



## 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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## 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 Gjøsaeter, 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 Gjøsaeter, 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 (*Mallothus 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 (Gjøsaeter 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

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