottom depths were >500 m, may be indicative of such adaptive behaviour and should be monitored in the years to come.

## 5. Conclusions

Temperature may be an important factor controlling the abundance, distribution and growth of 0-group polar cod. Thermal stress due to increased summer–autumn temperatures, especially in the Pechora Sea, and a reduction of ice cover resulting in a loss of suitable spawning habitat during the winter may have a negative effect on 0-group polar cod abundance, thereby leading to a further decline of polar cod in the Barents Sea. The consequences of that decline may influence both the Arctic and Barents Sea ecosystems. For 0-group redfish, the preferred thermal habitat has decreased in the southwestern region of the survey area due to a temperature increase in these waters in recent decades. Although CTH is available in the northeast, 0-group redfish do not seem to have extended their distribution to compensate for reduced habitat in the southwest. The resulting shrinkage of the preferred habitat may thus have a negative effect on 0-group redfish abundance in the Barents Sea, and future recruitment reductions may occur if the preferred thermal habitat continues to decrease. Suitable and favourable temperature and feeding conditions observed along the continental slope at the northwestern margin of the survey area may decrease the importance of the more central Barents Sea shelf as nursery area for 0-group redfish. This idea should be taken into consideration when future surveys are designed, and abundance indices should be estimated by extending these surveys by some nautical miles further to the west.

## Acknowledgements

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