Review

Spatial and temporal changes in the Barents Sea pelagic compartment during the recent warming

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ABSTRACT

The Barents Sea has experienced substantial warming over the last few decades with expansion of relatively warm Atlantic water and reduction in sea ice. Based on a review of relevant literature and additional analyses, we report changes in the pelagic compartment associated with this warming using data from autumn surveys (acoustic capelin, 0-group fish, and ecosystem surveys). We estimated biomass for 25 components of the pelagic community, including macroplankton, 0-group fish, and juvenile and adult pelagic fish, were examined for spatial and temporal variation over the period 1993–2013. 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 21-years period. Krill was the dominant biomass component (63%), whereas pelagic fish (capelin, polar cod and herring) made up 26% and 0-group fish 11% of the biomass on average. The spatial distribution of biomass 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. Dividing the Barents Sea into six regions, 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.

The total estimated biomass of the pelagic compartment remained relatively stable during 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. The pronounced increase reflected the warming between the relatively cold 1990s and the warmer 2000s and was driven mainly by an increase in krill due presumably 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 next years manifested as strong or weak year classes of dominant pelagic species. Associated with the warming there was also a northern or eastern extension of the distribution of several components although the broad-scale geographical pattern of biomass distribution remained similar between the first and the last parts of the investigated period. The capelin stock, a dominant species with a substantial contribution to total biomass, experienced two collapses followed by recoveries in the 1990s and 2000s. The apparent stability in total biomass in each of the two periods (before and after 2004) reflected compensating and dampening mechanisms. In the first period, krill showed an inverse relationship with capelin, increasing when the capelin stock was low. In the second period, other fishes including juvenile herring, polar cod and blue whiting increased to fill the 'void' of the low capelin stock. The syntheses reported here provides a basis for modelling some of the key players and dominating processes and drivers of change in the ecosystem.

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Contents

1. Introduction

Climate warming affects the distribution and biomass of marine species, reorganizing ecological communities and influencing ecosystem functions (Johannesen et al., 2012; Dalpadado et al., 2012; Michalsen et al., 2013; Wiedmann et al., 2014; Kortsch et al., 2015). Fish and zooplankton display some of the most rapid poleward shifts in distribution, with pelagic fish tracking climate velocities (Prokhorova, 2013; Fossheim et al., 2015). The biomass of pelagic species is also affected by warming, but the direction, magnitude and rate of change are harder to predict and interpret, as they depend on higher order effects of warming mediated by primary productivity and ecological interactions. Some of the most rapid and substantial climate driven changes in marine ecosystems are expected at high latitudes, in regions within, or bordering, the Arctic, where rates of warming are double the global average (Wiedmann et al., 2014; Fossheim et al., 2015; Kortsch et al., 2015).

Among the regions that have registered the highest rates of recent warming are the Arctic reaches of the Barents Sea. The Barents Sea ecosystem underwent a rapid environmental change during the last few decades displaying a warming trend with increasing peaks since the mid 1980s, with the last decade being the warmest on record (Ingvaldsen et al., 2003; Sakshaug et al., 2009; Jakobsen and Ozhigin, 2011; Boitsov et al., 2012; Dalpadado et al., 2012, 2014). During this period, both oceanic and atmospheric temperatures have increased substantially, and higher inflow of warm Atlantic water has increased the areal coverage of Atlantic waters in the southern Barents Sea, while decreased the area influenced by Arctic water in the north (Ozhigin et al., 2011). Associated with the warming trend, there was a push-back of sea-ice with a reduced extent of sea-ice cover in the winter (Boitsov et al., 2012; Johannesen et al., 2012; Dalpadado et al., 2012, 2014). As Atlantic water masses expand in the Barents Sea, zooplankton of Atlantic origin is gradually replacing arctic zooplankton (Dalpadado et al., 2012). This trend has mainly affected the commercial fish stocks positively, but opposite trends in abundance of zooplankton and plankton-eating fish have also been documented, pointing to a predator-prey feedback mechanism (Dalpadado and Skjoldal, 1996; Dalpadado et al., 2002; Stige et al., 2014).

The increasing water temperatures and changes in distribution of water masses and plankton communities have induced poleward shifts in the distribution of several boreal fish species (Ingvaldsen and Gjøsæter, 2013; Prokhorova, 2013; Fossheim et al., 2015). The same environmental changes have had negative implications for living conditions and feeding habitats of several arctic fish species feeding on arctic plankton (Wassmann et al., 2006a; Hop and Gjøsæter, 2013; Eriksen et al., 2015). Water temperature influences larvae and juveniles directly through metabolism and indirectly through food availability and habitat conditions (Brett, 1979). Increased inflow of Atlantic water and higher temperature are associated with increased recruitment of all the major fish stocks such as Atlantic cod, haddock, herring and capelin (Ottersen and Loeng, 2000; Eriksen et al., 2011, 2012b). However, Bogstad et al. (2013) concluded that at least for cod and herring, the association between recruitment success and high temperatures was weaker towards the end of the 100-year period they analysed although still positive. Johannesen et al. (2012) analysed four decades of data from 1970 onwards, over which the climate and the fishing pressure have changed substantially. The authors considered lowered fishing pressure and effects from warming to be the main reasons for the increased stock sizes in recent years. They concluded that trophic relationships in the Barents Sea were complex and dynamic and that there was no clear evidence for persistent ecological regimes (Johannesen et al., 2012). Kjesbu et al. (2014) made a detailed analysis of the Barents Sea cod stock and reached the same conclusion; that both reduced fishing pressure and warming had contributed to the strong build-up of the cod stock. On the other hand, Hjermann et al. (2010) concluded that the dramatic fluctuation in the dominating pelagic fish stock in the area, the capelin (*Mallotus villosus*), was mainly caused by trophic cascades initiated by the presence/absence of herring (*Clupea harengus*) sporadically entering the Barents Sea when rich year classes are recruited. In this case, fishing pressure played a minor role (Gjøsæter et al., 2016).

Recent literature on the implications of warming for the Barents Sea ecosystem indicates that, overall, production has increased, although single species may have suffered. Several species and ecosystem properties have been affected, as indicated by recent studies of recruitment processes (Ciannelli et al., 2007; Dingsør
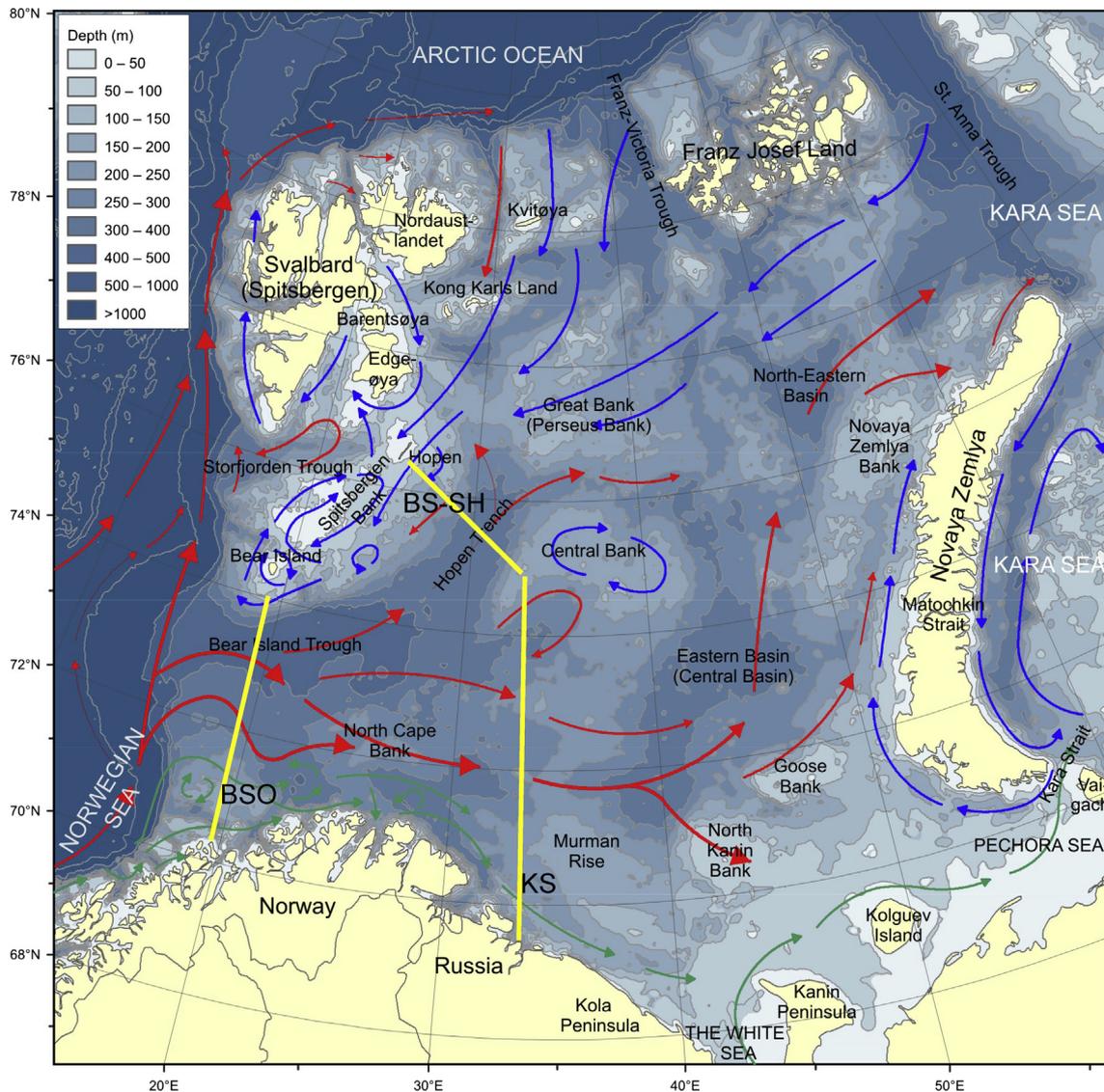
Fig. 1. The Barents Sea. Red arrows show Atlantic water currents, blue arrows Arctic currents and green arrows coastal waters. Yellow lines show positions of the Barents Sea Opening (BSO), Hopen (BS-SH) and Kola (KS) sections used for obtaining modelled fluxes of water. The BSO section corresponds to the Fugløya-Bjørnøya oceanographic transect.

et al., 2007; Hjermann et al., 2010; Stige et al., 2010; Eriksen et al., 2012b; Bogstad et al., 2013), fish population size and structure (Kjesbu et al., 2014), fish species and functional diversity (Wiedmann et al., 2014), food web topology (Kortsch et al., 2015), and ecosystem structure and functioning (Johannesen et al., 2012; Dalpadado et al., 2012, 2014; Michalsen et al., 2013; Kortsch et al., 2015). Despite changes in fish community structure (Aschan et al., 2013; Fossheim et al., 2015) and in biomass and structure of both lower and higher trophic levels, no clear regime shifts have been recognized (Johannesen et al., 2012). The Barents Sea is apparently an ecosystem characterized by high variability and resilience (Yaragina and Dolgov, 2009).

In this paper, we review recent literature on how climate warming and other drivers influence biomass variation of major pelagic components at different spatial and temporal scales. We also use data from trawl catches and acoustic recordings collected during the joint Norwegian-Russian surveys in autumn to estimate the biomass contributions of major species or groups in the pelagic compartment. Specifically, we analyse biomass changes of macro-zooplankton/micronekton and fish at small (grid cell), intermedi-

ate (subareas) and large (whole Barents Sea) scales during the years 1993–2013. This analysis is part of a review of changes in the Barents Sea ecosystem associated with a warming trend over the recent decades. We provide first an overview of the Barents Sea ecosystem and the recent warming event (Section 2). Next, we present the analysis of biomass changes in time and space (Sections 3 and 4), followed by a section on the overall state of the ecosystem expressed by a multivariate representation of biomass in the pelagic compartment (Section 5). We then go on to discuss the ecological interpretations and implications of the observed changes in the Barents Sea ecosystem in response to the climate warming (Section 6), before we end with some concluding remarks and suggestions for follow-on work (Section 7).

2. The Barents Sea ecosystem

2.1. Climate variability and change

The Barents Sea is a high latitude shelf ecosystem located between about 70 and 80°N in the northeastern Atlantic (Fig. 1).
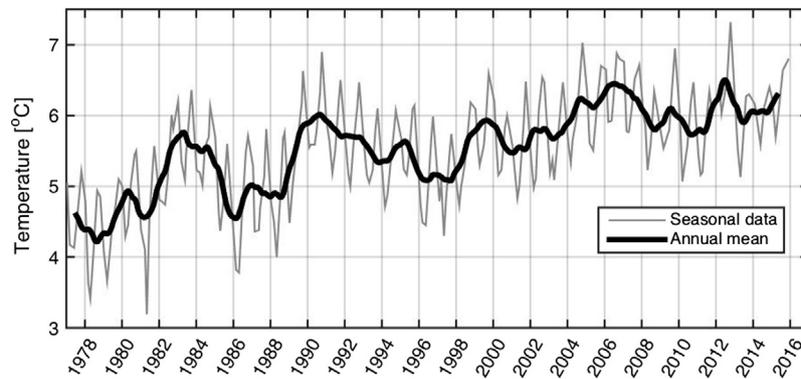
Fig. 2. Long term series (1980–2015) of annual temperature at the Fugløya-Bjørnøya section (FB, grey line) and 10 years moving average shown with black line.

The shelf area is relatively deep (mean depth of 230 m) and quite extensive (approximately 1.6 million km² in area). The Barents Sea constitutes a biogeographical transition zone between a warmer boreal southern part and a cold Arctic northern part (Fossheim et al., 2015). There are several recent overviews and reviews of the climate and ecosystem of the Barents Sea (e.g. Wassmann et al., 2006a; Loeng and Drinkwater, 2007; Drinkwater, 2011; Hunt et al., 2013; Smedsrud et al., 2013). Readers are referred to these and other sources for detailed accounts of the physical and biological conditions and variability of the Barents Sea ecosystem. Here we limit ourselves to a brief account of some key features of the climate and ecological system of the Barents Sea.

The North Atlantic Current (partially 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 and the other flowing around the western and northern flanks of the Barents Sea as the West Spitsbergen Current (Skagseth et al., 2008; Ingvaldsen and Loeng, 2009; Ozhigin et al., 2011). The heat content of the Atlantic water leads to relatively mild conditions in the western and southern regions, whereas more Arctic conditions prevail in the northern and eastern regions of the Barents Sea (Ozhigin et al., 2011; Smedsrud et al., 2010, 2013).

The bottom topography with banks and basins steers the currents and governs the distribution of water masses (Loeng, 1991; Fig. 1). The dominant Atlantic and Arctic water masses are separated by the oceanographic Polar Front, which is topographically determined and sharp in the western and central Barents Sea but more gradual and transitional in the eastern part where there is more mixing of water masses (Drinkwater, 2011). The inflow and throughflow of Atlantic water has a large impact on the ocean climate of the Barents Sea (Drinkwater, 2011; Hunt et al., 2013; Smedsrud et al., 2013). The hydrographic section (Fugløya-Bjørnøya, FB) across the southwestern Barents Sea opening records the temperature conditions of the inflowing Atlantic water (Fig. 1). A time series since 1980 at FB (Fig. 2) shows seasonal oscillations (with amplitude 1–2 °C between winter minimum and summer maximum) superimposed on an increasing although fluctuating trend. A typical pattern revealed in longer time series analysis with data from the Kola section (across the Atlantic current further into the Barents Sea, Fig. 1) has been an alteration of cold and warm years at about 3–4 year's interval (Loeng, 1991; Ingvaldsen et al., 2003; Boitsov et al., 2012). For the period 1993–2013, which we focus on in the analyses in following sections, the temperature of the inflowing Atlantic water decreased to a local minimum in 1997, followed by a pronounced increase in two steps up to a maximum in 2006–2007. After this time, conditions have remained
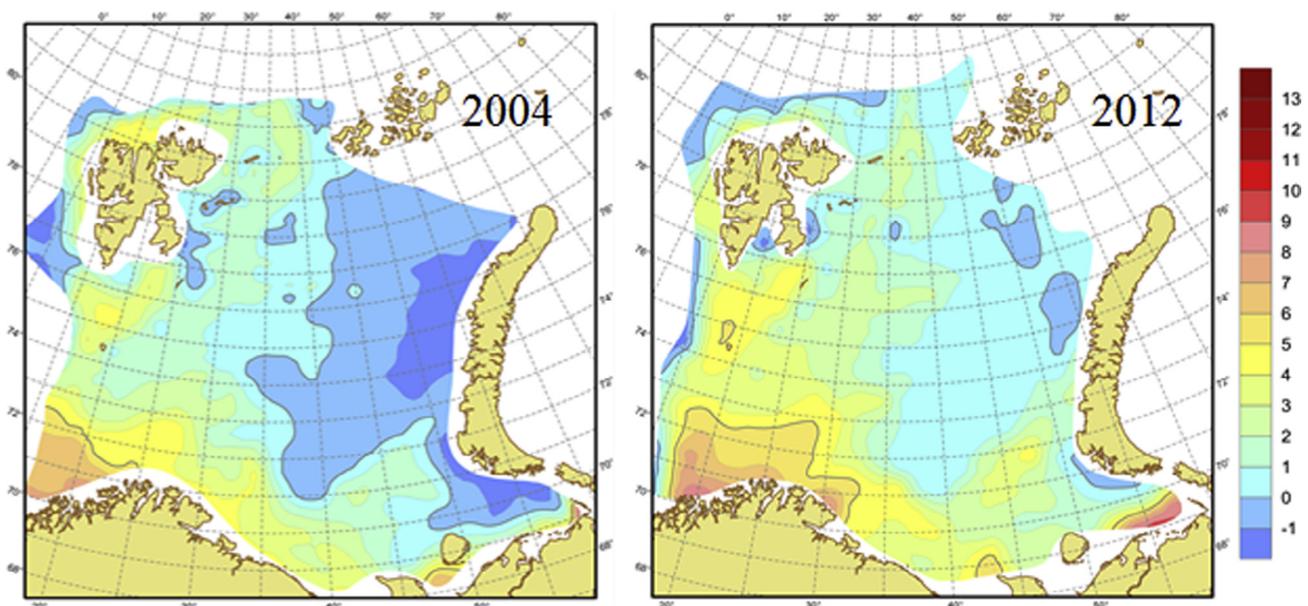

Fig. 3. Distribution of temperature (°C) at the bottom, August–September 2004 (left panel) and 2012 (right panel).

warm but with some cooling up to about 2010 followed by another warm event in 2012 (Fig. 2).

The inflowing Atlantic water became warmer by 1–1.5 °C between the local minimum in 1997 and the maximum in 2006/07. This was associated with increased area coverage of Atlantic and mixed water masses (defined as waters of temperature >3 °C and 0–3 °C, respectively) in the Barents Sea and a corresponding reduction of area of Arctic water (temperature <0 °C) (Johannesen et al., 2012; Dalpadado et al., 2014). There was also a concomitant reduction in the maximum area of sea ice in winter (typically in April), with a decline in trend of about 0.4 million km² since 1980, representing a loss of about half the area of winter sea ice during the warming of the recent decades. These climatic changes are quite dramatic and are reflected as a pronounced increase in the extent of near-bottom temperatures warmer than 0 °C (Fig. 3).

2.2. Biological components of the ecosystem

A spring bloom of phytoplankton is a prominent feature of the annual cycle of primary production in a high latitude ecosystem like the Barents Sea (Wassmann et al., 2006a; Sakshaug et al., 2009; Hunt et al., 2013). The spring bloom in Atlantic water is driven by seasonal heating (thermocline) which results in a slow and protracted development, while the bloom in the seasonal sea-ice zone (ice edge bloom) develops more rapidly in response to stabilization from ice melt (Skjoldal and Rey, 1989; Sakshaug and Skjoldal, 1989; Wassmann et al., 2006a). The stronger degree of stratification due to melting of sea ice limits the vertical admixture of nutrients from deeper water layers. This is reflected in lower annual primary production in seasonally ice-covered waters in the northern Barents Sea (30–70 g C m^{-2} y^{-1}) compared to Atlantic water in the southern part (100–150 g C m^{-2} y^{-1}). The mean annual primary production for the Barents Sea is estimated to be about 100 g C m^{-2} y^{-1}, with a suggested increase of possibly 20–30% associated with the warming and loss of sea ice during the two last decades (Sakshaug, 2004; Wassmann et al., 2006b; Arrigo et al., 2008; 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). The mesozooplankton in the Barents Sea is dominated by mainly herbivorous calanoid copepods with *Calanus finmarchicus* in Atlantic water in south and *Calanus glacialis* in Arctic water in north (Melle and Skjoldal, 1998; Wassmann et al., 2006a; Eiane and Tande, 2009). These copepods reproduce in spring nourished by the early spring growth of phytoplankton (and ice algae for the Arctic *Calanus glacialis*) (Melle and Skjoldal, 1998; Søreide et al., 2008; Falk-Petersen et al., 2009). The new cohorts (generations) of copepods develop during summer with one-year (*Calanus finmarchicus*) or two-year (*Calanus glacialis*) life cycles (Tande, 1991; Melle and Skjoldal, 1998; Falk-Petersen et al., 2009). The *Calanus* species make up the bulk of the mesozooplankton biomass which is monitored and mapped during joint IMR-PINRO autumn surveys. The mean zooplankton biomass is typically 5–10 g dry weight m^{-2} and the temporal and spatial variation have been related to both climate and predation by pelagic fish, notably by the large but varying capelin stock (Dalpadado et al., 2014; Kvile et al., 2014; Stige et al., 2014).

Krill and amphipods are important components of the macrozooplankton. There are four main species of krill in the Barents Sea, mostly associated with Atlantic water in the southern and western areas. *Thysanoessa inermis* is found mainly in the western and central parts, *T. raschii* is associated with shallow waters in the southeastern Barents Sea, whereas the smaller *T. longicaudata* and the largest species *Meganyctiphanes norvegica* are more strongly

associated with the inflowing Atlantic water in the southwestern Barents Sea (Drobysheva, 1994; Dalpadado and Skjoldal, 1991, 1996; Dalpadado and Mowbray, 2013; Orlova et al., 2015; Eriksen et al., 2016). Long-term monitoring of krill in Russian investigations (collected with a plankton net attached to bottom-trawl) since the 1950s has revealed an increasing trend in krill abundance associated with warming from the 1980s (Zhukova et al., 2009; Orlova et al., 2013, 2015). The general increase in krill reflected increased advection and abundance of *Thysanoessa inermis* and *Meganyctiphanes norvegica* in warm years, whereas *Thysanoessa raschii* showed an opposite trend in the southeastern Barents Sea (Orlova et al., 2013, 2015). Data from a joint Norwegian-Russian pelagic trawl survey (same as used in subsequent parts of the present paper; see Sections 3–5) has also shown an increased amount of krill in the Barents Sea in recent decades (Eriksen and Dalpadado, 2011; Eriksen et al., 2016).

There are two species of hyperiid amphipods which are important in the Barents Sea: the large Arctic *Themisto libellula* (up to 5–6 cm in length) found mainly in the northern Barents Sea and the smaller (2–3 cm) *T. abyssorum* which is a boreal-arctic species (Dalpadado, 2002; Dalpadado et al., 2008). Pelagic amphipods have shown a declining trend, opposite to that of krill, over the recent decades (Dalpadado et al., 2014). This reflects most likely the association of the *Themisto* species with the cold Arctic water mass which have declined in extent due to warming (Johannesen et al., 2012; Dalpadado et al., 2014).

The Barents Sea fish community is dominated by few large stocks, such as the Barents Sea cod (*Gadus morhua*), Barents Sea capelin (*Mallotus villosus*), Northeast Arctic haddock (*Melanogrammus aeglefinus*), and Norwegian spring-spawning herring (*Clupea harengus*). The Barents Sea serves as a nursery area for the offspring of several commercial fish stocks which spawn 'up-stream' along the coast. 0-group fish distributes over wide areas and are important in energy transport between different trophic levels and different geographical areas, thus playing a key role in the entire Barents Sea ecosystem (Eriksen et al., 2011, 2012b). The pelagic species capelin, polar cod (*Boreogadus saida*), young herring, and blue whiting (*Micromesistius poutassou*) constitute the bulk of pelagic fish biomass in the Barents Sea. These species are mainly plankton-feeders and constitute important links between lower and higher trophic levels in the Barents Sea ecosystem (Skjoldal and Rey, 1989; Dolgov et al., 2011a, 2011b). The total biomass of fish in the Barents Sea is of the order 10–12 million tonnes (1983–2011), whereas the total biomass of the four pelagic fish species has fluctuated between about 1 and 8 million tonnes (1973–2013), driven largely by the large fluctuations of the capelin stock (Fig. 4; Gjøsæter et al., 2009).

Since 1980 there have been three collapses of the Barents Sea capelin stock, followed by rapid recoveries within a few years (Fig. 4). Recruitment failure due to predation by juvenile herring on capelin larvae has been implied as a main cause for the capelin collapses (Gjøsæter and Bogstad, 1998; Gjøsæter et al., 2009, 2016). An opposite pattern of fluctuations in capelin and juvenile herring is seen in Fig. 4 where increased abundance of juvenile herring occurs when the capelin stock is declining at each capelin collapse. Increased predation from cod and poor individual growth of capelin due to lower availability of zooplankton food are also implied as contributing factors to the capelin collapses (Skjoldal and Rey, 1989; Gjøsæter et al., 2009; Hjermann et al., 2010). The first observed collapse in the 1980s had large repercussive effects in the ecosystem, reflected in poor state of the cod stock, seal invasions, and seabird breeding failure and mortality (Skjoldal and Rey, 1989; Hamre, 1994). The next two collapses had more moderate impacts, apparently due to dampening effects by other components of the ecosystem (Gjøsæter et al., 2009). These two collapses and subsequent recoveries are within the time period we consider
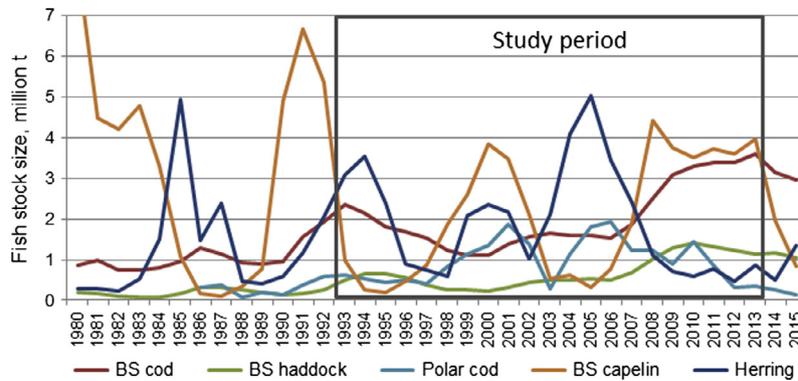
Fig. 4. Fluctuations of five of the main Barents Sea fish stocks during 1980–2015. The total stock biomass (million tonnes wet weight) is given for 3 years and older cod and haddock, one-year and older capelin and polar cod, and 1–3 years old juvenile herring. Based on data from joint Norwegian-Russian surveys and stock assessments by ICES (2015).
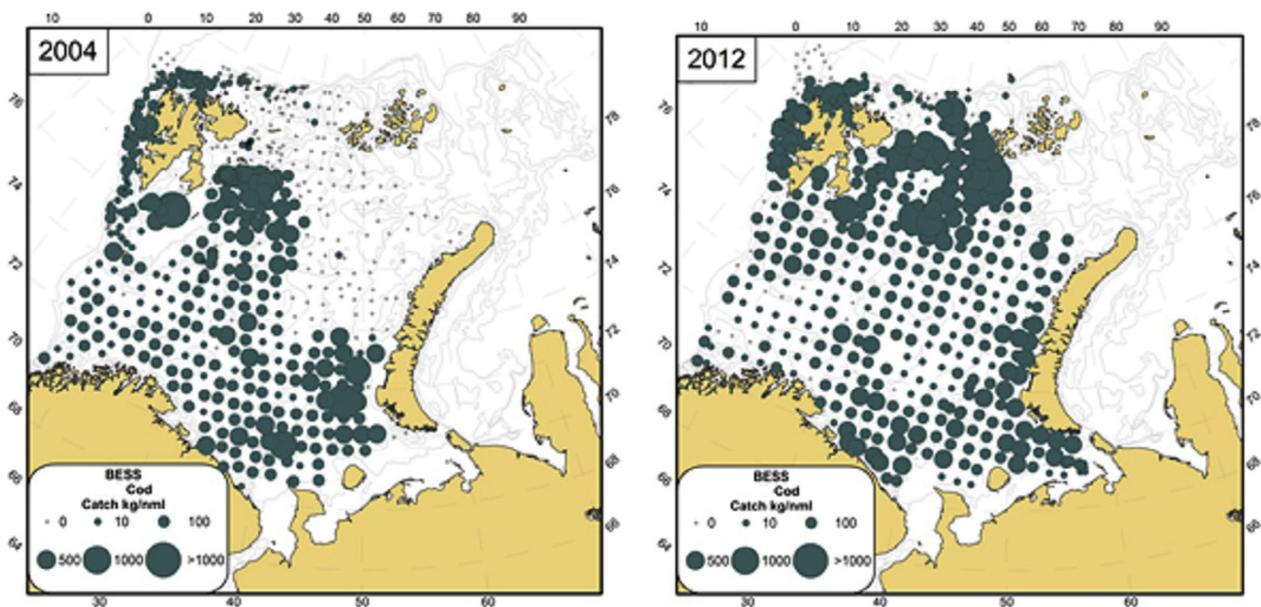
Fig. 5. Cod distribution in the autumn 2004 (left panel) and 2012 (right panel) in the Barents Sea.

specifically in the following sections of this paper (1993–2013, Fig. 4). A fourth collapse of the capelin stock took place after 2013 (Fig. 4). The same factors (recruitment, growth and predation) appeared to have played roles in this most recent collapse, with predation from the large cod stock being the most important factor this time around (ICES WGIBAR, 2016).

The Barents Sea is home to some major stocks of commercial demersal fish species. Of these, Atlantic cod of the Barents Sea stock is the most important (Kjesbu et al., 2014). The total biomass of the main demersal fish in the Barents Sea is of the order 2–6 million tonnes, and cod biomass has fluctuated between about 0.7 and 3.6 million tonnes (Fig. 4). While the stocks of pelagic fish have fluctuated without a clear trend in recent decades, the demersal stocks of cod and haddock have shown a pronounced increase to levels of more than 3 and 1 million tonnes, respectively, in the most recent years (Fig. 4). The increase of the stock of Barents Sea cod took place in steps to over 2 million tonnes in the early 1990s to 3–3.5 million tonnes from 2009 onwards. This is the highest level ever recorded for the cod stock, and reflects the climate warming combined with good management (low fishing mortality; Hylen et al., 2008; Kjesbu et al., 2014). The warming has allowed an expansion of cod distribution to include the northern part which

was previously in the Arctic domain and not available for cod (Fig. 5; Kjesbu et al., 2014; Fossheim et al., 2015; Kortsch et al., 2015).

In contrast to Atlantic cod, the polar cod stock has declined from nearly 2 million tonnes to a low level (<0.5 million tonnes) during the last 5 years (Fig. 4). This appears also to be a climate response, in this case a negative effect for an Arctic species (Eriksen et al., 2016). Increased spatial overlap and predation from Atlantic cod on polar cod may have played a role in the recent decline of the polar cod (Renaud et al., 2012; ICES WGIBAR, 2016). However, in 2015, the polar cod recruited a rich year class, and it remains to be seen whether this was an exceptional event or whether the negative trend for the polar cod has halted.

3. Compilation of biomass data for macrozooplankton, micronekton and pelagic fish

3.1. Surveys and sampling procedures

A joint Norwegian-Russian 0-group fish trawl survey has been carried out annually in August-September since 1965. The main goals of the 0-group survey have been to give an initial indication

of year class strength of the commercially important fish stocks and to map their spatial distribution in the Barents Sea (Eriksen and Prozorkevich, 2011). A small-meshed pelagic trawl ("Harstad") with 20 m * 20 m mouth opening has been used to cover the upper water layer (0–60 m) with the head-line at 0 m, 20 m and 40 m (Anonymous, 2004; Eriksen et al., 2009). 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 when dense concentrations of 0-group fish are recorded deeper than 60 m on the echo-sounder.

An acoustic capelin survey has been carried out annually (since 1972) in September-October. This survey provides abundance estimates of capelin which are used in the capelin stock assessment by ICES (Gjøsæter et al., 2002; ICES, 2013). In addition to capelin, the survey includes young herring, polar cod, and zooplankton. Acoustic data (nautical area scattering coefficients NASC (m^2·nmi^{-2} – MacLennan et al., 2002)) are integrated continuously along the survey tracks, and mean values of acoustic back-scattering per nautical mile (nm) are recorded for mapping and calculations of fish abundance and biomass. The distance between survey lines has varied, from 10–20 nm when special acoustic surveys were made targeting capelin, to 20–35 nm when the acoustic surveys became part of the ecosystem survey in 2004. The echo sounders are monitored continuously, and trawl hauls ("Harstad" trawl) are carried out whenever the recordings change their characteristics and/or the need for biological data makes it necessary. These hauls are carried out to identify acoustic recordings to species and to obtain biological information (individual length, weight, maturity stage, stomach content, and age) (Aglen and Gavrilov, 2011).

Since 2004, both the 0-group trawl survey and the acoustic capelin survey have been part of a Barents Sea ecosystem survey (BESS), designed and jointly carried out by the Institute of Marine Research (IMR, Norway) and the Polar Research Institute of Marine Fisheries and Oceanography (PINRO, Russia). In addition to covering fish, zooplankton and oceanography, the survey includes sampling and observations of benthos, seabirds, marine mammals, and contaminants (Michalsen et al., 2011, 2013; Eriksen and Gjøsæter, 2013). The timing of the BESS allows access by research vessels to most of or the whole Barents Sea, sea-ice being at its seasonal minimum. In August-September, migratory species such as capelin have reached their maximum northern distribution at the end of the summer feeding period. At this time of year, the juvenile 0-group fish of commercially and ecologically important species are sufficiently large to be caught by trawl, while 0-group demersal species such as cod and haddock have not yet settled to the bottom.

3.2. Sample processing and determination of biomass

During the 0-group fish, capelin and BESS surveys, the pelagic trawl samples were sorted and all captured organisms identified to lowest possible taxonomic level. Pelagic fishes (capelin, herring, blue whiting and polar cod) and 0-group fishes were identified to the species level, and other species among plankton and small fishes (see below) were identified to family or genus level due to difficulties in species identification and time constraints on board. Individual length and weight were measured for pelagic species. 100 specimens of each 0-group fish species and 30 specimens of other small fishes were length measured, while pooled weight was obtained for species or species groups. Krill and jellyfish were only weighted. Biomass data for 0-group fish were obtained for the main commercial fish species (cod, haddock, capelin, and herring) and for other species as listed in Table 1.

The 0-group data are expressed as kg wet weight biomass per sq nm (=3.43 km^2) by using tow length, number of depth layers and capture area of trawl (width of 20 m) (Eriksen et al., 2009). Small individuals pass through the coarser meshes in the front part of the trawl and the capture efficiency of the trawl differs between species and increases generally with fish length (Godø et al., 1993; Hylen et al., 1995). Therefore, correction factors based on empirical data for catchability (Hylen et al., 1995; Mamylov, 2004) have been established and used in the annual calculations of abundance (Mamylov, 2004; Dingsør, 2005) and biomass (3.8 for cod, 2.8 for haddock, 5.9 for herring, and 5.0 for capelin; Eriksen et al., 2011). Capture efficiencies for other 0-group fishes such as polar cod, redfish, saithe, long rough dab and other small fishes have not been estimated. We believe that these fishes (juveniles and adults) of 1–7 cm in length are only caught by the fine-meshed trawl sections before the cod end, and we have used a correction factor of 5 for these fishes, equivalent to that used for capelin (see also Eriksen et al., 2011).

Sampling of krill is problematic due to their intermediate size between macrozooplankton and micronekton, and their evasion abilities (Sameoto et al., 2000; Orlova et al., 2008, 2009; Skjoldal et al., 2013; Eriksen et al., 2016). The estimates of krill biomass were based on night catches only (most krill migrate to the upper pelagic layer to feed at night) and were calculated from tow length and an assumed effective filtering area of 10 m^2, based on the fine-meshed trawl sections before the cod end (Eriksen and Dalpadado, 2011; Eriksen et al., 2016). The biomass data for krill (assumed to be mainly individuals >15 mm in length; Eriksen et al., 2016) were expressed as kg wet weight per nm^2. For the estimates of large jellyfish (primarily *Cyanea capillata*) no correction factor was used due to the large size of the medusa bell (diameter of 20–60 cm; Eriksen et al., 2012a). Since jellyfish have a very high water content

Table 1
Overview of studied species, families and groups.

Group	Species
Macroplankton	Jellyfish, mostly lion's mane jelly *Cyanea capillata* Krill, not identified to species level
0-group fish	Capelin (*Mallotus villosus*), Barents Sea population Herring (*Clupea harengus*), Norwegian spring spawning population Cod (*Gadus morhua*), Northeast Arctic population Haddock (*Melanogrammus aeglefinus*), Northeast Arctic population Polar cod (*Boreogadus saida*) Beaked redfish (*Sebastes mentella*) Saithe (*Pollachius virens*), Northeast Arctic population Blue whiting (*Micromesistius poutassou*) Greenland halibut (*Reinhardtius hippoglossoides*) Long rough dab (*Hippoglossoides platessoides*) Wolffishes *Anarhichas* spp.
Pelagic fish species	Capelin (*Mallotus villosus*), Barents Sea population (immature: age1 + 2, mature: age 3+) Herring (*Clupea harengus*) (age 1–5), Norwegian spring spawning population Blue whiting (*Micromesistius poutassou*) Polar cod (*Boreogadus saida*) (immature: age 1 + 2, mature: age 3+) Lumpfish (*Cyclopterus lumpus*) (age 1+)
Other small fishes	Ammodytidae (mainly *Ammodytes marinus*) Agonidae (*Agonus cataphractus, Leptagonus decagonus, Ulcina olriki*) Cottidae (*Artediellus atlanticus, Artediellus scaber, Icelus bicornis, Icelus spatula, Gymnacanthus tricuspis, Myoxocephalus quadricornis, Myoxocephalus scorpius, Taurulus bubalis, Triglops murrayi, Triglops nybelini, Triglops pingelii*) Liparidae Stichaeidae (*Anisarchus medius, Leptoclinus maculatus, Lumpenus lampraetaeformis*)

Table 2
Mean and median biomass (kg wet biomass per sq nm) of the species and groups used in the study. The biomass values for each species have been categorized into 4 groups: no catches, low biomass (lower than 30% below mean), average biomass (mean ± 30% (over the study period)), and high biomass (higher than 30% above mean).

Group	Species	Mean	StDev	Median	StDev/Mean
Macro plankton	Krill	27,864	39,784	11,110	1.0
	Jellyfish	1184	1315	730	1.1
0-group fish	0 Herring	212	484	0.5	2.3
	0 Capelin	337	552	95	1.6
	0 Cod	363	735	44	2.0
	0 Haddock	122	257	2.9	2.1
	0 Polar cod	125	288	1.5	2.3
	0 Redfish	52	201	0.0	3.9
	0 Gr.halibut	0.2	0.7	0.0	3.9
	0 Long rough dab	0.8	3.1	0.1	4.0
	0 Wolffish	0.6	2.7	0.0	4.4
	0 Bl. whiting	0.0	0.2	0.0	9.4
	0 Saithe	2.6	5.3	0.3	2.0
Pelagic stocks	1–2 Capelin	2315	4666	202	2.0
	3–5 Capelin	970	1952	49	2.0
	1–2 Polar cod	1103	2133	40	1.9
	3–5 Polar cod	465	1437	2.3	3.1
	1–5 Bl.whiting	344	1147	0.0	3.3
	1–5 Herring	1321	2715	0.0	2.1
	Lumpfish	124	148	75	1.2
Small fish	Agonidae	0.2	0.5	0.0	3.0
	Liparidae	1.5	4.9	0.0	3.3
	Ammodytidae	6.8	19	0.1	2.8
	Cottidae	1.0	3.4	0.1	3.5
	Stichaeidae	1.6	4.6	0.3	2.9

(up to 95.6%, Lowndes, 1942; 95–96.5%, Cushing et al., 1958; Doyle et al., 2007), the jellyfish wet weight biomass values have been multiplied by the factor 0.04 to make them comparable to fish wet weight biomass values (assuming water content of jellyfish of 96% and salt content of 3.3%; this gives organic dry weight content of 0.7% of wet weight versus about 17% for fish).

Small fishes among the families of poachers (Agonidae), sculpins (Cottidae), snailfishes (Liparidae), pricklebacks (Stichaeidae), and sandeels (Ammodytidae) were only identified to family level, and therefore relative abundance indices represent fish families (Eriksen et al., 2012c).

Capelin, herring, polar cod and blue whiting were recorded acoustically and the abundance and biomass were calculated from the acoustic data by using information on species and size composition from trawl catches (Aglen and Gavrilov, 2011). The raw data are binned as 1 nm sections along the acoustic survey lines and the estimates calculated for squares of 1° (latitude) × 2° (longitude) using the stock size estimation program "BEAM" built on SAS GIS (Totland and Godø, 2001). These spatial data were used for biomass estimation expressed as kg wet weight per square nautical mile (nm^2). The biomass is calculated for age classes by using length-age keys from the trawl samples. We have used biomass data for young immature (1 and 2 years old) and older (3+) capelin and polar cod, while we have used the biomass for all juvenile age classes (1–5) for herring and blue-whiting (Table 2). For herring, the spatial estimations were missing for the years 1999, 2001, 2002 and 2003. We have used data for the total amount of juvenile herring (not spatially resolved) from the stock assessment for these years.

3.3. Abiotic data

For analytical comparison with the compiled biomass data, we have prepared time series of some climate related abiotic variables. The temperature conditions of the inflowing Atlantic water at the Fugløya-Bjørnøya (FB) section were expressed as the average temperature from 50 to 200 m depth at FB in August-September (FB-aug) and as annual mean temperature (FB50-200). The tempera-

ture conditions in the southern and eastern Barents Sea were expressed as the average temperature from 0 to 50 m (Kola 0–50) and 50 m to 200 m (Kola 50–200) at the Kola standard section (69°30′N–74°00′N, 33°30′E; Trofimov and Ingvaldsen, 2012) in August-September. See Fig. 1 for location of these hydrographic sections.

Time series of area coverage by Atlantic Water (AW, T > 3 °C), Arctic Water (ArW, T < 0 °C) and mixed water (MW, 0 °C < T < 3 °C) were taken from the WGIBAR report (ICES, 2014; see also Johannesen et al., 2012).

Modelled fluxes of water (integrated over the water column) have been calculated with a three-dimensional baroclinic ocean general circulation model (ROMS) set up with 4 km horizontal resolution and run with meteorological forcing for 1960–2013 (Lien and Ådlandsvik, 2011). We have used modelled fluxes at the Barents Sea Opening (BSO) in southwest, across the Hopen Deep (BS-SH) and at the Kola section (KS) for the 2nd and 3rd quarters of the year (April-June and July-September) (Fig. 1). These two quarters correspond to the time period when fish larvae are transported and spread by the currents flowing into the Barents Sea up to the time of the autumn 0-group survey.

We also included an index representing the atmospheric influence, the annual North Atlantic Oscillation index (NAO), which was downloaded from http://www.cgd.ucar.edu/cas/jhurrell/indices.html.

A hierarchical clustering routine was used to identify periods with similar oceanographic characteristics. Stratigraphically constrained clustering with unweighted pair-group average (UPGMA) algorithm, where clusters were joined based on the average distance between all members in the two groups, was conducted in the "PAST" (Hammer et al., 2001).

3.4. Data treatment and analyses

We have analysed data from the 0-group fish, capelin and BESS surveys for the 21-year timeperiod 1993–2013. 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 × 60 nm

grid cells covering the whole Barents Sea. The size of the grid cells corresponds to one degree latitude but due to the earth curvature they do not align with the latitude nor longitude lines. The gridded average biomass data (for 1993–2013) for each taxon (species or groups) have been plotted on maps using 4 biomass categories: zero, low, average, and high biomass (kg wet weight per nm^2). An interval of ±30% around the mean over all grid cells and years of the study period for a taxon was categorized as average biomass of that taxon. Mean biomass values of each grid cell (over the period 1993–2013) being more than 30% smaller or 30% larger than the mean over all grid cells were categorized as low and high biomass values respectively (see Table 2).

3.4.1. Spatial and temporal biomass variation

To investigate the spatial organization of the pelagic community and the biomass fluctuation at large scale we aggregated the data into larger areas. The Barents Sea was subdivided into six areas following broadly topographic and oceanographic features (Fig. 6). The **Southwestern** area includes the entrance region of Atlantic water between Norway and Bear Island (situated on the Spitsbergen Bank) and the deep Bear Island Trench with maximum depth of 500 m. The **South-Central** area includes the shallow Central Bank (about 150 m) and the area of deep banks (200–250 m) south to the North Cape Bank off Norway and the Murman Rise north of the Kola Peninsula. This area is influenced mostly by inflowing Atlantic water but with colder water generally residing over the Central Bank. The **Southeastern** area includes the shallow waters (<100 m) of the Goose Bank and North Kanin Bank, the Pechora Sea and the entrance region to the White Sea. This area is influenced by Atlantic water but also coastal water and river run-off to the White and Pechora seas, and it is largely covered by locally formed sea-ice in winter. The **Eastern** area includes the shallow Novaya Zemlya Bank and the deep Eastern Basin and is influenced by mixed and cold waters generated by ice formation in winter. The **North-central** area includes the Svalbard Bank, the northern part of the Hopen Deep, the Great Bank and the Olga Deep north to Kvitøya and southwestern Franz Joseph Land. This area is influenced by Arctic water overlying cold Atlantic water in deeper portions, and is generally covered by sea-ice in winter. The **Svalbard** area includes the shallower waters around the archipelago and the deeper shelf and slope regions to the west and north of Svalbard. The area is influenced by Atlantic water of the West Spitsbergen Current in deeper areas and Arctic and mixed waters in shallower parts. See Ozhigin et al. (2011) for a description of water masses and oceanographic conditions.
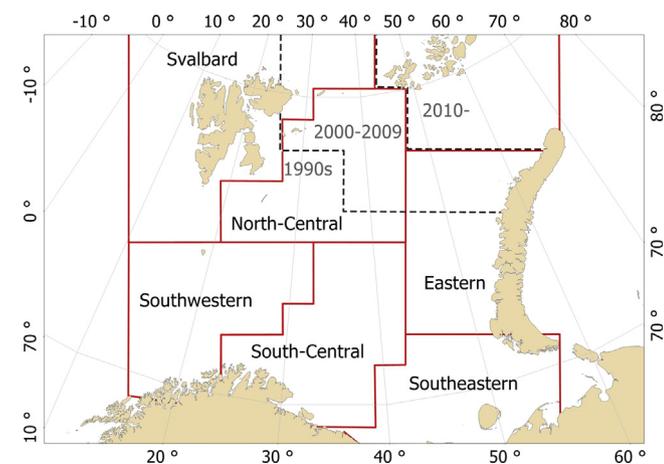

Fig. 6. Division of the Barents Sea into six subareas based on topography and general oceanographic conditions. Schematic northern boundaries for surveyed areas in the 1990s and the 2000s are shown as dashed lines.

The gridded biomass data were integrated and presented for each of the six subareas of the Barents Sea. We used non-metric multidimensional scaling (NMDS) to analyse the spatial structure of the data, visualizing the level of similarity among samples from different subareas by means of a NMDS map (Hammer et al., 2001).

3.4.2. The Barents Sea ecosystem state and changes

The environmental variables (size of areas occupied by AW, ArW and MW), water temperature at sections (FB-aug, FB50-200, Kola0-50 and Kola50-200), the NAO index, and modelled water fluxes (BSO, BS-SH, KS) were used to investigate possible abiotic sources of pelagic biomass variability in different areas and years by non-metric multidimensional scaling. Stratigraphically constrained clustering (using the UPGMA algorithm) of years based on abiotic variables for the period 1993–2013 were used to identify different time segments within the study period. Pearson correlation coefficients were used to analyse co-variation of sets of biotic variables (pelagic biomass values) and abiotic data (temperature, areas of water masses, modelled fluxes, and NAO). Multivariate multiple linear regression (MMRA, Johnson and Wichern, 1992) was used to study the association between groups of parameters. Non-metric Mann-Kendall test for trend in time series was used to identify whether the variable consistently increased (or decreased) through time, where the trend may or may not be linear (Gilbert, 1987). To compute MMRA, NMDS and Mann-Kendall test the software "PAST" (version 3.07, Hammer et al., 2001) was used. Results from the statistical tests are given in Supplementary material 1.

We used Principal Component Analysis (PCA) to integrate information across multiple time series comprising different components of the pelagic community and environmental factors (see e.g. Kenny et al., 2009). The time trajectories of the first two principal components were used to evaluate the temporal development of the pelagic community structure (Kenny et al., 2009). The PCA analysis was performed with the R packages 'vegan' and 'gclus'. Both biotic (pelagic biomass values) and abiotic data (temperature, areas of water masses, modelled fluxes, and NAO) were included, and all data were normalized and standardized to zero mean and unit variance before analysis. PCA loadings are given in Supplementary material 1.

3.4.3. Overlap between high concentrations

To determine the location of core areas and areas of potential competition between species, the spatial overlap of the species at a small scale (grid cell level) was estimated. The areas of high concentrations of each of the studied species were based on grid cells with high biomass values (higher than mean + 30%; Table 2). The degree of overlap between two species (X and Y) was calculated based on the number of grid cells with high concentrations for both species as a proportion of the total number of grid cells. This provides an index for how large area with high concentrations of species X overlapped with high concentrations of species Y.

4. Spatial and temporal patterns of pelagic biomass distribution

4.1. Oceanographic conditions

The first part of the studied period was relatively cold with low temperature in the Fugløya-Bjørnøya section and a small area occupied by Atlantic water (Fig. 7A). This was followed by a warm period with record warm years in 2006–2007 and large areas of warm waters, decreasing somewhat during the last three years of the study period. The areas of Atlantic and mixed waters were at their lowest extent in 1997–1998 followed by an increasing trend up to maximum in 2006–2007. The area occupied by ArW showed
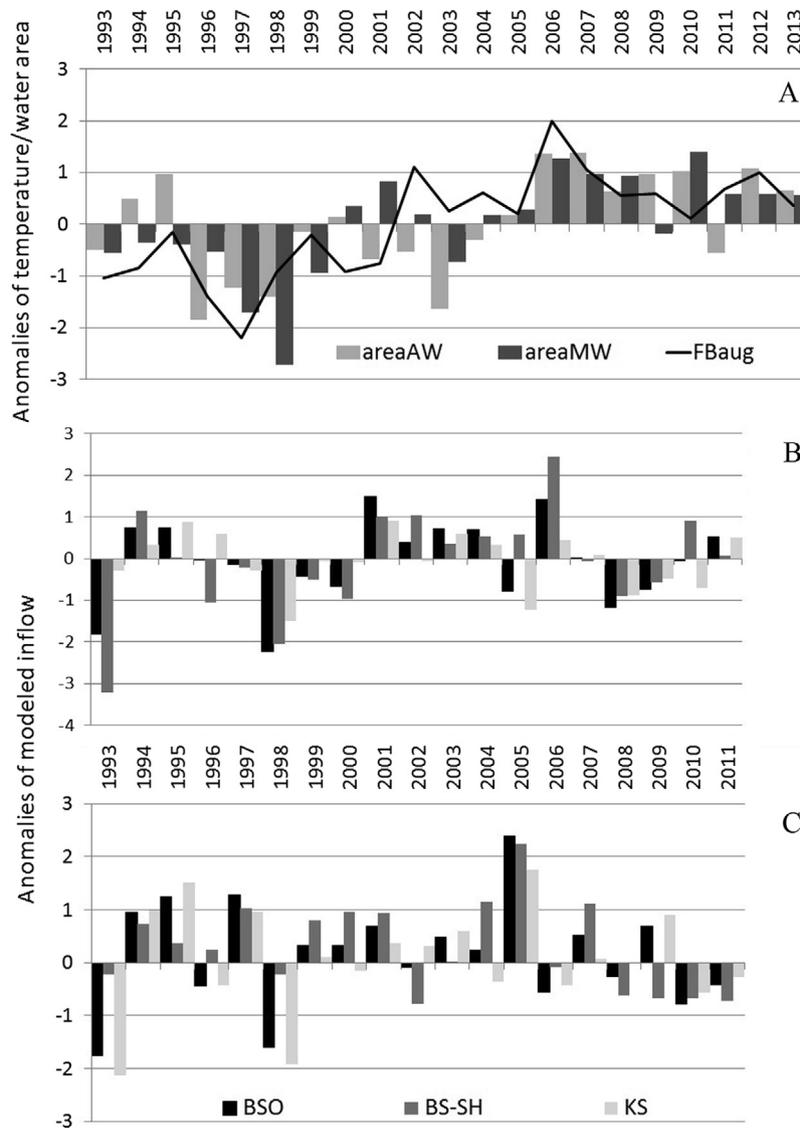
Fig. 7. Oceanographic conditions in the Barents Sea. A – temperature anomalies at the Fugløya-Bjørnøya section in August (FBaug), and anomalies of areas of Atlantic water (AW) and mixed waters (MW) in August-September 1993–2013. B and C – anomalies of modelled inflow of Atlantic water at the Barents Sea Opening (BSO), north into the Hopen Deep (BS-SH), and east across the Kola section (KS) during the second (B) and third (C) quarters of the year, 1993–2011.

opposite and generally decreasing trend during the period (S2, Trend test). The modelled inflow of Atlantic water during the second and third quarters of the year showed fluctuations with low fluxes in 1998 (and in 1993) and high fluxes in 2005–2006 (Fig. 7B and C). The modelled fluxes (for the spring and summer periods) tended to be above average in the first years after 2000 leading up to the maximum temperature in 2006, and below average in 2008–2010 when the temperature showed a decrease (Fig. 7).

The study period can be broadly divided into two segments based on differences in oceanographic variables before and after 2004 as shown by hierarchical clustering (Fig. 8). The first period before 2004 was characterized by relatively cold conditions with low temperature and a small area occupied by Atlantic water, while the second period after 2004 was warm with higher temperatures and larger areas of warm waters and a correspondingly decreased area of Arctic water.

4.2. Species distribution

A total of 50 taxa were recorded from the pelagic catches. During the BESS, 25 fish species or groups were recorded regularly

(Table 1). This included common and abundant commercial species like cod, haddock, saithe, herring, capelin, polar cod, blue whiting, beaked redfish, and Greenland halibut. Other common and abundant species were long rough dab, lumpfish, and sandeels.

The biomass (at grid cell level) from pelagic trawl catches and acoustic recordings are mapped and presented for main species and groups in Figs. 8 and 9. The pelagic fish stocks taken together occupied almost 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, blue whiting in southwestern, and herring were mainly found 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 (71%) between high concentrations of juvenile (1–2 years) and older (3–5 years) capelin (Fig. 9A and D). Young (1–2 years) and older (3+) polar cod were found mainly in the eastern subarea with a high degree (74%) of overlap of grid cells with high biomass of these two age groups (Fig. 9B and E).

Lumpfish was distributed in the Barents Sea with high catches in the Southwestern, South-central, the southern part of the North-Central, and the Svalbard subareas (Fig. 9G). The groups of
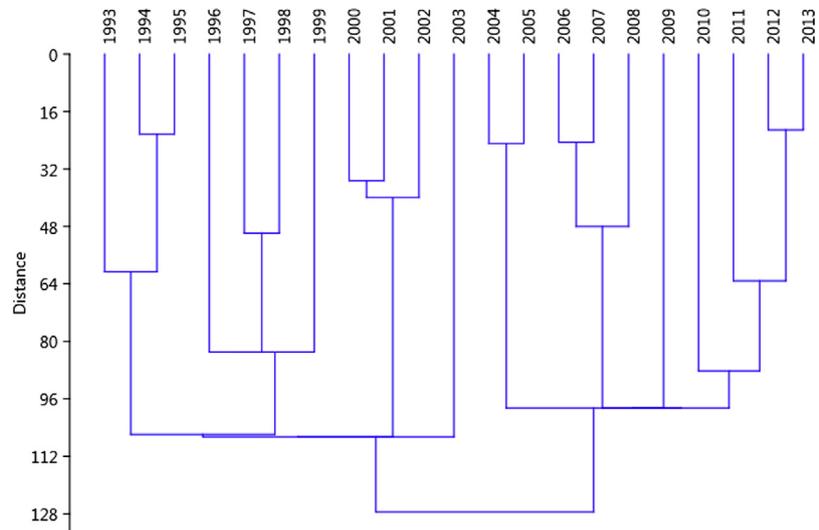
Fig. 8. Stratigraphically constrained clustering of years based on abiotic variables for the period 1993–2013. Lines show linkages of groups of years based on similarity from constrained cluster analysis (using UPGMA algorithm).
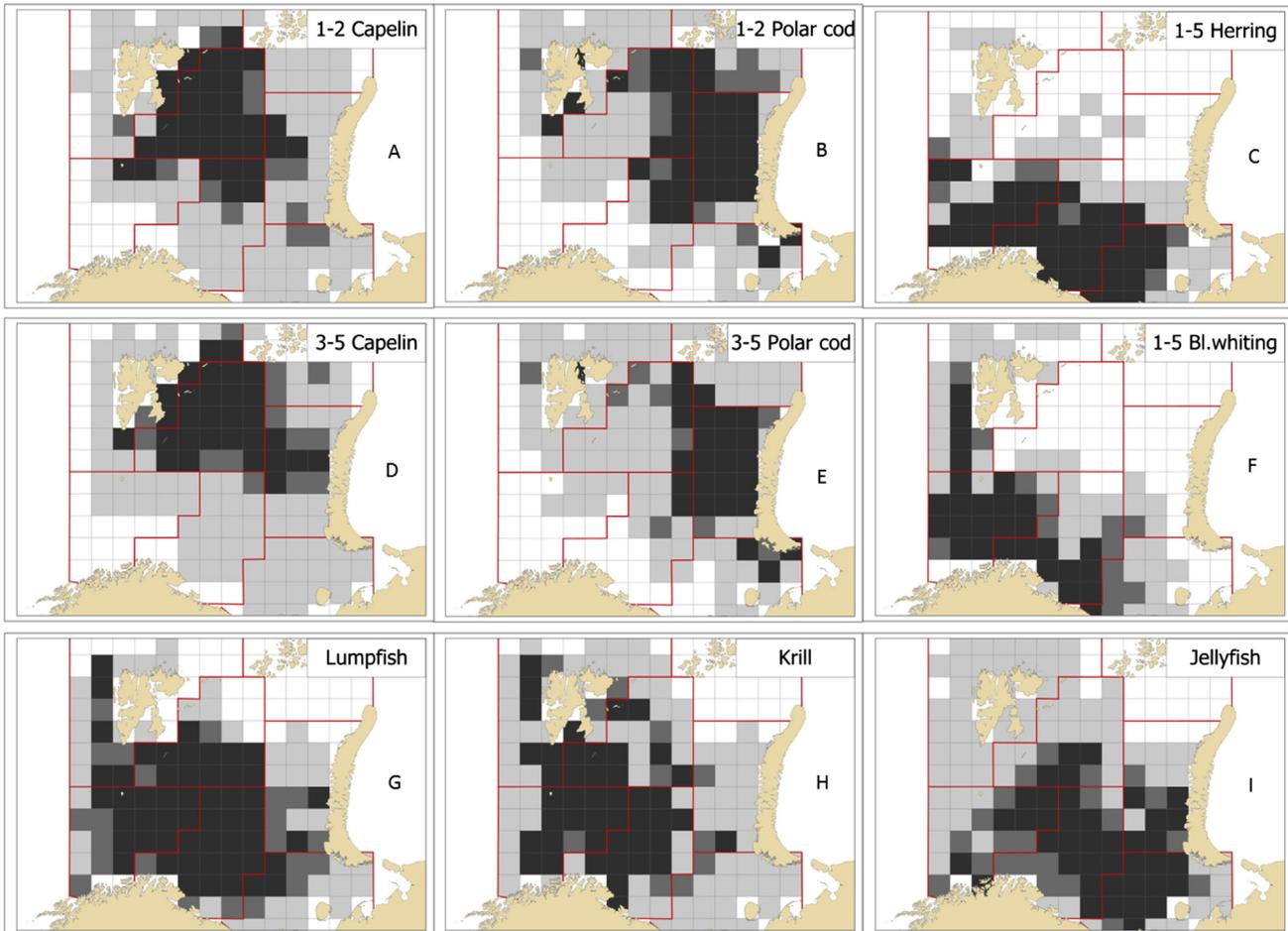
Fig. 9. A–I. Spatial distribution of biomass of pelagic fish stocks and macrozooplankton in the Barents Sea given as mean values by grid cells for the period 1993–2013. Low, average and high biomass values for the species and groups are given in Table 2 and are shown with light, medium and dark grey shading, respectively. Red lines show the boundaries of the six subareas (see Fig. 6). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

krill and jellyfish were widely distributed in the western and southern Barents Sea. The highest concentrations of krill were mainly found in the Southwestern, South-Central, the southern part of the North-Central, and the Svalbard subareas (Fig. 9H).

The highest concentrations of jellyfish were mainly found in the Southeastern, South-Central and Eastern subareas (Fig. 8I). High catches of jellyfish and krill overlapped only to a limited extent and mainly in the South-Central subarea. High catches of lumpfish
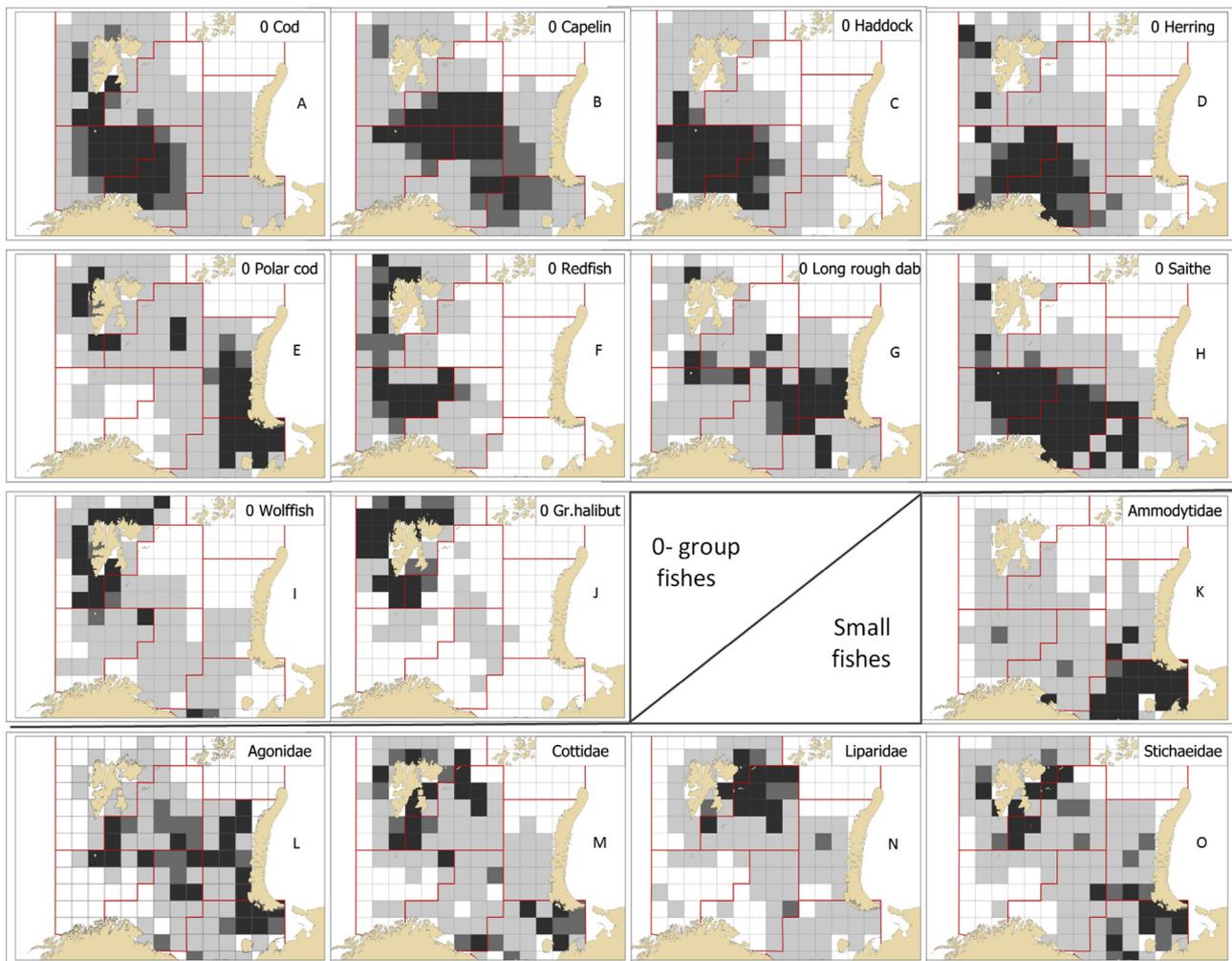
Fig. 10. A–O. Spatial distribution of biomass of 0-group and other small fishes in the Barents Sea given as mean values by grid cells for the period 1993–2013. Low, average and high values for the various species or groups are given in Table 2 and are shown with light, medium and dark grey shading, respectively. Red lines show the division of the Barents Sea into six subareas. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

overlapped to a high degree with high catches of krill (74%) and jellyfish (59%) and with high catches of some of the 0-group fish, notably cod, haddock, capelin and herring (72–88%). About one third (29%) of high catches of young (1–2) and older (3–4) capelin were found in areas with high krill catches.

0-group fish of the commercial species cod, haddock, herring, capelin, polar cod, and redfish were common and abundant with mean biomass values from 258 kg nm^{-2} for redfish to 1379 kg nm^{-2} for cod (Table 2). Other species (saithe, Greenland halibut, long-rough dab, wolffish and blue whiting) were much less abundant with mean biomass values of 0.1–13.0 kg per nm^2 (Table 2). 0-group cod, haddock, capelin and herring had wide distributions in the Barents Sea. High catches were mostly found in the Southwestern and South-Central subareas, with patterns of more western distribution for cod and haddock, northern distribution for capelin and southern distribution for herring (Fig. 10A–D). There were high degrees of overlap (63–79%) of high catches of cod, haddock and herring. The distribution of 0-group saithe resembled that of cod and haddock with high concentrations in the Southwestern and South-Central subareas (Fig. 10H).

0-group polar cod was found mainly in the Eastern and Southeastern subareas as were 0-group long rough dab (Fig. 10E and G). 0-group redfish was found in the western part of the Barents Sea in the Southwestern and Svalbard subareas, whereas wolffishes and

Greenland halibut were found mainly in the Svalbard subarea (Fig. 10F, I, and J).

Small fishes of various families showed different patterns in their distributions in the Barents Sea, with high catches typically found in limited areas. Sandeels were found with high concentrations mainly in the shallow Southeastern subarea (Fig. 10K). Sculpins and pricklebacks were found predominantly in the Southeastern and Svalbard subareas, whereas poachers were observed mostly in the North-Central, Eastern and Southeastern subareas (Fig. 10M, O, and L). Snailfishes were found mainly in the North-Central and Svalbard subareas (Fig. 10N).

4.3. Temporal and spatial distribution of estimated biomass

The estimated total biomass (wet weight) of the pelagic compartment ranged between 6.6 million tonnes in 2003 to a maximum of about 30 million tonnes in 2008 and 2011, with an average of about 16.9 million tonnes over the 21-years period (Fig. 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. Large scyphomedusae (mainly lion's
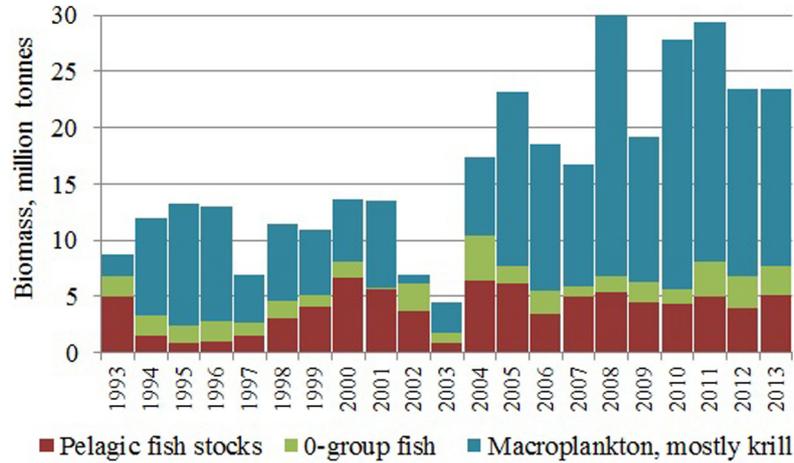
Fig. 11. Estimated biomass (million tonnes wet weight) of the pelagic compartment in the Barents Sea from 1993 to 2013.

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.

The study period can be broadly divided into two segments based on differences in abiotic variables before and after 2004 (Fig. 8). 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. 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 (Fig. 11). This reflected large and complex changes in the main species and groups that contributed to the total biomass. During the first period (1993–2003), capelin was generally the main component among pelagic fish (Fig. 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 (Fig. 4).
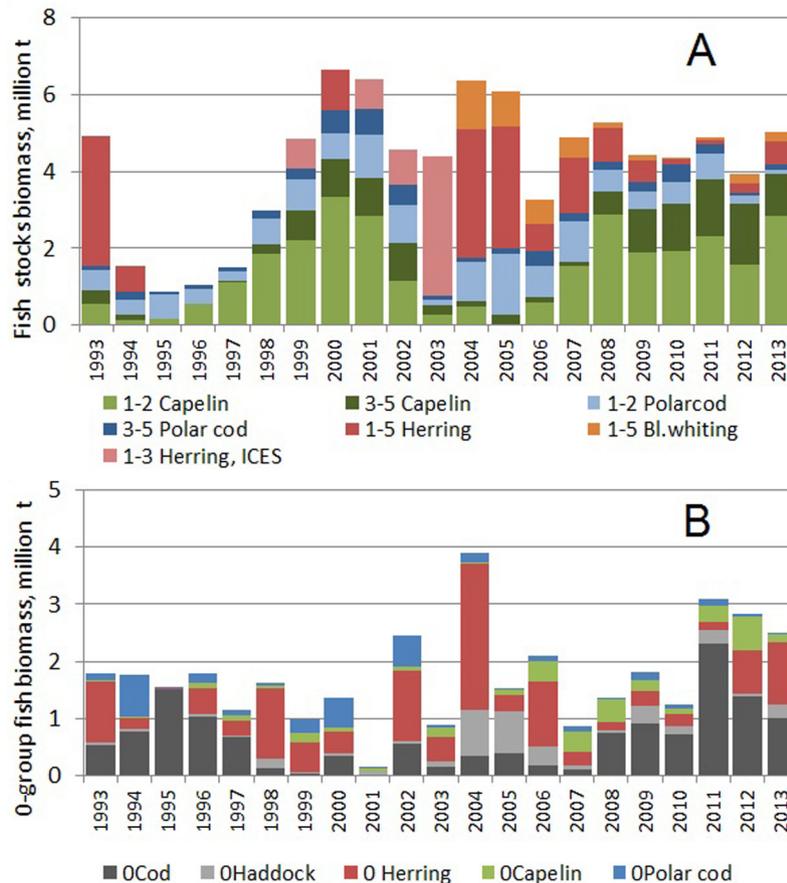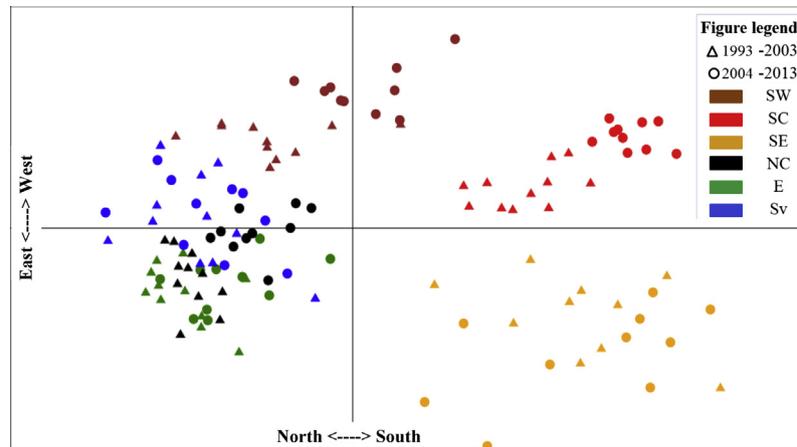

Fig. 12. Temporal development of biomass (million tonnes wet weight) of pelagic fish species (A) and 0-group fishes (B) in the Barents Sea from 1993 to 2013.

Fig. 13. Plot from non-metric multidimensional scaling of temporal variation (1993–2013) of biomass values of 25 species or groups in six subareas (SW – Southwestern, SC – South-Central, SE – Southeastern, NC – North-Central, E – Eastern, and Sv – Svalbard) of the Barents Sea. The data points (years) for the subareas are shown with different colors. The data points for each subarea are shown for the first and second time periods by triangles (1993–2003) and dots (2004–2013). The horizontal and vertical axes are interpreted as representing N-S and E-W gradients.
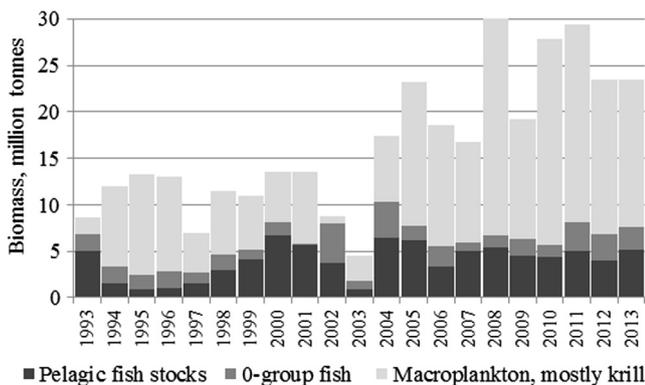
Fig. 14. Mean biomass values for 3 pelagic components in the Southwestern (SW), South-Central (SC), Southeastern (SE), Eastern (E), North-Central (NC), and Svalbard (Sv) subareas (see Fig. 3) over the period 1993–2013.

The second collapse of capelin in the early 2000s differed in that the void was filled by other species, notably polar cod and juvenile herring. These components decreased as capelin increased after 2006. At the same time there was a second 'surge' in krill which remained at a high level for some years when the capelin stock also remained high (2008–2013, Figs. 8 and 9). 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) (Fig. 11B). 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 0.5 million tonnes in 2000 and 2002.

The results from the non-metric multidimensional scaling to study spatial structure in the pelagic biomass distribution showed that the biomass patterns from the various subareas tended to show separate clusters, notably for the Southwestern, South-Central and Southeastern subareas, while there was more overlap of data points for the northern subareas (Svalbard, North-Central and Eastern) (Fig. 13). The arrangement of the data points in the NMDS plot suggested that the two axes separated along latitudinal and longitudinal gradients (Fig. 13). Krill biomass varied along the longitudinal gradient and was lowest in the eastern subareas (Southeastern and Eastern). The biomass of pelagic fish differed along the latitudinal gradient and depended on stock dominance (young herring versus capelin): with high stock level of young her-

ring, the capelin stock was general low (Fig. 9A, C, D and Supplementary material 2). The biomass of 0-group fishand krill varied along the longitudinal gradient; highest biomasses were observed in the western subareas, where cod, capelin, herring and haddock contributed, while eastern subareas were dominated by polar cod (Supplementary material 2).

The biomass distribution of the pelagic components differed among the 6 subareas (Figs. 14 and 15, Supplementary material 2). The highest average biomass values were found in the Southwestern and South-Central subareas with about 4.3–4.4 million tonnes in each, and in the North-Central subarea with about 3 million tonnes. Krill was the major biomass component in the Southwestern and South-Central subareas (around 3 million tonnes), whereas pelagic fish (mainly capelin) was the predominant component along with krill in the North-Central subarea (Figs. 14 and 15). 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 subareas (Figs. 14 and 15).

The total biomass in the Southeastern and Eastern subareas was lower with about 0.9 and 1.0 million tonnes, respectively, dominated by pelagic fish (mainly herring and polar cod). The total biomass in the Svalbard subarea was 2.5 million tonnes on average, with krill as the dominant component (Figs. 14 and 15). The temporal development of biomass of the main components of the pelagic compartment in the subareas is shown and described in more detail in Supplementary material 3.

4.4. The Barents Sea status and change

The overall state and trends of the pelagic compartment of the Barents Sea ecosystem is shown as an anomaly trend plot in Fig. 16 for 33 variables: 8 abiotic and 25 biotic variables of annual biomass values of the main species or groups (see Table 1). The plot shows an overall pattern with increasing trends for about half 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 predominantly red to green in the lower part of the plot).

The pattern of change in the 25 biotic and 8 abiotic variables has been examined by principal component analysis (PCA; Fig. 16). The first principal component (PC1) explained 26% and the second component (PC2) 14% of the total variation. The temporal trajectory for the years (1993–2013) in the PC1-PC2 plane showed large
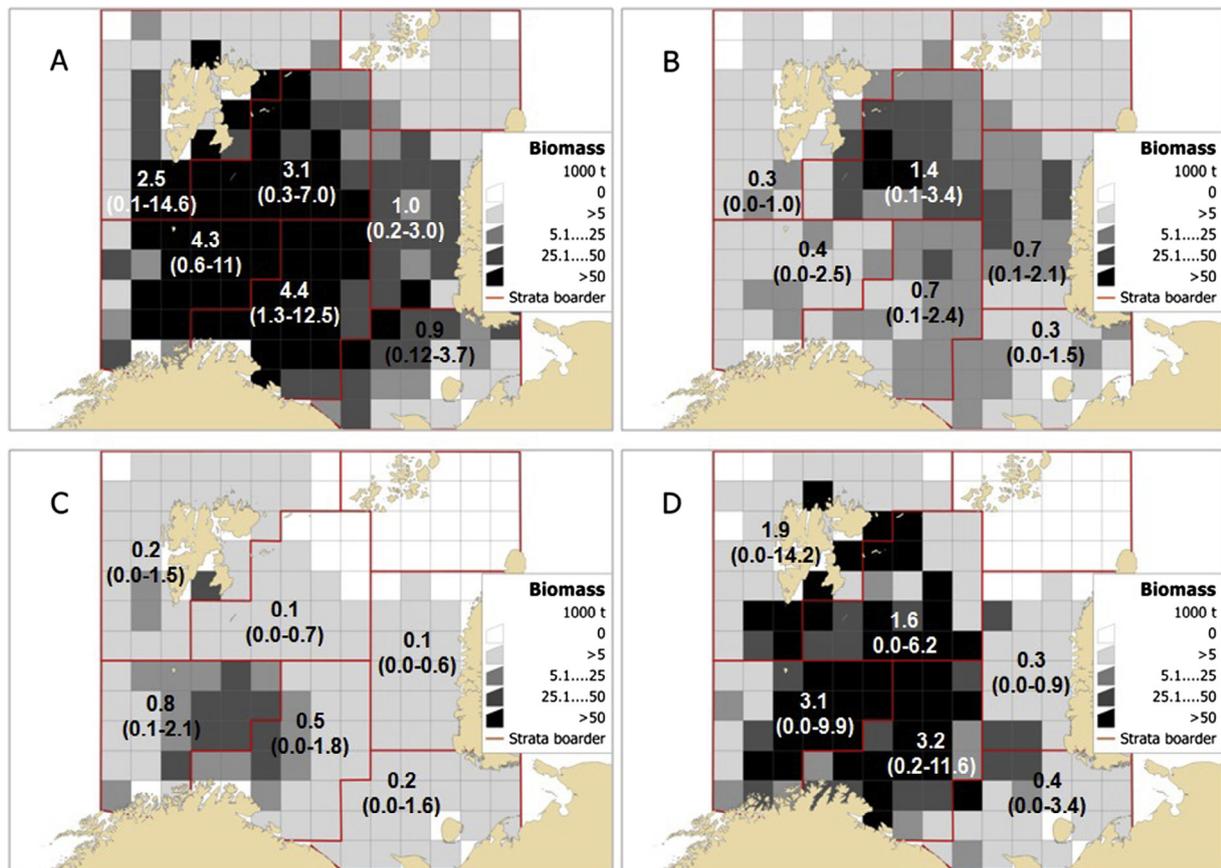
Fig. 15. Spatial distribution of mean biomass densities (10^3 tonnes wet weight per 60×60 sq nm grid cell; light/dark grey, darker shading indicates denser concentrations) and total average biomass values (million tonnes) for the six subareas (red lines). A – Total biomass for all components of the pelagic 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. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

variation along PC2 at negative values of PC1 (except for 2000) up to 2003, followed by a more stable situation with positive scores on PC1 from 2004 onwards (Fig. 17A). The physical variables (areas of water masses and seawater temperatures) were strongly correlated with PC1, suggesting that this can be interpreted as a "warming trend" axis (Fig. 17B). Thus, PC1 was significantly and positively correlated with Fugløya-Bjørnøya temperature ($r = 0.85$, $p < 0.01$) and areas of Atlantic water ($r = 0.74$, $p < 0.01$) and mixed water ($r = 0.82$, $p < 0.01$). Juvenile herring and blue whiting grouped together with the climate variables with high scores along PC1.

The variation along PC2 (Fig. 17A) appears to reflect the large fluctuations in the capelin stock which was low in 1994–1995 and high around 2000 (see Figs. 4 and 12A). Biomass values of juvenile and older capelin along with biomass of polar cod were positively related to PC2 while krill showed the opposite trend (Fig. 17B). The total biomass of the pelagic compartment remained relatively stable in each of the two main periods (before and after 2004) but shifted up by a factor of about 2 to a higher level in the last period (Fig. 11). This corresponded to the shift from negative to positive PC1 values (Fig. 17A).

## 5. Dynamics of the Barents Sea pelagic compartment

The Barents Sea ecosystem is dynamic and has been shown to undergo large fluctuations in response to climate variability at different time scales including multidecadal and interannual (Sætersdal and Loeng, 1987; Skjoldal and Rey, 1989; Loeng and Drinkwater, 2007; Drinkwater, 2011; Johannesen et al., 2012;

Dalpadado et al., 2014). The Barents Sea experienced a cold climate period around the beginning of the former century, followed by a warm period from the 1920s through the 1950s, a cold period from the 1960s into the 1980s, and has since been on a warming trend (Ingvaldsen et al., 2003; Ingvaldsen and Loeng, 2009; Ozhigin et al., 2011). Information on some of the major fish stock such as Barents Sea cod and herring dates back more than 100 years (Helland-Hansen and Nansen, 1909; Hjort, 1914; Dragesund et al., 2008; Hylen et al., 2008). The Barents Sea cod stock has shown long-term variations in response to the climate oscillations with high stock level in the warm period in the 1930s–1940s and again in the recent warm period after 1990 (Hylen et al., 2008; Kjesbu et al., 2014). Regular monitoring of fish recruitment and pelagic fish stocks in the Barents Sea dates back to the 1960s and 1970s with only sporadic information before that time (Jakobsen and Ozhigin, 2011; Eriksen and Gjøsæter, 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 (Rijnsdorp et al., 2009; Perry et al., 2010; Ottersen et al., 2010). Even small changes in temperature can directly influence the physiology and ecology of fish (Hochachka and Somero, 2001; Pörtner, 2001). Since about 1980, the Barents Sea has been on a warming trend with an increase of about 1 °C in the average temperature of the Atlantic water at the Kola section (Boitsov et al., 2012). The warming has been particularly large in the last decade when we have seen record warm conditions and northerly distributions of fishes such as cod in the Barents Sea (Johannesen et al., 2012; Renaud et al., 2012; Johansen et al., 2013; Michalsen
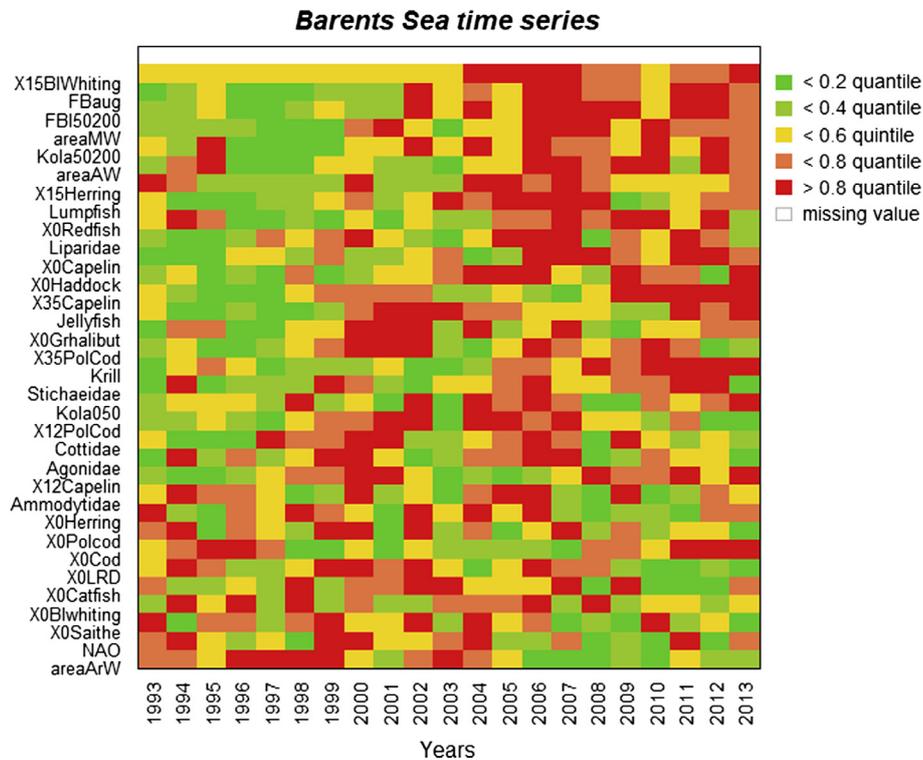
Fig. 16. Temporal trend plot of 25 biological variables (biomass of macrozooplankton, pelagic fish and 0-group fish; see Table 2) and 8 physical variables (NAO index, modelled water fluxes, area of water masses and water temperatures) used in PCA analysis for the period 1993–2013. The variables are standardized as anomalies (zero mean and unit SD) and shown with red (positive deviations) and green (negative) deviations. The variables are ordered according to their score on the first PCA axis.
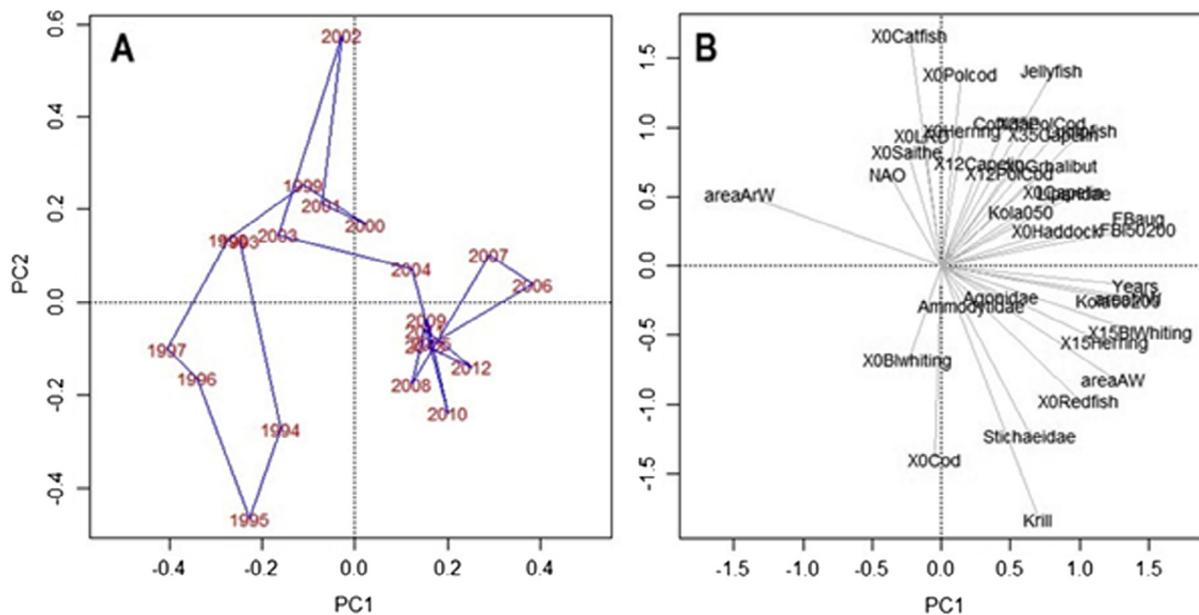
Fig. 17. Results from PCA analysis of 25 biological and 8 abiotic variables (see Table 2 and Fig. 16) for the time period 1993–2013. A – trajectories of the years 1993–2013 projected in the PC1-PC2 plane, B – projections of the 33 (25 + 8) variables onto the PC1-PC2 plane.

et al., 2013; Fossheim et al., 2015). The period 1993–2013, which we address in this paper, is therefore characterized by strong warming to a state which is unprecedented in our (relatively short) historic memory with proper scientific documentation.

Before we go on to consider spatial and temporal aspects of the observed changes in the Barents Sea ecosystem during this period, we note that there are methodological issues related to estimates of biomass from trawl catches and acoustic recordings. A discus-

sion of sources of errors of these data is found in Supplementary material 4.

5.1. Spatial pattern of pelagic biomass distribution

Krill was the dominant component of the pelagic biomass (after mesozooplankton; see Dalpadado et al., 2014; Stige et al., 2014), comprising nearly 2/3 of the total biomass of the larger-sized com-

ponents including 0-group fish considered in this paper (Fig. 11). Over the whole 21-years period krill biomass has shown an increasing trend. Krill was particularly abundant in the Southwestern and South-Central subareas but was also abundant in the North-Central and Svalbard subareas (Figs. 14 and 15). *Thysanoessa inermis* is the numerically dominant species with a core distribution in the Atlantic watermass of the western and central Barents Sea (Dalpadado and Skjoldal, 1991, 1996; Drobysheva, 1994; Orlova et al., 2011, 2013). The role of advection is not clear for this species but is probably important in supplying specimens with the inflowing Atlantic water, including larvae from upstream spawning areas in the adjacent Norwegian Sea (Drobysheva, 1982, 1994; Dalpadado et al., 2008; Orlova et al., 2015). Advection is known to play an important role for the occurrence of the larger krill species *Meganyctiphanes norvegica* in the region of inflowing Atlantic water in the western and southern Barents Sea (Drobysheva, 1979, 1994; Zhukova et al., 2009; Orlova et al., 2013, 2015). Although we lack species identification, we believe *Meganyctiphanes* contributed much to the high biomass values recorded in our trawl catches in the western and central Barents Sea. *Thysanoessa raschii* is found mainly in the shallow waters of the southeastern Barents Sea (Drobysheva, 1994; Orlova et al., 2013) where recorded krill biomass was relatively low in our study (Fig. 15).

Cod and herring were the two most important species contributing to the biomass of 0-group fish (Fig. 11B). Along with haddock they spawn 'up-stream' of (or at the entrance to) the Barents Sea. The larvae are transported with the coastal and Atlantic currents into the Barents Sea (Rass, 1934, 1949; Ottersen and Loeng, 2000; Eriksen and Prozorkevich, 2011) where they are prominent contributors to the pelagic biomass primarily in the Southwestern and South-Central subareas. The southern Barents Sea is the main nursery ground for juvenile herring of the Norwegian spring spawning stock (Aleev, 1938; Marty, 1956; Dragesund et al., 2008), and juvenile herring was the dominant component of the pelagic fish biomass in the Southwestern, South-Central and Southeastern subareas (Supplementary material 3). Capelin and polar cod spawn and have life cycle closures within the Barents Sea ecosystem (the distribution area for polar cod probably includes adjacent part of the northern Kara Sea) (Rass, 1933; Ponomarenko, 1968; Gjøsæter, 1998; Gjøsæter et al., 2011; Ajiad et al., 2011). While mature capelin migrates south to spawn along the coasts of northern Norway and Murman in winter, capelin is found mainly in the North-Central subarea in autumn where it is a dominant biomass component (Fig. 9). Capelin was also found occasionally with relatively high biomass in the Svalbard and Eastern subareas. Polar cod moves to spawning areas under ice in the southeastern Barents Sea (Ponomarenko, 1968; Eriksen et al., 2015) where it contributed to high biomass in the Eastern subarea in autumn (Fig. 9, Supplementary material 3).

The spatial pattern of biomass variations was resolved by the non-metric MDS which showed a separation of the subareas according to North-South and East-West gradients (Fig. 13). The three southern subareas were well separated whereas the northern subareas were only partially separated and showed considerable overlap. A possible interpretation is that the southern subareas form a sequence with changing ecological conditions along the main route of transport of Atlantic water from West to East, whereas the northern subareas are all more clearly affected by the recent warming and associated 'borealization' (Fossheim et al., 2015).

In summary, we can see that the spatial pattern of pelagic biomass in the Barents Sea in autumn is determined by two main features: the geographical distribution and spatial life cycle closure for dominant species of pelagic fish, notably capelin, polar cod and herring, and advection with inflowing Atlantic water which transports krill and 0-group fish (notably cod and herring) into the western and southern Barents Sea. These two features provide a general consistent and persistent pattern in the spatial distribution of pelagic biomass but they contribute also to the temporal (interannual and decadal) variability which we consider next.

5.2. Temporal variability in pelagic biomass distribution

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 (Fig. 11). This increase in krill took place apparently in two pulses, with an increase in the North-Central subarea (including the Hopen Deep area) in 2005–2007, followed by increases in the Southwestern and South-Central subareas from 2008 (Supplementary material 3). The increase in krill was associated with increased fluxes of Atlantic water into the Barents Sea and north into the Hopen Deep in 2005 and 2006 and increased area of Atlantic water with maximum in 2006 and 2007 (Fig. 7). This suggests that the increase in krill from 2004 was associated with increased transports of *Meganyctiphanes norvegica* and *Thysanoessa inermis* with Atlantic water into the Barents Sea. The observed increase in krill in the recent period agrees with results from a Russian winter survey (where krill is collected with a plankton net attached to a bottom trawl) which has shown an increasing trend in the abundance of krill including *Meganyctiphanes* in the 2000s compared to the 1990s (Zhukova et al., 2009; Orlova et al., 2011, 2013). Orlova et al. (2015) used increased abundance of *M. norvegica* and the smaller species *Thysanoessa longicaudata* to suggest increased advection of krill into the Barents Sea from the adjacent Norwegian Sea. A closer comparison between the krill results from the Russian winter bottom trawl survey and the results from the joint autumn survey, which we report here, is given in a separate paper (Eriksen et al., 2016).

Variable recruitment of fish stocks is a major source of variability in the whole 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 (Eriksen et al., 2011) and subsequently as juveniles and adults of the pelagic species over the next years. Strong year-classes of fish have therefore a 'snowball effect' as they develop and exert ecological cascading effects through their roles as predators and preys in the ecosystem (Eriksen et al., 2011). In our data, we can see the influence of 0-group herring of the year-classes 2002–2004 on the biomass of juvenile herring in the southern Barents Sea in 2004–2008 (Fig. 12, Supplementary material 2). Juvenile herring has apparently, a strong predatory impact on capelin larvae which is believed to cause recruitment failure and stock collapses of capelin (Gjøsæter and Bogstad, 1998; Huse and Toresen, 2000; Gjøsæter et al., 2009, 2012; Hallfredsson and Pedersen, 2009). The high biomass of juvenile herring in the southern Barents Sea coincided with the stock collapse and low biomass of capelin in the early 2000s (Fig. 12A). High biomass of juvenile herring in 1993 also coincided with the stock collapse and low biomass of capelin in the early 1990s (Gjøsæter et al., 2009).

The spatial distribution of capelin has been shown to vary with both climatic conditions and stock size, with distribution extending further north in warm years and when the stock size is high (Huse et al., 2004; Carscadden et al., 2013; Ingvaldsen and Gjøsæter, 2013). Capelin was found mainly in the North-Central subarea where it constituted almost the total pelagic fish biomass. Capelin also contributed to the biomass in the eastern subarea in some years (notably 2000 and 2009) as it did also in the Svalbard subarea (notably in 2001, 2010, 2011 and 2013; Supplementary material 3).

Atlantic cod contributed to the pelagic biomass as 0-group fish in the Southwestern and South-Central subareas as two 'waves' in

the mid 1990s (1994–97) and in the late 2000s (2008–2012). Good recruitment contributed to a strong increase in the Barents Sea cod stock to a record high level and a northward expansion of distribution in the most recent warm years (Johannesen et al., 2012; Bogstad et al., 2013; Johansen et al., 2013; Kjesbu et al., 2014).

Polar cod has shown an opposite trend with a substantial decline in recorded stock size and a northeastward retreat in autumn distribution in the recent warm years (Prokhorova, 2013; ICES, 2014; Eriksen et al., 2015). Polar cod contributed to the pelagic biomass as 0-group fish in the Eastern and Southeastern subareas with peaks in 1994 and 2002 (Supplementary material 3). Juvenile and older polar cod dominated the biomass of pelagic fish in the Eastern subarea with three 'waves' of population increases, one in the mid 1990s, a second around 2000, and a third in the mid to late 2000s (Supplementary material 3). The virtual disappearance of polar cod in the surveys in 2012 and 2013 has resulted in low biomass in the Eastern subarea and is a major concern for the overall functioning of the Barents Sea ecosystem due to the large role of polar cod in the Arctic food webs (Ajiad et al., 2011; Renaud et al., 2012; Hop and Gjøsæter, 2013; ICES, 2014; Eriksen et al., 2015).

6. Concluding remarks

Based on a review of relevant literature and additional analyses, we have described large changes and shifts in the pelagic part of the Barents Sea ecosystem associated with the recent warming event over the last 10–15 years. The biomass level of the larger fractions of the pelagic community (not including mesozooplankton) was recorded to shift up with about a doubling from the 1990s (up to 2003) to the 2000s, driven primarily by a substantial increase in the amount of krill. The warming was associated with stronger inflow events of Atlantic water and an expanded area of relatively warm Atlantic and mixed water. It is possible that the increase in the amount of krill reflects stronger advection of krill (notably *T. inermis* and *M. norvegica*) with the inflowing Atlantic water into the Barents Sea and increased transport and extended range northwards and eastwards with the expansion of Atlantic water (Orlova et al., 2015).

Capelin is a key species in the Barents Sea ecosystem linking the cold arctic waters in the north with the warmer Atlantic water in south through its seasonal feeding migration and life cycle closure. Capelin has a strong influence on zooplankton stocks through predation (Dalpadado et al., 2002; Stige et al., 2014), which has been found to be particularly pronounced for krill in the central Barents Sea (Dalpadado and Skjoldal, 1996). The inverse relationship between capelin and krill is reflected in the diet of Atlantic cod which shifts to feed more on pelagic crustaceans at times when capelin is scarce (Orlova et al., 2005, 2013). It appears that the role of capelin in the Barents Sea ecosystem has become less dominant in the recent period of warming, with other species filling the 'void' and dampening the effect of lack of capelin during the collapse in the early 2000s (Gjøsæter et al., 2009). The effect of capelin predation on krill may also be dampened during warm conditions when advection brings a supply of new individuals into the Barents Sea to replenish the stocks depleted by predation (Eriksen and Dalpadado, 2011; Orlova et al., 2005, 2013).

To describe how parts of the ecosystem have responded to observed fluctuations and trends in abiotic and biotic factors in the past is by no means straightforward. To understand how the system will react to further changes in climate is even more complicated. Effects may for instance be linear over a range of temperatures observed so far, but may enter a nonlinear phase for higher temperatures. Time lags between causes and effects may obscure actual co-variations. Small differences in environmental factors may cause huge variation in recruitment success, which might have cascading effects affecting the whole ecosystem. Further ecosystem analyses and studies need to be guided by identified research questions that are based on our current understanding and formulated as testable hypotheses where possible.

The Barents Sea can be regarded at the same time as a simple and a complex ecosystem. It is simple in the sense that there are a limited number of species that play the dominant roles as actors in the drama that unfolds on the ecosystem scene. However, it is sufficiently complex with many couplings and time-delays in trophic interactions to make it difficult to unravel and ascertain the combined effects (both direct and indirect) of climate variability and trophic interactions in the ecosystem. Our data suggest that there is a fair amount of spatial structure and consistency resulting from the spatial life cycle closure (geographical belonging) of main species of fish with spawning grounds both inside and up-stream outside the Barents Sea, and the role of advection in transporting and distributing fish larvae, juveniles and zooplankton with the Atlantic inflow. Climate variability (reflected in fluxes, properties and distribution of water masses) has a particularly important effect on recruitment variability of the major pelagic fish stocks. The variable year class abundance affects the ecosystem during the whole lifetime of these fish species, from the 0-group stage and during the subsequent years, when 'waves' of the major pelagic fish stocks surge through the ecosystem with cascading effects both upwards to predators (e.g. Atlantic cod, harp seal and others) and downwards to prey populations such as krill and other zooplankton.

Based on what we have seen so far, we may conclude that spatial aspects are indispensable in any hypotheses regarding the dynamics and future development of the Barents Sea ecosystem. The Barents Sea is by no means spatially homogeneous, and is a highly dynamic and shifting ecosystem with large amplitude fluctuations (see Fig. 4). Recruitment to the main fish stocks seems to be pivotal in this ecosystem, and recruitment mechanisms are by no means understood, despite considerable research effort in this field for many decades. The role of jellyfish in these recruitment mechanisms should be further investigated. Trophic interactions and trophic control mechanisms under various environmental conditions are other highly relevant research fields. Effects on growth and reproduction of the pelagic fish stocks from changes in biomass and composition of plankton is another research topic that is highly relevant to improve our understanding of possible effects of climate variability and change in the Barents Sea ecosystem.

Development and use of mathematical models is one approach to address research questions and test identified hypotheses for the Barents Sea ecosystem. Balancing complexity to obtain realism and simplicity to meet data needs is often the most difficult task when choosing models. Even though the Barents Sea is a data-rich ecosystem with long time series and reasonably good spatial and temporal resolution of sampling, models should be made as simple as possible, starting with the key players and the dominating processes and drivers of change in the ecosystem. Estimates reported here provides a basis for next steps to identify some of these key factors.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2016.12.009.

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