

Three-dimensional zooplankton distributions seen through the lens of fish in the Barents Sea



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Scientific environment

The PhD candidate Johanna Myrseth Aarflot has been affiliated with the Ecosystem processes group at the Institute of Marine Research (IMR) and the Theoretical ecology group at the University of Bergen (UoB). The work was financed by the Norwegian Research Council through the IMR strategic institute programme TIBIA (Trophic Interactions in the Barents Sea – steps towards an Integrated Ecosystem Assessment), project number 228880.

Preface

Over the past three years, I have developed a passion for zooplankton. How these creatures have adapted to life in a three-dimensional, viscous environment never stops to amaze me. Working on a PhD has been challenging and exciting, hard and frustrating - but most of all it has been a privilege. A privilege to be employed for enhancing your own knowledge and developing the necessary skills to become a scientist, and a privilege to be guided by a wide range of people who inspire you.

I thank my supervisors Hein Rune Skjoldal, Padmini Dalpadado, and Øyvind Fiksen, for input, guidance and support during this period. Special thanks to Øyvind for challenging me to aim high and make my research appeal to a broader audience. I also thank my group leader and co-author Mette Skern-Mauritzen for invaluable support, and co-authors/collaborators Dag Aksnes and Anders F. Opdal for constructive feedback that really improved my manuscripts. Many other colleagues both at the IMR and UoB have offered their views, advice and training without expecting anything in return, and I am grateful to all of you.

Analyses presented in this dissertation rests on countless hours of work by technicians, scientists and crew onboard IMR monitoring surveys in the Barents Sea, and in laboratories on shore. It has been a pleasure to work with these datasets, and I acknowledge all who have contributed in their making. Also, thanks to Andrey Dolgov, Irina Prokopchuk and Anna Gordeeva (PINRO) for allowing me to use the “Russian” part of capelin stomach data from the Barents Sea in my dissertation.

Thanks to family and friends for believing in me and supporting me, I love you all so much. Hogne, thank you for being there and loving me also in the darkest phases of the past three years. Sigvald and Kanutte, thank you for always brightening up my days and taking my focus off work. Only the coolest kids know which animal is the strongest in the world.

Johanna Myrseth Aarflot, Bergen 2019

Summary

My aim with this dissertation is to enhance our knowledge of food availability and foraging opportunities for planktivorous fish over the Barents Sea bathymetry.

The Barents Sea is a highly productive sub-Arctic shelf sea supporting some of the largest fish stocks in the world. Lipid-rich calanoid copepods are key prey for fish and other planktivore predators in northern latitude ecosystems. Visual detection of individual prey is the dominant foraging mode in planktivorous fish, and prey detection is arguably the most limiting phase in the predation process. Light is a prerequisite for visual foraging and decreases exponentially with depth in aquatic systems. Furthermore, vertical movement has become a widespread strategy among *Calanus* and other zooplankton for avoiding visual predation. The bathymetry may, however, constrain vertical distributions and force zooplankton into more illuminated parts of the water column. Environmental constraints on distributions may be important for fish searching for zooplankton and affect predator-prey dynamics in pelagic ecosystems.

In **Paper I**, we focus on *Calanus* spp. and use an extensive (30-year period) dataset on zooplankton biomass and species-specific abundance to show that calanoid copepods are a major driver of variation in zooplankton biomass in this ecosystem. *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* constitute on average 80 % of the total biomass, and older copepodites (stages CIV and CV) make the largest contribution. The *Calanus* species co-occur in all areas, and interspecific variation in spatial biomass distribution may be related to the distribution of water masses. Biomass of *Calanus* spp. increases with bottom depth, but does this mean that prey is more available to fish in deeper parts of the Barents Sea?

In **Paper II**, we utilize a unique dataset on vertical zooplankton distributions to determine the weighted mean depth (WMD) of zooplankton in three size fractions and assess the effect of topography and light on the depth distributions. The vertical dimension of the prey field is important for fish that are constrained by light in their search for prey. We show that the bathymetry constrains the zooplankton depth

distribution; all size fractions have deeper distributions with increasing bottom depth. Distributions are shallower when the water is less clear, however the effect of water clarity is secondary compared to the effect of topography, and most pronounced in deeper (> 300 m) areas. Furthermore, zooplankton over banks are exposed to several orders of magnitude more light compared to zooplankton in deeper areas where distributions are less constrained by the bathymetry. This has a large effect on the theoretical visual range of fish, which declines as zooplankton WMD deepens.

Zooplankton WMD does, however, only indicate where the weight of zooplankton is standing in the water column. To further investigate how the bathymetry structures foraging opportunities for fish, we use the vertical zooplankton biomass profiles as input to a visual foraging model and quantify the integrated prey encounter rate for fish over the bathymetry (**Paper III**). Our results demonstrate that fish may encounter significantly more large zooplankton (> 2 mm) in areas shallower than 200 m, even though the abundance is higher in deeper areas. Banks in the northern Barents Sea appear to be particularly attractive foraging habitats, as prey here is forced into greater light exposure. Furthermore, analyses of copepod filling in capelin stomachs support these predictions and suggest that capelin foraging on copepods have been more successful over shallow bathymetries < 200 m. Due to visual constraints on prey detection, the fish' ability to utilize the zooplankton biomass m^{-2} is non-linearly related to the zooplankton WMD, and greater in shallow areas.

Evaluating food availability for planktivorous fish using vertical zooplankton distributions presents a different picture than the spatial patterns in prey abundance. Results in my dissertation highlight the importance of bathymetry for fish foraging efficiency and predator-prey dynamics in pelagic ecosystems. Furthermore, my results convey a new perspective on capelin feeding migrations and regional variation in trophic control, which may increase our general understanding of ecosystem structure and function.

List of Publications

Paper I

Aarflot, JM, Skjoldal, HR, Dalpadado, P & Skern-Mauritzen, M. (2017) Contribution of *Calanus* species to the mesozooplankton biomass in the Barents Sea. *ICES Journal of Marine Science* **75** (7): 2342-2354, doi: 10.1093/icesjms/fsx221.

Paper II

Aarflot, JM, Aksnes, DL, Opdal, AF, Skjoldal, HR & Fiksen, Ø. (2018) Caught in broad daylight: Topographic constraints of zooplankton depth distributions. *Limnology and Oceanography* (Early View), doi: 10.1002/lno.11079.

Paper III

Aarflot, JM, Dalpadado, P, Skjoldal, HR & Fiksen, Ø. Hide and seek: Foraging opportunities for planktivorous fish shaped by constraints on vertical zooplankton distributions. *Manuscript*.

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Introduction

Spatial structures in the environment shape habitats and outline the space where species interact through reproduction, competition and predation (Tilman 1994). In the ocean, space below the surface is defined by the topography. The vertical size of this space, that is the distance from the surface to the sea floor, affects physical processes like advection, mixing and sinking time of organic matter, and it can also structure biological interactions. Bottom depth alters for instance the strength of the biological coupling between benthic and pelagic parts of the ecosystem, thereby modifying predator-prey interactions and food-web structure (Schindler and Scheuerell 2002). Depth shapes trophic structure gradients in shallow continental seas, where the degree of benthic *versus* pelagic prey in the diet of fish changes along the depth slope. Benthic and pelagic fish can access both prey sources and have a more variable diet in shallow waters, and the strength of the benthic-pelagic coupling weakens as depth increases (Kopp et al. 2015; Giraldo et al. 2017). In deeper waters off the continental slope, interactions between the bathymetry and vertically migrating prey species may structure the functional composition of demersal fish communities. Benthic feeding fish have access to vertically migrating prey sources only down to depths where the migrators reach the sea floor. In contrast, benthopelagic feeders who are also able to consume prey above the sea floor have a competitive advantage and dominate in biomass at greater depths (Trueman et al. 2014).

Few studies have investigated how bottom depth affects biological interactions between species associated with the upper part of the ocean, i.e. in the pelagic zone. Marine pelagic ecosystems are possibly the largest ecosystems on earth measured by area (Verity et al. 2002), and host a variety of zooplankton and planktivorous fish. Both zooplankton and pelagic fish are often considered key species in marine ecosystems, feeding many species at higher trophic levels and supporting economically important fisheries (e.g. Pikitch et al. 2014; Record et al. 2018). Life in pelagic ecosystems is highly influenced by the properties and flow of water masses (Manderson 2016), but can it also be structured by the topography?

Pelagic organisms must choose where to position themselves within the water column, as it will determine both access to food and susceptibility to predation. Many species have evolved vertical migration strategies, adapting to the trade-off between maximizing growth and survival in dynamic environments (Pearre 2003; Ji 2011). Vertical migrations represent an active flux of carbon out of the productive surface and down to deeper waters, which contributes to the “biological pump” (Isla et al. 2015), supports mesopelagic species (Steinberg et al. 2008) and affects biological interactions in the upper ocean (Hays 2003; Brierley 2014). However, environmental barriers such as subsurface oxygen minimum zones (Ekau et al. 2018) or bottom topography (Genin 2004; Krumhansl et al. 2018) may constrain migrations and potentially force species to inhabit sub-optimal vertical distributions. These constraints are likely important for predator-prey dynamics in pelagic ecosystems.

Enhanced knowledge of how spatial structures in the environment affect vertical zooplankton distributions is central for our understanding of predator-prey dynamics between zooplankton and pelagic fish. It may also serve to improve our general understanding of marine ecosystems with respect to fish stock productivity and biomass distributions. In the following, I will describe vertical migration strategies in zooplankton and key aspects of planktivore foraging, before I introduce the ecosystem at focus (the Barents Sea). Finally, I present key findings from my 3 papers with a discussion aimed at putting my results into both a system-specific and a more general context.

Vertical migration strategies in zooplankton

Vertical migrations of zooplankton have been studied since the late-19th century (review in Russell 1927; Banse 1964), and possibly represents the largest movements of biomass on earth (Hays 2003). Diel vertical migration (DVM) is principally viewed as a predator avoidance mechanism (reviewed in Hays 2003), where the normal pattern of DVM is to occupy deeper waters in the day and migrate to shallower depths at night. Migration patterns may also be in the opposite direction, i.e. reverse DVM, and some species can alter migration behaviour or cease migrations altogether based on the presence of different types of predators (Ohman 1990).

Seasonal vertical migrations are common among zooplankton species at northern latitudes, where calanoid copepods undertake ontogenetic descents and overwinter at great depths for several months each year (Conover 1988). During overwintering they reduce their metabolic activity and enter a phase of diapause, before they ascend to the surface again for feeding and reproduction the following spring (Hirche 1983). Factors like temperature (Hirche 1991; Heath and Jónasdóttir 1999), light (Miller et al. 1991), food availability (Bandara et al. 2016), presence of predators (Kaartvedt 1996) and endogenous clock genes (Häfker et al. 2018) have been suggested as proximate cues for triggering these migrations.

Common for both DVM and seasonal migrations is that deep distributions have lower mortality risk from visual predation, due to the exponential decay of light in the water column (Aksnes and Giske 1990). Considering that migrations are related to fitness and survival, environmental barriers (e.g. oxygen minimum zones or bathymetry) restricting organisms from migrating to deeper, darker waters may i) amplify mortality risks of the migrators, and ii) provide important food sources to their predators.

Visual foraging in planktivorous fish

Planktivorous fish can feed on zooplankton using different modes of filtering and visual search (Eggers 1977; Batty et al. 1990). Particulate feeding, i.e. visually selecting individual prey, is considered the common feeding mode in these fish, due to the large size of prey in their stomachs and since filtering requires a certain amount of prey in the environment for it to be efficient (Blaxter and Hunter 1982; Batty et al. 1990).

In visual foraging, ambient light is important for success. Studies have shown that fish react to prey at greater distance under high light intensity (Link and Edsall 1996; Aksnes and Utne 1997), and that water clarity affects both the choice of prey and the amount consumed. Fish select large prey more frequently when the water is turbid, and consumption rates decline with increasing turbidity (Helenius et al. 2013). This may be related to prey visibility. Large prey are detected at greater distances by the fish (O'Brien 1979), and increasing turbidity shortens the visual range (Aksnes and Giske 1993) and reduces the clearance rate (Huse and Fiksen 2010). Observations of fish abundance and zooplankton size distributions have indeed been related to the degree of light absorption in the water column when comparing different fjord systems (Eiane et al. 1999; Aksnes et al. 2004).

Since zooplankton visibility is a function of body size, large individuals must go deeper to reduce their visibility (Giske et al. 1994). Water clarity affects how deep surface irradiance penetrates the water column, and consequently how deep the zooplankton must go to reduce the visual predation risk. Zooplankton observations have shown that large sizes tend to occupy deeper waters (Fortier et al. 2001; Ohman and Romagnan 2016; Paper II), and that water clarity can account for variations in depth distributions (Dupont and Aksnes 2012; Ohman and Romagnan 2016; Paper II). The vertical dimension of the (size-structured) prey community and optical properties of the water column is therefore important to consider when assessing food availability for planktivorous fish.

Aim

The scope of this dissertation is to enhance our knowledge of how zooplankton distributions in a three-dimensional space structures foraging opportunities for planktivorous fish across a large, sub-Arctic ecosystem. Extra emphasis is put on the lipid-rich *Calanus* species which are considered key zooplankton in high-latitude ecosystems. **Paper I** is therefore devoted to *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, and aims to establish a better understanding of their relative contribution to the zooplankton community in the Barents Sea, and describe interspecific differences with regards to spatial distributions and key environmental drivers. In **Paper II** I look more closely at the vertical dimension and aim to assess the effect of topography and light on vertical zooplankton distributions in this ecosystem. I also evaluate size-related differences in the vertical distributions, and how the observed patterns may impact the visual range of planktivorous fish over the topography. The fish predator perspective is elaborated further in **Paper III**, where the objective is to examine how the observed vertical zooplankton distributions and interactions with the bathymetry structures foraging opportunities for planktivorous fish over the seascape.

The Barents Sea ecosystem

Physical properties

The Barents Sea is a large marine ecosystem (~1.6 million km²) (Carmack et al. 2006) on the Arctic continental shelf bordering the northern Norwegian and Russian coasts in the south. It is a relatively shallow sea with a mean depth of 230 m, and the 500 m depth contour is frequently used to delimit its borders to the surrounding Norwegian and Greenland Seas and the polar basins (Ingvaldsen and Loeng 2009). Complex bathymetry characterizes the Barents Sea, and large oceanic banks (< 200 m depth) are mainly found in the central and northern areas (Svalbard Bank, Central Bank, Great Bank and Novaya Zemlya Bank, Fig. 1). One of the deepest areas is the Bear Island Trench (400–500 m depth), located at the western entrance where Atlantic water flows into the system.

The Barents Sea is a flow-through shelf system (Carmack et al. 2006) dominated by water masses of both Atlantic and Arctic origin (Fig. 1). Warm, saline Atlantic water originates from the Norwegian Atlantic Current in the south, while cold (< 0° C) and less saline Arctic water enters the system from the polar basins in the north and north east (Ingvaldsen and Loeng 2009). Atlantic and Arctic water masses meet at the topographically steered Polar Front (Loeng 1991; Gawarkiewicz and Plueddemann 1995). Coastal water from the Norwegian Coastal Current is found in the southern parts of the sea, influenced by low-saline water from the North Sea and fresh water river runoffs along the Norwegian coast (Ingvaldsen and Loeng 2009). The strength and properties of Atlantic inflow coupled with local atmospheric conditions affects climatic conditions in the Barents Sea, and there have been large interannual trends in ocean temperature and ice cover (Smedsrud et al. 2010; Boitsov et al. 2012). Northern parts of the sea where Arctic water is present are covered by ice during several months each year, and the minimum sea ice extent is usually found in mid-September (Kvingedal 2005). Increased heat transport of warmer Atlantic water has caused a substantial warming trend over the past decades (Årthun et al. 2012), and the seasonal ice extent has been reduced since the 1950s (Onarheim et al. 2018).

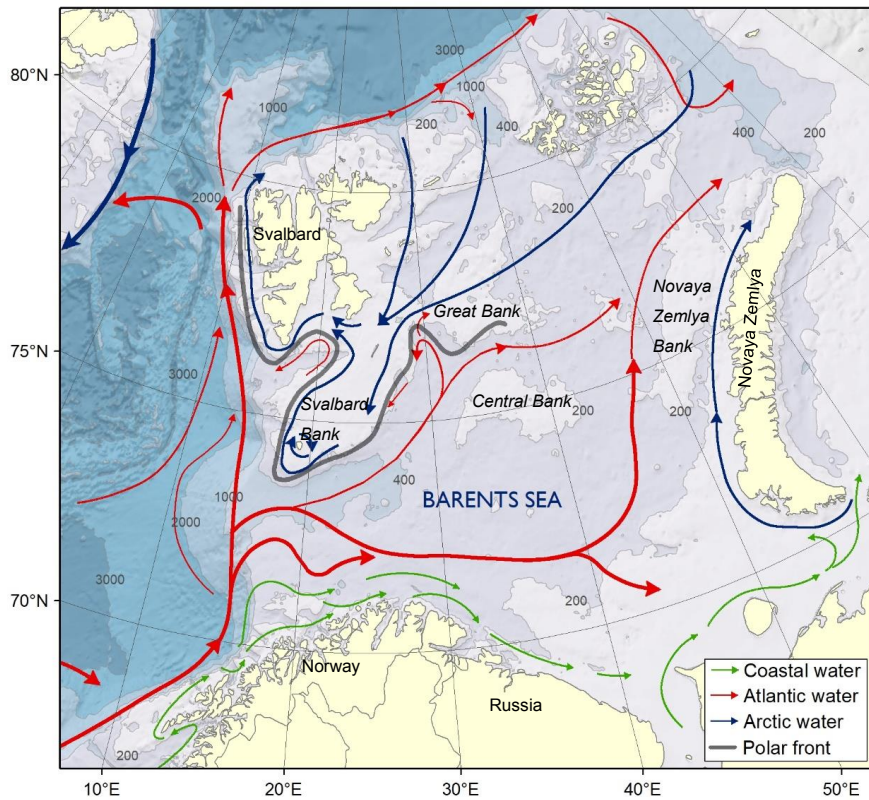


Figure 1: Map of the Barents Sea, showing main pathways for the major currents and location of the Polar Front. More detailed bathymetry maps are given in **Papers II** and **III**. Land areas and major banks have been labelled by the PhD candidate. Courtesy: R. Ingvaldsen and K. Gjertsen, Institute of Marine Research.

Planktivorous fish

The Barents Sea is a highly productive ecosystem hosting some of the largest fish stocks in the world (Eriksen et al. 2017). Capelin (*Mallotus villosus*) is a key, planktivorous fish species here, and several species at higher trophic levels depend on capelin as their main prey (Dolgov 2002). Other planktivorous fish are the Norwegian Spring-Spawning herring (*Clupea harengus harengus*), which use the southern parts of the sea as nursery area for young fish (Dragesund 1970), and polar cod (*Boreogadus saida*) commonly found in eastern and northern areas (Eriksen et al. 2017). Stomach analyses have shown that calanoid copepods are key prey items for capelin, herring and polar cod in the Barents Sea (Ajiad and Gjørseter 1990; Huse and Toresen 1996; Prokopchuk 2009). Krill (and to some degree amphipods) become progressively important for capelin with increasing fish size (Orlova et al. 2002; Dalpadado and Mowbray 2013). I have largely focused on capelin in this dissertation, due to its key ecological role in the Barents Sea ecosystem (Wassmann et al. 2006; Gjørseter et al. 2009). Some of the key findings do, however, apply to planktivorous fish in general.

Calanoid copepods

Zooplankton in the Barents Sea are both produced locally and advected into the sea with Arctic and Atlantic water masses (Wassmann et al. 2006; Kvile et al. 2017). The zooplankton community is diverse, with copepods and krill being the most important prey for fish (references above). Calanoid copepods dominate in abundance (Wassmann et al. 2006) and biomass (Arashkevich et al. 2002; Paper I), and three *Calanus* species with different sizes and life cycles are common here. *Calanus finmarchicus* is the smallest and most abundant, generally associated with Atlantic water masses (Tande 1991; Paper I) and characterized by a 1-year life cycle producing one new generation per year (Melle and Skjoldal 1998). Calanoid copepods are recognized for their high plasticity in diapause influenced by local

environmental conditions (Conover 1988; Baumgartner and Tarrant 2017), and recent studies suggest that *C. finmarchicus* may produce two generations per year at these latitudes with continued ocean warming (Paper I; Weydmann et al. 2018). Its Arctic congener, *C. glacialis*, has primarily been associated with Arctic water masses in the Barents Sea, where it displays a 1–2 years life cycle overwintering both at copepodite stages IV and V (Tande 1991; Melle and Skjoldal 1998; Paper I). The largest *Calanus* species in the Barents Sea, *C. hyperboreus*, is also of Arctic origin but displays a 3–4 years life cycle (Conover 1988). It generally occurs in low numbers in the Barents Sea compared to the other two *Calanus* species (Hirche and Kosobokova 2003; Paper I), and has its center of origin in the deep Greenland Sea (Hirche 1997).

Methods

Data

Two zooplankton datasets collected by the IMR during monitoring surveys in the Barents Sea have been central in this dissertation. One was a joint dataset of mesozooplankton biomass and abundance identified to species and copepodite stage, with a high seasonal resolution over a 30-year sampling period (**Paper I**). This combined dataset provided a unique opportunity to quantify which contribution *Calanus* species make in the total mesozooplankton biomass, and to evaluate *Calanus* spp. distribution in relation to key environmental drivers (**Paper I**). Furthermore, continuous sampling from the “Fugløya-Bear Island transect” (western entrance to the sea) facilitated analyses of temporal changes in the *Calanus* community between 1995–2016. Results from **Paper I** also provided better grounds for interpreting the zooplankton data utilized in **Papers II** and **III**.

In **Papers II** and **III**, I worked with an extensive dataset of vertical zooplankton distributions collected with MOCNESS sampling gear during ecosystem monitoring surveys in autumn (Eriksen et al. 2018). Accumulation of MOCNESS data over a 25-year period enabled us to analyse vertical zooplankton data over a wide spatial scale in the Barents Sea (Figure 1 in **Paper II**). Samples had been sorted into three different size fractions (> 2 mm, 1–2 mm and 0.18–1 mm) but did not include information on species in the samples, apart from large zooplankton like krill and amphipods which are measured separately (see Methods **Paper II**). During the Barents Sea ecosystem survey in 2016, eight samples from different sampling locations were processed for species identification after sorting into the three size fractions (unpublished data). Despite a low sample size, this gives some insight to what we expect to find in the three fractions and is added here as additional information (Fig. 2).

Sampling net avoidance of krill is influenced by ambient light (Wiebe et al. 1982), and since we largely focused on daytime samples in **Papers II** and **III**, we excluded

krill and other macrozooplankton from the analysis where possible (Methods **Paper II**). The majority of the data utilized in **Paper I** came from WP2 plankton nets which are not efficient in capturing krill and other large zooplankton due to their swimming (avoidance) capabilities (e.g. Eriksen et al. 2016). I therefore consider the contribution of macrozooplankton to be insignificant also in analyses presented in **Paper I**.

In addition to the zooplankton data, I have used data on temperature (**Paper I**), salinity (**Papers I and II**), chlorophyll *a* (**Paper II**) and capelin stomachs (**Paper III**) collected during the same monitoring surveys in the Barents Sea. Metadata on spatial position (longitude, latitude) and bottom depth were employed in analyses in **Papers I and III**. Since irradiance is not routinely measured during these surveys, I employed an algorithm from the HYCOM model (Bleck 2002) as a proxy for surface irradiance in **Paper II**.

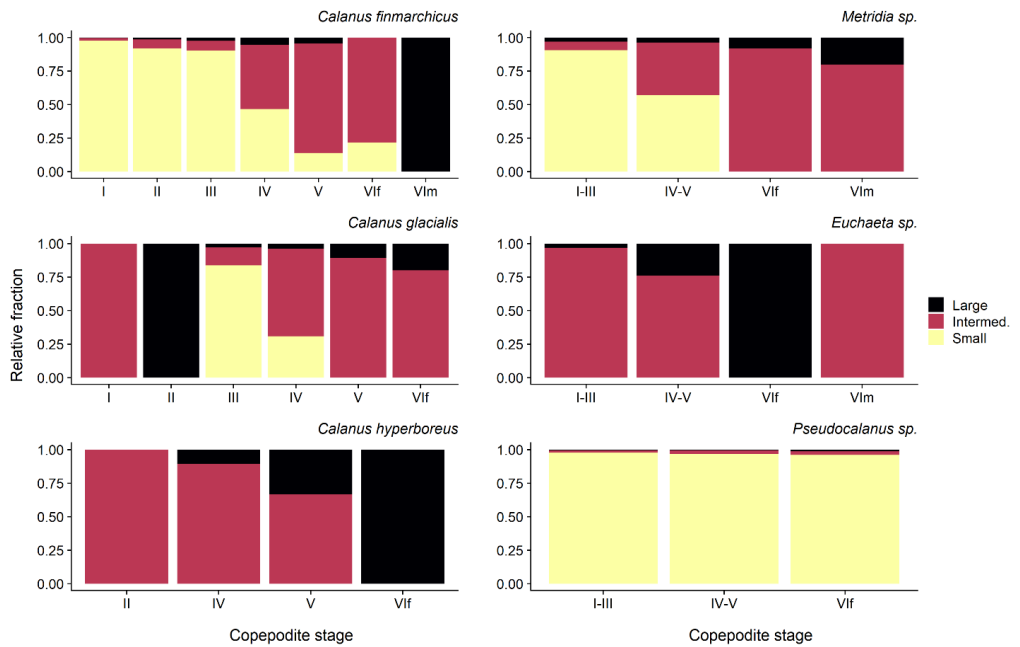


Figure 2: Appearance of copepodite stages from *Calanus* spp. and other copepod species sorted into the three size fractions large (> 2 mm), intermediate (1–2 mm) and small (0.18–1 mm). Samples originate from the Barents Sea ecosystem survey in 2016, where eight samples were processed for species identification after sorting into the three size fractions. Due to the low sample size, the data is likely not representative for all copepodite stages shown here.

Statistical analyses

I have used a combination of linear and non-linear statistical models when analysing data in this dissertation, the models are described and justified in the respective papers.

In **Paper I**, I employed linear modelling techniques to evaluate i) the relationship between total mesozooplankton biomass sampled and the estimated biomass of *Calanus* species in the respective samples, and ii) the relationship between *Calanus* species biomass and key environmental drivers. Temporal changes in the *Calanus* complex at the Fugløya-Bear Island transect were, however, assessed using General additive modelling (GAM). This is a more flexible statistical approach useful for capturing non-linear trends in the data (Wood et al. 2016).

In **Paper II**, I used linear models to test *a priori* defined hypotheses regarding the effect of bathymetry, light absorption and individual size on the vertical zooplankton distributions, and to assess whether the vertical distributions changed between day and night.

GAM was used in **Paper III** to evaluate stomach filling of copepods in capelin as a function of bottom depth. Considering that the MOCNESS data were employed as input in the theoretical foraging model, further statistical analyses in this paper was considered inappropriate.

Theoretical foraging model

Prey abundance is not necessarily a good measure of how much food a predator has access to (Gawlik 2002). Since planktivore fish are searching for small prey relative to their own body size, locating prey is presumably the most limiting phase in the foraging process (O'Brien et al. 1990). Ambient light is necessary for prey detection, and may be an important top-down constraint on fish foraging (Aksnes and Giske 1993). Combining the vertical zooplankton observations with a theoretical foraging

model of a fish that is limited by light in its search for prey (Aksnes and Giske 1993; Aksnes and Utne 1997) enabled me to theoretically assess how the prey detection distance (**Paper II**) and encounter rates (**Paper III**) for the fish are structured by actual observations of vertical zooplankton distributions. A similar modelling framework has previously been employed to investigate how fish abundance and zooplankton body size varies between fjord systems with different water clarity (Aksnes et al. 2004), seasonality in fish growth in relation to prey abundance and solar irradiance (Varpe and Fiksen 2010) and the relationship between prey size and growth of planktivorous fish (van Deurs et al. 2015).

As with all modelling exercises, assumptions needed to be made, here concerning e.g. prey size and contrast against the background, fish visual capabilities and the ambient light environment (see Supplementary material **Paper II** and Methods **Paper III**). Furthermore, I did not include processes like prey handling time or capture success (Discussion **Paper III**), these would have required more assumptions of unknown parameters and the goal was not to quantify realistic ingestion rates for the fish. My results do, however, bring new insight to the foraging opportunities (or prey availability) for planktivorous fish in an ecosystem where zooplankton are both forced into the light and allowed to stand in darker parts of the water column.

Results and discussion

System-specific perspectives

Previous studies from the Barents Sea have analysed the interaction between zooplankton and planktivorous fish mainly based on data of stomach content in fish and biomass (m^{-2}) fluctuations within the two trophic levels (an exception is Hassel et al. 1991). Results from my dissertation bring additional insight to this interaction and can shed new light on previous observations from the ecosystem. Furthermore, results presented here are also important from a fisheries management and monitoring perspective.

Calanus in the Barents Sea ecosystem

Copepods of the genus *Calanus* are a central part of pelagic food webs in high latitude ecosystems, where they concentrate lipid-poor energy from primary production into a lipid-rich food source for higher trophic levels (Conover 1988; Kattner and Hagen 2009). With an individual lipid content up to 50–60 % of their body weight (Scott et al. 2000), these copepods are valuable prey for their predators. Earlier studies have described *Calanus* as key zooplankton in the Barents Sea ecosystem due to their large size and abundance (e.g. Hassel 1986; Melle and Skjoldal 1998; Wassmann et al. 2006), though few have quantified the overall contribution of *Calanus* species in terms of biomass. In **Paper I**, we demonstrated that the joint contribution of *Calanus* species to the zooplankton biomass may be as large as 80 % or higher, though varying at spatial and seasonal scales. This is in accordance with a study by Arashkevich et al. (2002) conducted over a smaller spatial and temporal scale than ours. Older copepodites (stages CIV and CV) make the largest contribution to biomass (**Paper I**), and are also the most important calanoid prey for capelin in this ecosystem (Hassel et al. 1991; Huse and Toresen 1996).

There has been a discussion during the recent decade on whether one can reliably separate between the *Calanus* species when visually examining specimens in the laboratory (see Discussion **Paper I**). In one of the most recent studies examining this question, Choquet et al. (2018) showed that misidentifications may occur also when examining the curvature of the fifth thoracic pair of legs of the copepodites. This morphological trait has traditionally been used by the IMR for separating between the species in addition to size (see Methods **Paper I**). Thus, it is difficult to assess the possible uncertainties associated with the IMR dataset on *Calanus* species abundance. However, considering the clear association we found between *Calanus* species in different water masses, I am confident that our results in **Paper I** are representative though there may be misidentifications in individual samples. The potential for misidentification (and hybridization) is probably greatest in the mixed water masses where the largest co-occurrence of *C. finmarchicus* and *C. glacialis* was observed (**Paper I**). A general trend is that large *Calanus* copepodites tend to dominate in colder waters associated with northern, central and eastern areas of the Barents Sea (**Paper I**). This fits well with our analyses of copepods in capelin stomachs (**Paper III**), which is elaborated further below.

Daase et al. (2008) demonstrated that surface waters around Svalbard were dominated by young stages of *Calanus* spp., while larger calanoid copepodites had deeper distributions. We also found significant differences in depth distributions of the three size fractions (**Paper II**), and the smallest fraction which contains most of the young *C. finmarchicus* copepodites (Fig. 2) had the shallowest distributions. Variation in the depth distributions may have been caused by the presence of different species with different vertical strategies (**Paper II**, Fig. 2), e.g. the omnivorous *Metridia longa* which has been associated with a wider distribution (Daase et al. 2008). The presence of *M. longa* in the Barents Sea appears to be more variable than the *Calanus* species (Arashkevich et al. 2002).

In **Paper II** we presumed that the large size fraction had descended for overwintering, considering the strong (and similar) effect of bottom depth on distributions in both day and night. Bandara et al. (2016) described vertical descents

of older copepodites between August and October in a zooplankton community around Svalbard, which corresponds to the time-period for our own observations. Comparison of day- and night-time distributions did, however, suggest a pattern of inverse DVM for the small and intermediate size fraction (**Paper II**), which most stages of the dominant *C. finmarchicus* (**Paper I**) sort into due to its size (Fig. 2). Inverse DVM may be a response to the presence of other vertically migrating predators (e.g. Ohman 1990). Previous studies have described midnight sinking behaviour of *C. finmarchicus* corresponding to the arrival of krill (*Meganyctiphanes norvegica* and *Thysanoessa raschii*) in surface layers at night time (Tarling et al. 2002). In the Barents Sea, *Thysanoessa longicaudata* and *M. norvegica* are known to feed on copepods, while the dominant *Thysanoessa inermis* is regarded a predominantly herbivore species (Falk-Petersen et al. 2000; Dalpadado et al. 2008). However, the patterns we observed were relatively weak and may have been confounded by the presence of different species in the individual samples (e.g. Hays et al. 1997).

Greater prey availability for fish over banks

The spatial distribution of capelin in the Barents Sea varies with stock size and ocean temperature (Ingvaldsen and Gjørseter 2013), and it undertakes large seasonal migrations each year. Northwards feeding migrations from overwintering areas in the central Barents Sea take place when the ice melts in summer and early autumn (Gjørseter 1998; Carscadden et al. 2013). These migrations are potentially costly in terms of energy (e.g. Nøttestad et al. 1999) and should be associated with clear gains for capelin itself. Trailing plankton blooms following the receding ice edge can be advantageous for capelin that possibly migrate into previously unpredated areas (Sakshaug and Skjoldal 1989; Hassel et al. 1991). Migrations can also be a response to greater mortality risk from cod in the south (Fiksen et al. 1995) or longer day lengths enhancing feeding opportunities in the north (Nøttestad et al. 1999).

A new perspective on capelin migrations is that zooplankton is more available in the areas where capelin migrates to feed, not due to higher biomass but arising from the vertical zooplankton distributions and interactions with the bathymetry. Deep areas have more zooplankton biomass m^{-2} (**Papers I and III**), however zooplankton have access to darker parts of the water column and are less available to the fish (**Papers II and III**). Topographic constraints on depth distributions creates attractive foraging habitats for planktivorous fish over banks in the central and northern parts of the Barents Sea (**Paper III**). Since zooplankton are forced into more illuminated parts of the water column in shallow areas (**Paper II**), fish that forage over these topographies have presumably greater probability of encountering prey and may utilize a larger part of the available prey population m^{-2} (**Paper III**). Predicted autumn distributions of capelin based on acoustic data (Fall et al. 2018) correspond well with our theoretical predictions of attractive foraging habitats for capelin. Furthermore, our theoretical predictions were supported by capelin stomach data analyses. Capelin caught over banks had greater probability of having copepods in their stomachs, and the ones who had fed on copepods had more copepods in their stomachs when caught over banks compared to capelin sampled from deeper areas (**Paper III**). Greater stomach filling of copepods in fish sampled from shallow areas may, however, also reflect greater availability of large *Calanus* in Arctic water domains (**Paper I**).

Capelin are in general believed to exert a significant predation pressure on zooplankton in the Barents Sea, and are frequently described as the most important planktivorous fish in this ecosystem (e.g. Gjørseter 1998; Wassmann et al. 2006). Interactions between the bathymetry and prey depth distributions will potentially affect the strength of the top-down and/or bottom-up regulation between zooplankton and fish. In areas shallower than 200 m, we found a tight relationship between zooplankton density and the theoretical prey encounter potential for fish, which was more variable for deeper areas (**Paper III**). Top-down control of fish on zooplankton has been demonstrated for the central and northern parts of the Barents Sea (Stige et al. 2014), where we predicted that the fish will be able to utilize a larger part of the available prey population (Figure 3 in **Paper III**). The strength of this relationship is

weaker in the southwest (Stige et al. 2014), where the topography allows deeper zooplankton distributions and they are less available to the fish (**Papers II and III**).

Are banks risky habitats for capelin?

In addition to greater foraging opportunities, shallow areas may also represent elevated predation risk for capelin. Fall et al. (2018) did not find a strong relationship between capelin density and bottom depth, though McGowan et al. (2018) observed higher densities of capelin over banks in the Gulf of Alaska. Atlantic cod (*Gadus morhua*) is a key predator on capelin in the Barents Sea, and the abundance of cod is negatively associated with bottom depth (Johannesen et al. 2012). Furthermore, studies from Newfoundland have demonstrated a negative association between bottom depth and the amount of capelin measured in cod stomachs (Fahrig et al. 1993). A similar association is also found in cod stomach analyses from the Barents Sea (Johanna Fall, unpublished data). Banks might therefore be risky habitats for capelin which is faced with a trade-off between greater foraging opportunities and elevated risk of predation. Habitat use by another mesopredator fish species (*Gasterosteus aculeatus*) has been associated with habitat complexity providing varying degrees of shelter from predation (Gagnon et al. 2019). Local scale processes and structures at the banks may be important also for capelin foraging in shallow areas.

Calanus in a changing Barents Sea

Climatic conditions in the Barents Sea are changing dramatically, and the sea is getting warmer (Lind et al. 2018). Both the minimum (September) and maximum (March) ice extent has decreased since 1950, and the sea is predicted to become ice free all year round within the next 30-40 years (Onarheim et al. 2018). Fish communities are already responding to these changes by transitioning towards dominance of Atlantic (boreal) species also in northern areas traditionally hosting

Arctic associates (Frainer et al. 2017). Changes in zooplankton communities may propagate through the ecosystem (e.g. Beaugrand et al. 2003), so revealing ongoing changes in the *Calanus* community is key for assessing the future state of this ecosystem.

Calanus glacialis has its core distribution in seasonally ice-covered areas on the Arctic shelves (Conover 1988; Falk-Petersen et al. 2009), where ice algae is considered important for its success. Early egg production is fuelled by ice algae blooms, so that offspring may utilize the phytoplankton bloom occurring a couple of months later (Hirche and Kosobokova 2003; Søreide et al. 2010). Changes in the primary production regime caused by earlier break up of sea ice in the northern Barents Sea might lead to a mis-match between spring bloom conditions and *C. glacialis* phenology (Søreide et al. 2010). It is, however, uncertain if *C. glacialis* can adapt to a warmer climate with no ice algae. Recent molecular studies do suggest that this species has a wider distribution than previously reported (Choquet et al. 2017).

Sea ice may be important for *C. glacialis* for another reason than food supply, namely survival through the overwintering stage. According to our theoretical predictions, planktivorous fish can utilize a larger part of the water column in the core distribution areas of *C. glacialis* areas in the Barents Sea (**Papers I and III**). Topographic constraints forcing vertical distributions into the light (**Paper II**) presumably makes *C. glacialis* and other large copepodites more vulnerable to visual predation in these areas (**Paper III**). Since ice reduces the amount of light entering the water column (Grenfell and Maykut 1977; Varpe et al. 2015), it is likely critical for the winter survival of zooplankton in areas with shallow bathymetries. Reduced sea-ice extent may lead to a tremendous increase in the search efficiency of fish (Langbehn and Varpe 2017), and can be a serious threat to the future persistence of large zooplankton in historically ice-covered areas of the Barents Sea.

Increasing temperatures may shift the size-structure of zooplankton communities through temperature-size relationships (Daufresne et al. 2009) and visual predation (Varpe et al. 2015), both leading to a dominance of smaller sized individuals. We

observed indications that this type of change is already occurring in the Barents Sea (**Paper I**), though our data only covered the western area (Fugløya-Bear Island transect). Potential changes in the zooplankton size-structure give rise for concern. Large zooplankton are important for fish since they support higher growth rates (van Deurs et al. 2015), and because their visibility makes the fish able to sustain high encounter rates at lower densities of prey (**Paper III**). Changes in the zooplankton size-structure may also bring negative consequences for other planktivores than fish in the ecosystem (e.g. Karnovsky et al. 2003; Steen et al. 2007).

General perspectives on fish-zooplankton trophic dynamics

Research on the structure and dynamics of pelagic ecosystems has traditionally taken a resource-driven view (Verity and Smetacek 1996), and it was recently argued that properties (e.g. temperature) and dynamics (e.g. current velocity) of seawater are the primary factors controlling ecological dynamics in the ocean (Manderson 2016). However, considering the results in **Paper II** and **Paper III** of my dissertation, it is intriguing to reflect upon which role the bathymetry and light might have played in shaping the patterns we observe in marine ecosystems.

Ocean banks as hotspots for fish

Physical structures in habitats creates patches where predators are more successful foragers, and areas where prey have a greater chance of survival (e.g. Crowder and Cooper 1982; Carter et al. 2018). The subsurface topography may have this kind of role in the predator-prey dynamics between zooplankton and visually orienting planktivore predators (**Papers II and III**). Banks and shelves are often productive zones of the ocean (Simpson and Sharples 2012) where fish tend to aggregate. Fish aggregation over shallow topographies has traditionally been viewed as a result of enhanced prey availability due to increased primary production from upwelling over

the topography. However, evidence for bottom-up effects on zooplankton and fish caused by increased primary production has rarely been demonstrated in the literature (Rogers 1994).

When zooplankton are advected onto shelves and banks, they are forced to occupy shallower parts of the water column. Increased light exposure makes them more vulnerable to predation (**Paper II**) and can create attractive foraging opportunities for visually orienting predators (**Paper III**). Topographic blockage of vertically migrating zooplankton was first described by Isaacs and Schwartzlose (1965), who suggested that this mechanism could be important for sustaining resident fish populations over these topographies (illustrated in Fig. 3). Later studies have suggested that topographic blockage of vertically migrating zooplankton is important for both demersal fish (e.g. Genin et al. 1988), seabirds (Hunt et al. 1996) and penguins (Perissinotto and McQuaid 1992) foraging over shallow topographies.

Environmental constraints on *Daphnia* depth distributions caused by hypolimnetic anoxia in freshwater lakes (e.g. Sakwińska and Dawidowicz 2005) is a parallel mechanism forcing zooplankton to remain in more illuminated parts of the water column. Similarly, the oxygen minimum zone may constrain vertical zooplankton distributions in oceanic habitats (Ekau et al. 2018). Constraints on distributions by shallow oxygen minimum zones has recently been suggested to benefit predators feeding on vertically migrating myctophid fish species (Stewart et al. 2018).

Since light attenuates exponentially with depth in the ocean, the fish' ability to utilize the available prey population m^{-2} becomes a non-linear relationship of the weighted mean depth (WMD) of the zooplankton population (Figure 3 in **Paper III**). With similar densities of prey, shallow and deep topographies may differ by several orders of magnitude with regards to foraging opportunities (prey detection potential) for planktivores (**Paper II**). The prey encounter potential may also be significantly greater over shallow topographies even at lower zooplankton biomass m^{-2} compared to deeper areas (**Paper III**). Advection of water masses (Genin 2004) and vertical strategies of zooplankton will of course also structure feeding opportunities for

planktivores over these topographies (see Discussions **Papers II** and **III**). Nevertheless, topographic blockage of zooplankton may be an important mechanism attracting fish to shallow topographies in oceanic ecosystems.

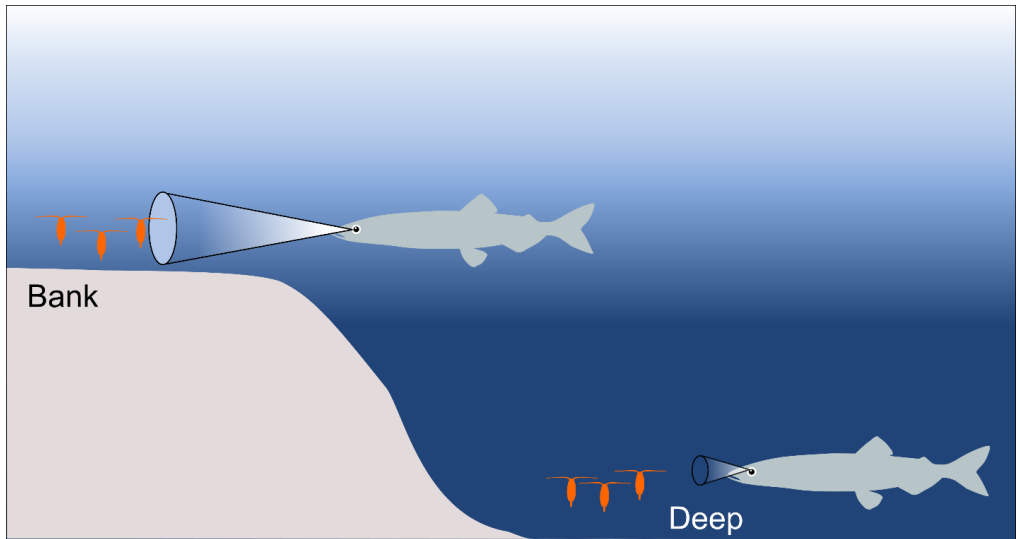


Figure 3: Illustration of topographic blockage of zooplankton and consequences for visual foraging in fish.

Does the bottom topography shape larger scale ecosystem structures?

Which role has the topography played in the evolutionary arms race between zooplankton and their visual foraging planktivore predators? Different life history strategies of *Calanus* species in the northern hemisphere is often explained as adaptations to different types of environmental conditions (e.g. Falk-Petersen et al. 2009). However, the patterns we observe may also have been shaped by predation (Berge et al. 2012). Bottom depth is important to consider in this regard, as it may be key for the survival of seasonally migrating zooplankton throughout the overwintering stage. Core overwintering areas of *C. finmarchicus* and *C. hyperboreus* allows descents down to 1000 m depth or deeper in the Norwegian and Greenland Sea (Østvedt 1955; Hirche 1991), well out of reach for both pelagic and mesopelagic fish (Kaartvedt 2000). *Calanus finmarchicus* also occupies shallower overwintering habitats in the North Atlantic, though mainly below 200 m depth where the bathymetry allows it (Heath et al. 2000). Variation in overwintering depth of *C. finmarchicus* may be related to different types of predators present in the environment (Kaartvedt 1996). It may also be affected by optical properties in the water column (Dupont and Aksnes 2012; Paper II), since high light attenuation provides reduced light exposure at shallower depths.

The combined effects of bathymetry and optical water properties on predator-prey interactions between zooplankton and planktivorous fish can potentially explain variation in both zooplankton size-structure and abundance (survival). *Calanus hyperboreus* is, for instance, presumably more constrained by the bathymetry in the Barents Sea than smaller *Calanus* species (**Paper II**), making it difficult to survive during multiple overwintering stages in this ecosystem. This is reflected in the low abundance of *C. hyperboreus* here, compared to other *Calanus* species with smaller body size and shorter life spans (Arashkevich et al. 2002; Hirche and Kosobokova 2003; Paper I).

The bathymetry constrains the overwintering distribution of *Calanus* species over shelves in the North Atlantic (Krumhansl et al. 2018; Paper II), and possibly also in the North Sea (see Discussion **Paper II**). Fish feeding on seasonally migrating

zooplankton must adapt to seasonally fluctuating foraging opportunities, when key prey become absent from the illuminated parts of the water column during large parts of the year. Occupying areas where seasonal migrators become constrained by the bathymetry in their vertical descents (**Paper II**) may be successful adaptations to the predator-avoidance strategies carried out by their prey. Indeed, small pelagic fish are often associated with continental shelves or shelf seas, such as capelin in the North Atlantic (Carscadden 2002).

Future perspectives

Evaluating how life is structured through predation is important to enhance our knowledge of pelagic ecosystems (Verity and Smetacek 1996). Results in my dissertation have demonstrated that the bottom topography likely plays a key role in the predator-prey dynamics between zooplankton and fish in the pelagic zone. Consumption of zooplankton by pelagic fish channels a large part of the energy flow from primary production to both commercially and non-commercially important species in marine ecosystems (Pikitch et al. 2014; Robinson et al. 2014). Including bottom depth as a variable in analyses of trophic control between fish and zooplankton populations may reveal regional differences in predator-prey dynamics between the two, and further our understanding of ecosystem function and productivity. In general, one may expect a tighter coupling between fish and zooplankton in areas with shallow bathymetry, where fish are able to utilize a larger part of the zooplankton population due to topographic constraints on vertical zooplankton distributions (**Paper III**).

Advection of zooplankton is important for sustaining profitable foraging habitats for fish over shallow topographies (Genin 2004). Without advection, it is likely that zooplankton over shallow topographies will be quickly depleted due to lack of refuge from visual predation (**Paper II**). Variation in advective transport of zooplankton over these topographies may cause variation in food availability and

growth rates of fish. The vertical distribution of zooplankton affects their advection rates within different water masses, creating additional variation in zooplankton transport (Basedow et al. 2018). Studies combining particle tracking and hydrodynamics (e.g. Harms et al. 2000) with vertical zooplankton strategies might be useful to further identify important foraging habitats and variations in food supply for planktivorous fish.

Krill is an important prey item for planktivorous fish that has not been considered in my dissertation. I do, however, expect that the bathymetry is important also for predator-prey interactions between planktivorous fish and krill (see Discussion **Paper III**). Use of other sampling techniques such as broadband acoustics are promising tools for obtaining finer scale measurements of vertical krill distributions and interactions with pelagic fish (e.g. Skaret et al., *submitted*), and may be important to further our understanding of pelagic ecosystem dynamics.

Using a mechanistic foraging model in combination with vertical zooplankton observations, we have demonstrated how the prey availability for fish is structured by the vertical zooplankton distribution and interactions with the bathymetry. Due to visual constraints on fish foraging, two areas with similar zooplankton biomass m^{-2} may represent significantly different foraging opportunities. Zooplankton biomass m^{-2} is therefore a poor measure of food availability for fish. Our results (**Papers II and III**) have shown that topography may be a useful proxy for assessing food availability for planktivores when vertical zooplankton data is lacking.

Arctic ecosystems are warming faster than the global average (Hoegh-Guldberg and Bruno 2010), and predictions for the Barents Sea give cause for concern (e.g. Onarheim et al. 2018; Lind et al. 2018). Continued warming may become serious for zooplankton like *C. glacialis* which for various reasons may be dependent on sea ice for their persistence in Arctic systems. Changes in zooplankton size-structures may be difficult to detect with the existing zooplankton data from the Barents Sea, as these contain only limited information (3 size fractions) on individual size. Novel observation methods such as plankton-imaging-systems (Benfield et al. 2007) are

promising tools for future monitoring of zooplankton-size structure in this ecosystem. Changes in the zooplankton size-structure may propagate to higher trophic levels and should be given high priority in future research and monitoring of the Barents Sea and other Arctic ecosystem.

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I



Contribution of *Calanus* species to the mesozooplankton biomass in the Barents Sea

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Copepods from the genus *Calanus* are crucial prey for fish, seabirds and mammals in the Nordic and Barents Sea ecosystems. The objective of this study is to determine the contribution of *Calanus* species to the mesozooplankton biomass in the Barents Sea. We analyse an extensive dataset of *Calanus finmarchicus*, *Calanus glacialis*, and *Calanus hyperboreus*, collected at various research surveys over a 30-year period. Our results show that the *Calanus* species are a main driver of variation in the mesozooplankton biomass in the Barents Sea, and constitutes around 80% of the total. The proportion of *Calanus* decreases at low zooplankton biomass, possibly due to a combination of advective processes (low *C. finmarchicus* in winter) and size selective foraging. Though the *Calanus* species co-occur in most regions, *C. glacialis* dominates in the Arctic water masses, while *C. finmarchicus* dominates in Atlantic waters. The larger *C. hyperboreus* has considerably lower biomass in the Barents Sea than the other *Calanus* species. Stages CIV and CV have the largest contribution to *Calanus* species biomass, whereas stages CI–CIII have an overall low impact on the biomass. In the western area of the Barents Sea, we observe indications of an ongoing borealization of the zooplankton community, with a decreasing proportion of the Arctic *C. glacialis* over the past 20 years. Atlantic *C. finmarchicus* have increased during the same period.

Keywords: *C. finmarchicus*, *C. glacialis*, Fugløya-Bear Island transect, key drivers, mesozooplankton, temperature effects.

Introduction

Herbivorous zooplankton plays an important role in the marine pelagic food web converting energy from primary production to food for higher trophic levels in the ecosystem. Copepods of the genus *Calanus* are predominantly herbivores and the most important zooplankton in the Nordic and Barents Sea ecosystems, largely due to their high abundances and lipid contents (Jaschnov, 1970; Tande, 1991; Melle and Skjoldal, 1998; Søreide *et al.*, 2008; Falk-Petersen *et al.*, 2009). Being a high latitude ecosystem, the Barents Sea is characterized by strong seasonality in light and sea-ice conditions, with large impact on the marine biota. Three *Calanus* species are common here; *Calanus finmarchicus* is an Atlantic boreal species, while *Calanus glacialis* and *Calanus hyperboreus* are of Arctic origin (Conover, 1988; Tande, 1991; Melle and

Skjoldal, 1998). Calanoid copepods are particularly well adapted to fluctuating environmental conditions due to reduced metabolic activity (diapause-like state) in winter when food is low, and capabilities of building large lipid reserves during the growing season. The individual lipid content in these species may be as large as 50–70% of the body weight (Lee, 1975; Scott *et al.*, 2000), which make them valuable food sources for higher trophic levels in the system. Indeed, the calanoid copepods constitute a key part of the diet for many ecologically and economically important fish species in the Barents Sea (Wassmann *et al.* 2006; Orlova *et al.*, 2011; Dalpadado and Mowbray, 2013).

Calanus finmarchicus overwinters in deep waters (>500 m) of the Norwegian Sea, and is advected into the Barents Sea with the Atlantic current when it ascends to surface layers in spring

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(Skjoldal *et al.*, 1992; Torgersen and Huse, 2005). Advection from the Norwegian Sea is vital for sustaining the population in the Barents Sea (Torgersen and Huse, 2005; Skaret *et al.*, 2014), though local reproduction within the Barents Sea is also important (Kvile *et al.*, 2017). This species generally has a predominantly 1-year life cycle in these waters, with the new generation produced at the onset of the phytoplankton spring bloom (Tande *et al.*, 1985; Melle and Skjoldal, 1998). *Calanus glacialis* is a shelf species largely associated with Arctic water masses in the Barents Sea, and can have both 1- and 2-year life-cycles (Conover 1988; Tande, 1991; Melle and Skjoldal, 1998). The larger congener *C. hyperboreus* has in general low abundances in the Barents Sea (Hirche and Mumm, 1992; Melle and Skjoldal, 1998; Arashkevich *et al.*, 2002), with its centre of origin in the deep basins of the Greenland Sea and Baffin Bay where it can have up to a 4-year life cycle (Conover, 1988; Hirche, 1997).

Since around 1980, the Barents Sea has experienced a warming trend which has been particularly pronounced during the last two decades (Boitsov *et al.*, 2012; Smedsrud *et al.*, 2013). Warming has led to a northward shift in the spatial distribution of fish communities (Fosheim *et al.*, 2015) and to a marked increase in the amount of krill and cumulative biomass of pelagic species (Eriksen *et al.*, 2016, 2017b). Continued warming has increased the dominance of Atlantic species and negatively impacted the Arctic communities (Hirche and Kosobokova, 2007; Kjellerup *et al.*, 2012; Dalpadado *et al.*, 2014; Fosheim *et al.*, 2015; Frairer *et al.*, 2017). Short-lived species like plankton are expected to show rapid responses to a changing climate (Hays *et al.*, 2005), and changes at the base of the marine food chain may propagate through the system with consequences at an ecosystem scale (Beaugrand *et al.*, 2003; Helaoût and Beaugrand, 2007). Revealing ongoing changes in marine plankton (e.g. Beaugrand *et al.*, 2002) is therefore vital for predicting the future of marine ecosystems in a warmer climate.

The Barents Sea zooplankton community has been studied extensively (e.g. Hassel, 1986; Tande, 1991; Unstad and Tande, 1991; Melle and Skjoldal, 1998; Arashkevich *et al.*, 2002). Many studies point to the importance of the *Calanus* species due to their size, abundance and lipid contents, though few have quantified their contribution to the total mesozooplankton biomass. Furthermore, most studies have analysed samples from a restricted time-period of one or a few years with low seasonal resolution. We explored an extensive dataset of species abundance for *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*, originating from various research and monitoring surveys in the Barents Sea, conducted by the Institute of Marine Research (IMR), Norway, over a 30-year period. IMR has used a standard method of splitting each zooplankton sample in two halves: one for determination of dry weight (dw) biomass, and the other preserved for species counts (Melle *et al.*, 2004). Our aim was to quantify the relationship between sampled mesozooplankton biomass and estimated biomass of *Calanus* species in the Barents Sea using the pair-wise samples. We further investigated the spatial patterns of the three species in relation to water masses and bottom topography, and evaluated whether there has been a change in the copepod community concurrent with the recent warming in the area. A transition towards dominance of smaller-sized, Atlantic copepods could affect the lipid structure and energy flow in the ecosystem with consequences for many trophic levels in the food web.

Material and methods

Zooplankton sampling and analyses

The standard procedure for zooplankton sampling at the IMR, Norway, is described in detail in Melle *et al.* (2004) and Skjoldal *et al.* (2013). Briefly, samples are divided in two halves with a Motoda plankton splitter, one part for determining the biomass (g dw per m² or m³), and the other half for species identification and abundance estimation. The biomass subsample is separated into three size fractions using mesh gauzes of 2000, 1000, and 180 µm (for details, see Skjoldal *et al.*, 2013). The second subsample is preserved with buffered 4% formalin solution and stored for later processing. The three *Calanus* species are identified based on size limits (Supplementary Table S1) and morphological characteristics including shape of the curvature of the coxopodite of the fifth leg (P5) (Knutsen and Dalpadado, 2009), and counted separately for each copepodite stage (CI–CV and CVI females and males). Consistent size-limits have been used throughout the period of the samples used in our study (see Hassel, 1986; Melle and Skjoldal, 1998). The size frequency data typically follow normal distributions for each of the species, with some (and variable) overlap between them, particularly for *C. finmarchicus* and *C. glacialis* (Hassel, 1986; Unstad and Tande, 1991; Melle and Skjoldal, 1998; Parent *et al.*, 2011; Gabrielsen *et al.*, 2012). Use of fixed size limits to separate the species is therefore an approximation, and the potential for misidentifications is present, particularly in areas where the species co-occur. Individuals of intermediate size are therefore routinely examined for curvature of the coxopodite to reduce the degree of misidentification from the use of fixed size limits.

Data description

Sample processing for species identification is labour-intensive, and only a fraction of the samples collected by the IMR are processed (all samples are stored in a long-term repository). Over the years, there has still been an accumulation of processed samples originating from various researches and monitoring surveys. We extracted all samples in the IMR database with data on both mesozooplankton biomass and species abundance from the same sampling stations in the Barents Sea (Tables 1 and 2). When multiple samples had been taken at a station, only one (WP2 gear, bottom to surface haul) was included in this study. In total, we analysed 616 samples covering an extensive geographical area (Figure 1). Samples were grouped into five oceanographic regions based on bathymetry and advection (Table 2), and aggregated into the following seasons: winter (November–March), spring (April–May), summer (June–July), and autumn (August–October). The Fugløya-Bear Island transect (FB transect, grey line in Figure 1) is a standard oceanographic transect in the western region, hereafter called “West”, covered by IMR five to eight times each year. Samples from this transect are regularly processed for species identification, and have consistent seasonal coverage since 1995. Region West therefore contributed a large part (~70%) to the data analysed in this study. Samples from the 1980s (the Pro Mare programme; Sakshaug *et al.*, 2009) were mainly from the spring and summer period.

Most of the samples were from near-bottom to surface hauls, though ~10% had shallower sampling depths (Table 1). Samples with a unit of abundance or biomass m⁻³ were converted to m⁻² by integrating over the water column down to the lowest

Table 1. Gear characteristics of the sampling equipment in the dataset.

Sampling gear	Net opening (cm)	Mesh size (μm)	Lower sampling depth (m)	Sample unit	Samples (n)
WP2	56	180	100, bottom	m^{-2}	569
Juday	80	250, 375	40, 50	m^{-2}	14
Hufsa	–	180, 375	30, 40, 50, 100	m^{-3}	28
MOCNESS	100	180, 333	bottom	m^{-3}	5

For detailed gear descriptions, see Sameoto *et al.* (2000), Wiebe and Benfield (2003), and Skjoldal *et al.* (2013). Upper sampling depth for all gears is surface (0 m).

Table 2. Overview of regions as defined in this study, and number of samples analysed per region.

Region	Latitude ($^{\circ}\text{N}$)	Longitude ($^{\circ}\text{E}$)	Bottom depth (m) ^a	Dominating water mass ^b	Main sampling period ^c	Samples (n) per season	
West	70–75	15.5–21	266	Atlantic	1994–2016	Summer	65
						Autumn	170
						Winter	177
						Spring	89
South	70–73.5	21–40	317	Atlantic	1983–2016	Summer	9
						Autumn	7
						Winter	0
						Spring	3
Central	74–78	21–38	221	Arctic/mixed	1983–2009	Summer	33
						Autumn	15
						Winter	2
						Spring	6
North	78–82	25–36	211	Arctic/mixed	2005–2016	Summer	1
						Autumn	22
						Winter	0
						Spring	0
East	71–80	41–61	234	Arctic/mixed	1983–1994	Summer	5
						Autumn	11
						Winter	1
						Spring	0

Samples were aggregated into the seasons winter (November–March), spring (April–May), summer (June–July), and autumn (August–October).

^aMean of sampling stations.

^bDominating water mass in samples analysed: Atlantic ($T > 3^{\circ}\text{C}$), Arctic ($T < 0^{\circ}\text{C}$), mixed ($0^{\circ}\text{C} < T < 3^{\circ}\text{C}$) based on temperature at 50-m depth.

^c>90 % of samples taken during this period.

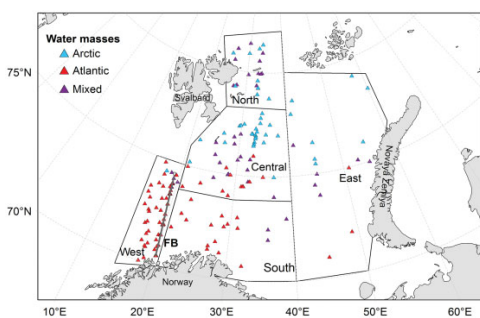


Figure 1. Geographical distribution of samples analysed in this study ($n = 616$). The Barents Sea was divided into five oceanographic regions as defined in Table 2. Outer bounds of the polygons are included as a visual aid. Samples were defined as Arctic ($T < 0^{\circ}\text{C}$), Atlantic ($T > 3^{\circ}\text{C}$), or mixed ($0^{\circ}\text{C} < T < 3^{\circ}\text{C}$) based on temperature data from 50 m depth. The FB transect, where a large part of the data originates from, is marked with a line.

sampling depth. Differences in sampling gear and depth were accounted for in the statistical analyses.

Biomass estimation of *Calanus* species

Copepodite abundances of *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* were converted to biomass estimates using individual weight-at-stage data from the literature (Table 3). The individual weight can vary considerably, by up to an order of magnitude within a copepodite stage (Figure 2). Part of this variation is due to weight increase as individuals grow through a stage between successive moults. There is also systematic variation in relation to thermal habitat, where individuals tend to become larger when they grow at low compared with higher temperature (Campbell *et al.*, 2001; Melle *et al.*, 2014). Mean weights from studies in or near the Barents Sea were considered representative of those for our study region (Table 3). We also performed length measurements on individuals of *C. finmarchicus* and *C. glacialis* stages CIV, CV and adult females, to evaluate the propriety of the weight-data employed for estimating species biomass. Based on these measurements we were confident that the weight-data (Table 3) were reasonable (results are available in the Supplementary Material).

Table 3. Dry weight (μg) per copepodite stage (CI–CVI female and male) for *Calanus* spp. used to estimate biomass in this study.

Species	CI	CII	CIII	CIV	CV	CVIf	CVIm	References
<i>C. finmarchicus</i>	1.5	4	13	70	250	235	235	Tande (1982), Tande and Slagstad (1992)
<i>C. glacialis</i>	8	16	40	185	600	810	600	Hanssen (1997), Hirche and Kosobokova (2003)
<i>C. hyperboreus</i>	10	40	140	500	2000	3500	3500	Hirche (1997)

See also Figure 2 for an overview of dry weight measurements of *C. finmarchicus* and *C. glacialis* from the literature.

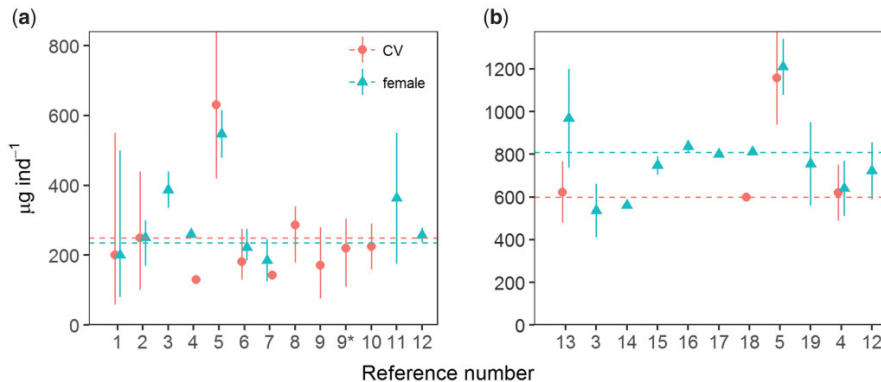


Figure 2. Mean weight ($\mu\text{g ind}^{-1}$, points in figure) for copepodite stage CV and adult females of (a) *C. finmarchicus*, and (b) *C. glacialis*, as reported by the scientific literature (x-axis). (i) Carloti *et al.* (1993), (ii) Tande (1982), (iii) Ikeda and Skjoldal (1989), (iv) Scott *et al.* (2000), (v) Diel (1991), (vi) Hirche *et al.* (2001), (vii) Gislason (2005), (viii) Båmstedt and Ervik (1984), (ix) Jónasdóttir (1999) (*deep water), (x) Heath and Jónasdóttir (1999), (xi) Runge *et al.* (2006), (xii) Kjellerup *et al.* (2012), (xiii) Båmstedt and Tande (1985), (xiv) Hirche (1987), (xv) Hirche and Kattner (1993), (xvi) Hirche *et al.* (1994), (xvii) Hirche and Kwasniewski (1997), (xviii) Hirche and Kosobokova (2003), (xix) Tourangeau and Runge (1991). Vertical lines show the range of weights, or mean \pm SD, when this information has been available. Horizontal lines show the values employed in this study when estimating species biomass for stage CV (dotted) and females (dashed).

Physical environment

Temperature and salinity profiles from CTD casts from the respective sampling stations were available for most of the dataset. Samples were classified as Atlantic ($T > 3^{\circ}\text{C}$), Arctic ($T < 0^{\circ}\text{C}$), or mixed ($0^{\circ}\text{C} < T < 3^{\circ}\text{C}$) based on temperature at 50 m, where the core of Arctic water is usually found (Lind and Ingvaldsen, 2012; Lind *et al.*, 2016). Temperature and salinity at 50 m were used as continuous variables in the statistical analyses explaining variance in *Calanus* sp. biomass (see ii below), and sampling depth as a proxy for bottom depth since some samples were not taken from bottom to surface.

Data analyses

Statistical analyses were performed to:

- (i) Estimate the relationship between *Calanus* biomass (sum of the three species) and the mesozooplankton biomass in the pair-wise samples.
- (ii) Evaluate interspecific differences in biomass between the three *Calanus* species with regard to key environmental drivers.
- (iii) Analyse inter-annual changes in the *Calanus* species group regarding species biomass and % contribution to total biomass.

For (i) and (ii), we employed the complete dataset with 616 samples (613 samples in (ii) due to missing temperature data from three stations). For (iii), we used summer and autumn data from region West (mainly FB transect) where we had annual observations since 1995. Analyses were performed on log-transformed estimated dw biomass plus a constant (0.01) to enable log-transformation of samples with species absence (zero biomass).

Total *Calanus* vs. mesozooplankton biomass

We used Major Axis regression (MA) to estimate the relationship between the observed (log-transformed) mesozooplankton biomass and the estimated total biomass of *Calanus* spp. This regression technique is suitable for describing the functional relationship between two variables of the same units of measurement when both are subject to observation error (Helsel and Hirsch, 1992; Sokal and Rohlf, 2012). We also performed an ordinary least squares (OLS) regression for comparison with the MA, to evaluate how results would change by the choice of regression model.

Calanus biomass at species level

OLS regressions with species biomass as response variable was used to evaluate interspecific differences between the *Calanus* species with regard to environmental factors (temperature, salinity and sampling depth as continuous variables, season as

categorical). Data on *C. glacialis* and *C. hyperboreus* had considerable zero-inflations as a large portion of the data came from the Atlantic sector of the Barents Sea, so analyses for these species were performed on all samples as well as only presence-data. We also ran separate analyses with presence/absence as a response, using Generalized Linear Models with a binomial distribution.

Model selection (i.e. deciding on the optimal models describing estimated biomass at species level) was based on the Akaike information criterion (AIC; Akaike, 1974) which considers the trade-off between model fit and model complexity, and backwards selection (stepwise removal of the least significant term).

All analyses were run both on the complete dataset and on data only including samples taken from bottom to surface. To account for differences in sampling gear characteristics like mesh size and net opening, equipment was included as a fixed covariate in the analyses. Due to an overweight of samples from the WP2 sampling gear, this dataset was not suitable for concluding on differences in sampling gear performance.

Temporal changes in region West

Changes in biomass at species level and changes in the proportion of *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* in the total mesozooplankton biomass over the period (1995–2016) were analysed with generalized additive models (GAMs) to catch potential non-linear trends in temporal variation. We used a spline based smoother with four degrees of freedom. In analyses of proportions, estimates >1 were set to 1, and analyses were run on arcsine transformed values.

All analyses were done in the statistical software package R (R Core Team, 2016), using the mgcv library for GAMs (Wood, 2017).

Results

Correlation between *Calanus* spp. and total mesozooplankton biomass

There was a strong correlation between the observed mesozooplankton biomass and the estimated biomass of *Calanus* species in the samples ($r^2 = 0.79$, $p = 0.005$) (Figure 3). Results were similar both with the complete dataset and when excluding samples that did not cover the entire water column. The observed biomass spanned a range of about three orders of magnitude, from 0.01 to 48 g dw m^{-2} , with a similar range also for the estimated biomass of *Calanus* species (0.003–50 g dw m^{-2}). On average, the *Calanus* species comprised 78% of the mesozooplankton biomass, though this varied between the different regions (see below).

The scatter around the regression line in Figure 3 was approximately one order of magnitude (corresponding to one unit on the log scale). The estimated dw of the three *Calanus* spp. surpassed the observed mesozooplankton dw sampled at the station (i.e. observations above the 1:1 dotted line in Figure 3) in 19% of the cases. Overestimations occurred in all seasons, both at high and low biomass levels.

The MA regression slope was steeper than unity (1.24 on the log-log scale), which means that the % contribution of *Calanus* species to the observed biomass increased with increasing biomass values. In fact, the regression line crossed the 1:1 line at a log value about 1.5 (32 g dw m^{-2}). The OLS regression had a lower slope (1.1) and did not cross the 1:1 line. OLS in bivariate regressions tends to underestimate the slope of the regression line when both variables are subject to observation error not

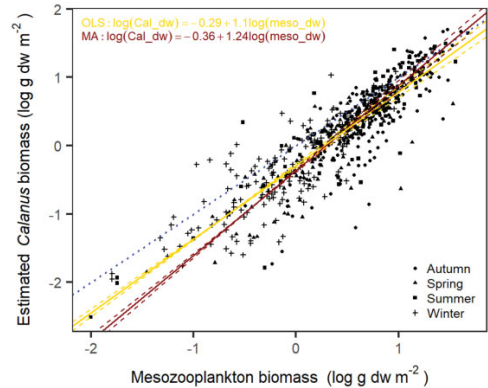


Figure 3. Observed mesozooplankton biomass and estimated total biomass of three *Calanus* species in the samples. Samples are shown with symbols by season; winter (November–March), spring (April–May), summer (June–July), and autumn (August–October). The dotted line shows a 1:1 relationship between mesozooplankton and *Calanus* spp. biomass. Regression results (MA and OLS) are plotted with 95% confidence bands, $r^2 = 0.79$ and $p = 0.005$ for both regressions.

controlled by the researcher (Sokal and Rohlf, 2012), which may be reflected in our data as well (Figure 3). We therefore conclude that predictions from the MA regression more accurately described the relationship between *Calanus* spp. and mesozooplankton biomass in the Barents Sea.

Hydrographic and spatial differences between *Calanus* spp.

There was considerable variation in the estimated % contribution of each species to mesozooplankton biomass in the water masses defined as Arctic, Atlantic and mixed (large interquartile ranges, Figure 4). However, the water masses were distinctively different regarding which of the three *Calanus* species that contributed to the mesozooplankton biomass. In Atlantic water, *C. finmarchicus* constituted a large part of the mesozooplankton biomass whereas *C. glacialis* had a low contribution to the total. In Arctic water *C. glacialis* prevailed, with low contribution by *C. finmarchicus*. Both *C. finmarchicus* and *C. glacialis* contributed to the total in mixed water masses. *Calanus hyperboreus* was generally a small part of the mesozooplankton biomass in all water masses, though relatively more abundant in the Arctic than the other two.

A summary of biomass estimates and estimated proportions of the three *Calanus* species in the five regions shown in Figure 1 is available in the Supplementary Material (Supplementary Table S2). The total contribution by the three *Calanus* species to the mesozooplankton biomass differed across the regions, from $\sim 50\%$ in the East to $>90\%$ in the South. On species level, the % contribution in each area reflected differences between the water masses as illustrated in Figure 4. The West and South regions where Atlantic water prevails was dominated by *C. finmarchicus*, while *C. glacialis* was a larger fraction of the total in the North and East regions where Arctic water is present (Figure 5). Both species had a similar contribution to the biomass in the Central

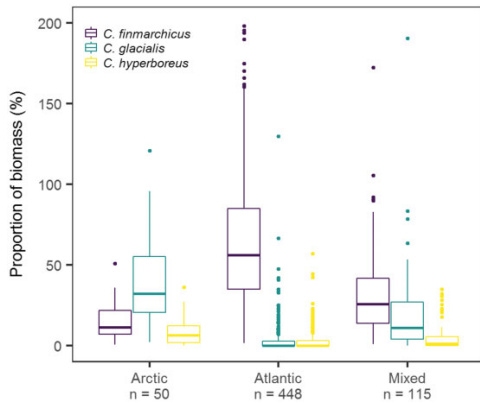


Figure 4. Estimated proportions of total mesozooplankton biomass for *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* in different water masses defined as Atlantic ($T > 3^{\circ}\text{C}$), Arctic ($T < 0^{\circ}\text{C}$), and mixed ($0^{\circ}\text{C} < T < 3^{\circ}\text{C}$). Number of samples (n) from each water mass is indicated in the x-axis labels. The graph presented excludes 12 observations with estimated proportions $>200\%$. The boxes are divided by the median value, and framed by the upper and lower quartile. The whiskers extend to the first outlier in each direction; other outliers are shown by separate points. Outliers are defined as data points >1.5 times the upper quartile.

region which contains the oceanographic polar front with cooled Atlantic and mixed water masses. Species other than *Calanus* appeared to have a larger contribution to the mesozooplankton biomass in the North, Central and East regions than in the West and South (Figure 5). The “other” category is usually dominated by species like *Metridia* spp., *Pseudocalanus* spp., *Microcalanus* spp., *Oithona* spp., *Oncaea* spp., and *Clione limacina* (IMR database).

The total variation in estimated biomass within the pooled datasets was large, with coefficient of variation (CV) typically greater than one (Supplementary Table S2). CV values tended to be higher at low estimated biomass values and were generally higher for *Calanus* biomass estimates than for the total mesozooplankton biomass. High CV values suggest a skewed distribution (relative to normal) which is reflected in median values being lower than arithmetic means (by 5–40% for total mesozooplankton biomass, and 20–60% for estimated biomass of *C. finmarchicus* and *C. glacialis*).

Environmental drivers of *Calanus* biomass

Selected linear regressions based on the AIC and backwards selection, showed that the best model for describing the estimated biomass at species level included season, sampling depth, equipment and temperature (50 m) for all three species ($r^2 = 0.38$ for *C. finmarchicus*, 0.51 for *C. glacialis* and 0.31 for *C. hyperboreus*). Model coefficients with standard errors are available in the Supplementary Table S3. Among the predictors, temperature revealed clear differences between the species (Figure 6a). *Calanus finmarchicus* had a positive relationship with temperature ($p < 0.001$), while it was negative for *C. glacialis* ($p < 0.001$). Also *C. hyperboreus* had a negative relationship with temperature ($p < 0.001$), though weaker than for

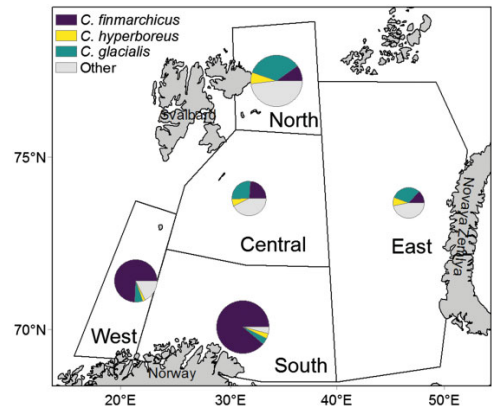


Figure 5. Estimated proportion of *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* biomass to total mesozooplankton biomass in different regions of the Barents Sea, based on arithmetic means (g dw m^{-2}) per region. The size of the cakes is proportional to the total mesozooplankton biomass. “Other” represents the total minus the estimated mean biomass of the *Calanus* species. Winter samples from region West are not included in the figure.

C. glacialis. Sampling depth was positively related to estimated biomass for all three species (Figure 6b), giving higher *Calanus* spp. biomass in deep vs. shallow water. The model for *C. finmarchicus* predicted a higher mean biomass in summer compared with autumn, and lower for winter and spring. For *C. glacialis* and *C. hyperboreus*, the models predicted lower mean biomass in winter, spring and summer compared with autumn. Salinity had no significant effect for neither species. These trends were consistent across all datasets (complete, bottom to surface and presence-only data for *C. glacialis* and *C. hyperboreus*). Further, binomial models on presence/absence for *C. glacialis* and *C. hyperboreus* confirmed the negative relationship of these species with temperature.

Temporal changes in region West

The total mesozooplankton biomass in June and August in region West showed an increasing trend in recent years (Figure 7a). This coincided with an increase in the medium (1000–2000 μm) and small (180–1000 μm) mesozooplankton size fractions, while the large ($>2000 \mu\text{m}$) size fraction has decreased since around 2002. GAM analyses on the estimated proportion of the three *Calanus* species in the corresponding samples revealed a linear decrease in the % contribution to total biomass of *C. glacialis* over the period (Figure 7b, $p = 0.04$). Meanwhile, the proportion of *C. finmarchicus* has increased since the early 2000s ($p = 0.003$). *C. hyperboreus* constituted a very small part of the mesozooplankton biomass in region West. Its contribution to the total was generally below 5% except between the years 2002 and 2004 when it had a “peak” contribution (Figure 7b, $p = 0.002$). Model outputs are available in the Supplementary Figure S1.

GAM analyses on estimated species biomass over the same period showed increasing biomass of *C. finmarchicus* since around 2005 ($p = 0.05$) (see Figure 8b). At the same time, the biomass of *C. glacialis* decreased (apart from the most

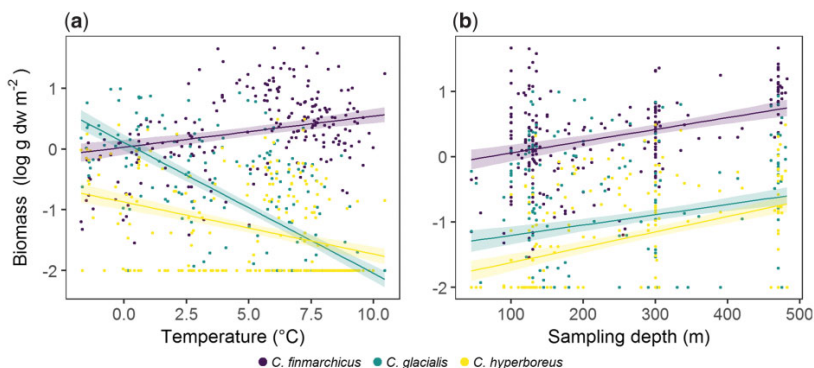


Figure 6. Estimated biomass of the three *Calanus* species against (a) temperature and (b) sampling depth, with data from equipment WP2 and season autumn. Predictions (straight lines with 95 % confidence bands) are from the linear models $\log(\text{Calanus sp. dw}) \sim \text{temperature} + \text{season} + \text{depth} + \text{equipment}$ ($r^2 = 0.38$ for *C. finmarchicus*, 0.52 for *C. glacialis*, and 0.31 for *C. hyperboreus*), with mean levels of depth (a) and temperature (b).

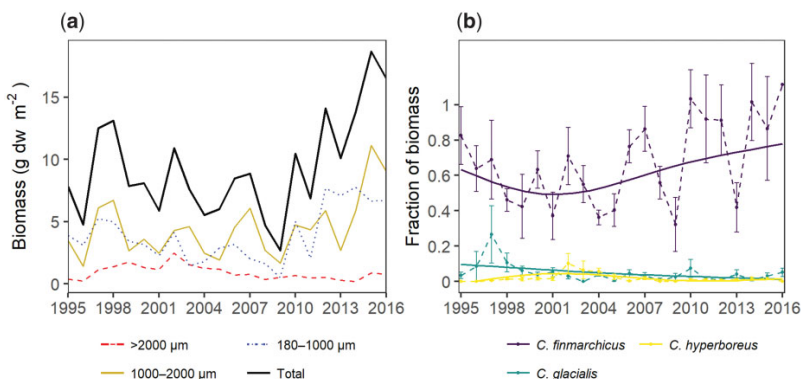


Figure 7. (a) Mean sampled June and August mesozooplankton biomass (g dw m^{-2}) in the Barents Sea, region West, from 1995 to 2016. Figure shows total biomass and biomass divided into three size fractions. (b) Mean estimated proportion (%) of *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* in the corresponding samples. Error bars show \pm the SEM proportion. One potential outlier with estimated proportion of *C. finmarchicus* >500 % was removed in the figure. The trend lines are results from GAM models with species proportions as response and year as explanatory variable; $p = 0.003, 0.04$, and 0.002 for *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, and deviance explained is 10, 4.2, and 12%, respectively.

recent years), though the trend was not significant at the 0.05 level ($p = 0.07$).

Stage specific contribution to biomass

Calanus finmarchicus was a consistently large part of the mesozooplankton biomass in region West, where Atlantic water dominates. Samples from this region revealed that copepodite stages CIV and CV dominated the total species biomass for *C. finmarchicus* (Figure 8). The new generation consisting of younger copepodites (CI–CIII) appeared in May. However, they comprised a very small part of the estimated total biomass in all months analysed. Stages CIV and CV of the new generation created a seasonal maximum biomass in

June–August. Samples from winter months (January, March) indicated that *C. finmarchicus* overwinters mainly as stage CV in this area.

Stages CIV and CV dominated the biomass also for *C. glacialis* in regions Central, North and East (Figure 9) where this species was a large fraction of the mesozooplankton biomass. Winter samples for *C. glacialis* indicated overwintering mainly as stage CIV and adults. The younger stages, particularly CIII, had a larger contribution to the total species biomass for *C. glacialis* during summer and autumn than with *C. finmarchicus*. The maximum mean monthly estimated biomass of *C. glacialis* of about 3.6 g dw m^{-2} was comparable to (but slightly lower than) the maximum biomass of *C. finmarchicus* apart from the higher values for the latter species after 2005 (Figure 8b).

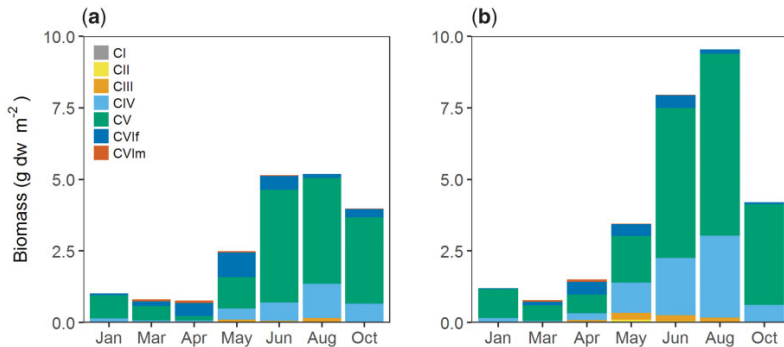


Figure 8. Mean biomass (g dw m^{-2}) per stage (CI to CV and CVI female and male) for *C. finmarchicus* in the western region of the Barents Sea between (a) 1995–2004 and (b) 2005–2016. The figure only displays months which have been consistently sampled over the period.

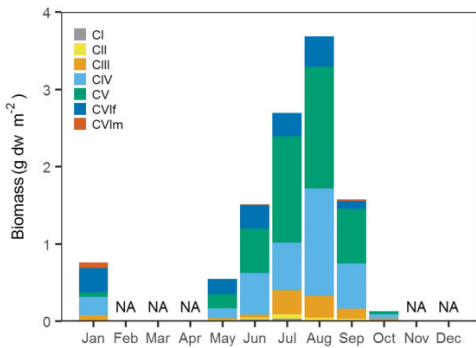


Figure 9. Mean biomass (g dw m^{-2}) per stage (CI to CV and CVI female and male) for *C. glacialis*, with data from the Central, North and East regions considered as most representative for this species. Months with no observations are indicated by NA.

Discussion

Estimated biomass of *Calanus* species

Calanus spp. are key species at high latitudes spanning from boreal to Arctic ecosystems (Jaschnov, 1970; Conover, 1988; Falk-Petersen et al., 2009). Yet, few studies have quantified the contribution of *Calanus* species to the total zooplankton biomass. Biomass of *Calanus* is typically estimated by combining stage-abundance data with mean individual body weights of the respective stages (e.g. Tande, 1991; Hirche and Kosobokova, 2003; Soreide et al., 2008). Using this method, we found a mean biomass of *C. finmarchicus* around 5 g dw m^{-2} in June and August (1995–2005) in the western region of the Barents Sea dominated by Atlantic water. After 2005, the biomass of *C. finmarchicus* has increased. Our estimates for the later years (2005–2016) are in the high end of the range of values reported from other areas. A detailed sampling at Station M in the Norwegian Sea gave a mean biomass of 1.7 g dw m^{-2} with a temporary maximum of 12.5 g dw m^{-2} (Hirche et al., 2001). Simulations with a coupled physical-biological model system (NORWECOM) gave a seasonal maximum biomass of *C. finmarchicus* of $4\text{--}5 \text{ g dw m}^{-2}$ in

the Norwegian Sea and the Atlantic part of the Barents Sea (Hjøllo et al., 2012; Skaret et al., 2014, see review of estimated biomass of the three *Calanus* species provided in the Supplementary Table S4). Our estimates for the colder waters of the central, eastern and northern Barents Sea were lower, and similar to values obtained in the same region by Hirche and Kosobokova (2003).

Estimated biomass of *C. glacialis* in the North, Central and East regions was slightly lower than the biomass of *C. finmarchicus* in the West, with a seasonal maximum around 3.6 g dw m^{-2} . This is comparable to studies of *C. glacialis* both from the Barents Sea and other areas (Tande, 1991; Madsen et al., 2001; Hirche and Kosobokova, 2003; Daase et al., 2013). Our biomass estimates for *C. hyperboreus* were $0.1\text{--}0.7 \text{ g dw m}^{-2}$ as means for the different areas. These are similar to values reported from the Barents Sea by Tande (1991) and Hirche and Kosobokova (2003). Higher values of up to $4\text{--}6 \text{ g dw m}^{-2}$ have been reported from the Greenland Sea (Hirche, 1991; Møller et al., 2006) and Disco Bay (Madsen et al., 2001).

Misidentification of *Calanus* species from the use of fixed size limits (see “Materials and methods” section) may have influenced the results. The most frequent cases of misidentifications are small individuals of *C. glacialis* wrongly identified as *C. finmarchicus* (Gabrielsen et al. 2012). A hybrid species is expected to have intermediate prosome lengths (Parent et al., 2012). Species distributions were in our study highly related to water masses; and in Atlantic water where *C. finmarchicus* dominated, the overall contribution by *C. glacialis* was low. Co-occurrence between *C. finmarchicus* and *C. glacialis* was more prominent in the mixed water masses, and here the potential for misidentification (and possible hybridization) may have been greater.

One could expect that increasing water temperatures in the Barents Sea would lead to decreasing size of *C. finmarchicus* copepodites (Campbell et al., 2001). Albeit a small sample size, the length measurements we performed as part of this study did in fact indicate that *C. finmarchicus* have become smaller between 1997 and 2010 (Supplementary Table S5). Smaller *C. finmarchicus* reduces the probability of overlapping in size with its congener *C. glacialis*. It is also reasonable to expect that warmer conditions would favour the dominance of *C. finmarchicus* (Kjellerup et al., 2012). We therefore believe that the general trends we observe in

this study would be consistent despite the possibilities of species misidentification (due to size overlap and possible hybridization) in our data.

Variation in weights of *Calanus* copepodites

Variation in size (weight) can be a considerable source of error and uncertainty in *Calanus* biomass estimates from species counts. Our *Calanus* biomass estimates surpassed the observed total biomass in one out of five samples. Responding to the overestimations, we repeated species counts on a selection of samples (formalin preserved) from years with large discrepancies between estimated dw of *C. finmarchicus* and observed mesozooplankton biomass. The new measurements did, however, not reveal any abundance estimation errors that could explain the biomass overestimations. We believe the overestimations reflect uncertainties in the weight-at-stage data employed when estimating species biomass, as well as variance introduced by subsampling when estimating species abundances (see e.g. Skjoldal *et al.*, 2013).

Most studies where *Calanus* spp. biomass is estimated have used mean weights of copepodite stages from the literature. It is difficult to quantify the uncertainty, but from the variation in mean weights of the older copepodite stages shown in Figure 2 it may be of order 20–30% for *C. finmarchicus* and *C. glacialis*, or even larger. In some studies (e.g. Hirche *et al.*, 1991) the weights of individuals have been determined as part of the study, thereby reducing this uncertainty. Size measurements performed on representative material to reveal changes in mean weights over space and time would greatly improve the precision of biomass estimates from zooplankton species abundance data. This may, however, induce a considerable increase in the effort spent on sample analysis. Using some form of plankton-imaging-system (Benfield *et al.*, 2007) may facilitate the approach to make it more practical in routine studies.

Calanus spp. as drivers of the mesozooplankton biomass in the Barents Sea

Calanus finmarchicus, *C. glacialis*, and *C. hyperboreus* are major players in the herbivore zooplankton community of the Barents Sea ecosystem. Our study has shown that *Calanus* species constitute a major part of the mesozooplankton biomass in all regions of the Barents Sea, and on average around 80% of the total. Large mesozooplankton biomass samples ($>16 \text{ g dw m}^{-2}$) were associated with correspondingly large estimated biomass of *Calanus* species, indicating that biomass “peaks” in the Barents Sea are mainly driven by *Calanus* spp. The combined biomass of these species explained a major part of the variation in the observed mesozooplankton biomass. Though the total biomass of *Calanus* spp. contributed in similar proportion to the mesozooplankton biomass across the regions, the highest contribution was observed in regions West and South where there is a high abundance of *C. finmarchicus*. The proportional contribution of *C. glacialis* to the zooplankton biomass in its core Arctic water area was lower than the contribution of *C. finmarchicus* in Atlantic water, and other species than *Calanus* seem to comprise a larger part of the mesozooplankton biomass here. The larger species *C. hyperboreus* had a rather low contribution to the mesozooplankton biomass ($<10\%$ in all regions), similar to earlier observations (Melle and Skjoldal, 1998; Arashkevich *et al.*, 2002; Hirche and Kosobokova, 2003). *Calanus hyperboreus* generally overwinters below 500–1000 m in its core areas (Hirche, 1997), and has probably difficulties in

completing a generation cycle in the (relatively shallow) Barents Sea due to its large size and longer life-span making it more vulnerable to predation (e.g. Falk-Petersen *et al.*, 2009; Berge *et al.*, 2012).

Our data showed that the contribution of *Calanus* to the mesozooplankton biomass is lower when the total zooplankton biomass is low (see regression in Figure 3). Considering that a major part of our data was from Atlantic water areas, we believe part of this result can be explained by a seasonal/advective effect of *C. finmarchicus*. During winter when the mesozooplankton biomass is low, there will be lower concentrations of *C. finmarchicus* in the inflowing Atlantic water when it has descended (over-winter in deep Norwegian Sea basins) from the surface layers of the advective Atlantic current (Skjoldal *et al.*, 1992). Hence, there will be a lower contribution of *Calanus* spp. to the total in winter vs. summer periods. A biological explanation is selective foraging by predators. The little auk *Alle alle* actively selects larger stages of *C. glacialis* when feeding in the Arctic, and avoids the smaller *C. finmarchicus* (Karnovsky *et al.*, 2003). Baltic herring has shown size-selective preferences when feeding on copepods (Sandström, 1980), and planktivore fish in the Barents Sea can exert a significant top-down control on their zooplankton prey (Hassel *et al.*, 1991; Stige *et al.*, 2014).

Calanus spp. biomass and hydrography

Both this and previous studies (Tande, 1991; Melle and Skjoldal, 1998; Hirche and Kosobokova, 2003) have demonstrated that the contribution of *C. finmarchicus* and *C. glacialis* to the zooplankton biomass in the Barents Sea is highly related to which water mass dominates. Weydmann *et al.* (2014) described temperature and bottom depth as the main drivers for zooplankton variability in the West Spitsbergen Current. Daase *et al.* (2007) demonstrated similar temperature-relationships as our study for the *Calanus* species in waters off Svalbard, and related the findings to advective processes. The steep, negative biomass-temperature relationship of *C. glacialis* in our study reflected large difference in biomass of *C. glacialis* in Arctic vs. Atlantic water masses.

The area of Arctic water in the Barents Sea has been declining over the last few decades (ICES, 2017). This could possibly be associated with a reduction in the habitat (extent and conditions) of *C. glacialis* in the northern Barents Sea. It has been suggested that *C. glacialis* will decrease in Arctic areas of the Barents Sea if continuous warming leads to a greater mismatch between phytoplankton production and *C. glacialis* development due to earlier break-up of the winter ice (Hirche and Kosobokova, 2007; Søreide *et al.*, 2010). The decrease of this species at the southwestern entrance (region West) could reflect a general decline in the core area further north. However, our data from the northern Barents Sea are limited ($n=23$; Tables 2) and too heterogenous in time to allow us to examine if this has been the case. This is an important issue from an ecosystem perspective which we plan to address in a future study, using archived samples dating back to the 1980s.

Calanus finmarchicus is an expatriate in Arctic water masses, and its reproductive cycle is limited by the low temperature environment (Melle and Skjoldal, 1998; Hirche and Kosobokova, 2007; Ji *et al.*, 2012). Previous studies have also established a positive relationship between *C. finmarchicus* biomass and temperature (Dalpadado *et al.*, 2003; Daase *et al.*, 2007; Dvoretzky, 2011). High temperatures may indicate higher inflow of Atlantic water

and thus larger concentrations of advective organisms like *C. finmarchicus* (Dalpadado et al., 2003). Furthermore, *C. finmarchicus* has higher growth rates (Campbell et al., 2001) and augmented egg production (Kjellerup et al., 2012) at increasing temperatures. The optimum temperature for this species appears to be about 6–10°C based on abundance data over its geographical range (Helaouët and Beaugrand, 2007; Helaouët et al., 2011; Reygondeau and Beaugrand, 2011; Melle et al., 2014). The temperature of the inflowing Atlantic water at the FB transect has been increasing by about 1.5°C since around 1980 to an annual mean level of about 6–6.5°C after 2004 (Eriksen et al., 2017b). This may have improved the conditions and expanded the optimal habitat for *C. finmarchicus* in the southern Barents Sea.

The number of generations produced per year by boreal *Calanus* decreases with increasing latitude (Conover, 1988). Though previous studies have suggested that *C. finmarchicus* produces one generation per year in the Barents Sea (e.g. Tande et al., 1985; Melle and Skjoldal, 1998), there are indications for a second generation of *C. finmarchicus*, particularly related to warm periods (Timofeev, 2000; Skaret et al., 2014). A second generation of *C. finmarchicus* may have contributed to the marked increase in biomass of *C. finmarchicus* in region West during the most recent period analysed here (after 2005).

Coupled with the decrease in Arctic water masses in the Barents Sea is an increase of mixed water with intermediate temperatures of 0–3°C (Eriksen et al. 2017b). Related to the issue of whether *C. glacialis* has declined as a response to the ongoing warming is therefore also a question of how the *Calanus* species are coping with the conditions in the mixed water masses. Temperature-driven stage-duration coupled with food availability and the length of the growth season in these waters, will largely determine the ability of *C. finmarchicus* to reach diapausing stage over the season (e.g. Ji et al., 2012). *Calanus glacialis* should persist physiologically at these cool temperatures, as suggested by its dominance in the White Sea (Kosobokova, 1999), though it is an open question as to how changes in ice conditions and water masses will affect the species in the mixed waters. Model predictions by Slagstad et al. (2011) have suggested that the secondary production by *C. glacialis* and *C. finmarchicus* combined will decrease in a future warmer climate in the northern Barents Sea, due to a temperature regime that is too warm for *C. glacialis* and sub-optimal for *C. finmarchicus*.

Concluding remarks

Plankton are good indicators of climate change occurring in the oceans (Hays et al., 2005). We have shown that the recent warming in the Barents Sea is likely affecting the composition of the mesozooplankton community, increasing the abundance of Atlantic *C. finmarchicus* in the west. With increased inflow of Atlantic water into the system, we would not expect these changes to be restricted only to the western area, as both fish species and macrozooplankton have shown responses to the warming in extended areas of the Barents Sea (Fosheim et al., 2015; Eriksen et al., 2017b; Frainger et al. 2017). A transition in the mesozooplankton community in certain areas from dominance of *C. glacialis* towards the smaller *C. finmarchicus* could be detrimental for higher trophic levels, particularly the size-selective particulate feeders (e.g. Karnovsky et al., 2003; Hirche and Kosobokova, 2007). Consistent time-series like ours from the FB transect and from the joint Norwegian-Russian ecosystem survey in autumn (Eriksen et al. 2017a) are crucial for revealing ongoing changes in

zooplankton communities. Progress of the *Calanus* species in a future, warmer Barents Sea, particularly changes towards dominance of smaller sized individuals over a larger geographical area, deserves high priority in future research considering the key role of these species in the ecosystem.

Supplementary data

Supplementary material is available at the ICESJMS online version of the article.

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Supplementary Material Tables, figures and analyses not included in main article

Table S1: Prosome length (mm) of copepodid stages CI–CV and adult females, used for separation between the *Calanus* species at the Institute of Marine Research (IMR), Norway. Separating *C. finmarchicus* and *C. glacialis* stage CV and females is, in addition to size, also based on morphological characteristics of the coxopodite of the 5th leg, visualized in Knutsen and Dalpadado (2009) page 34.

Stage	<i>C. finmarchicus</i>	<i>C. glacialis</i>	<i>C. hyperboreus</i>
CI	<0.75	0.75–1.0	>1.0
CII	<1.1	1.1–1.4	>1.4
CIII	≤1.6	1.6–2.0	>2.0
CIV	<2.2	2.2–2.9	>2.9, acute spine on 5 th thoracic segment
CV	<2.9	2.9–4.0	>4.1, acute spine on 5 th thoracic segment
CVI female	<3.1	3.1–4.1	>4.3, acute spine on 5 th thoracic segment

West (÷ winter)	325	Total zooplankton	5.00	2.98	6.18	1.23	2.42			
		<i>C. finmarchicus</i>	4.99	2.26	7.42	1.49	2.00	0.74	0.49	0.49
		<i>C. glacialis</i>	0.40	0.00	1.29	3.23	0.04	0.06	0.00	0.01
		<i>C. hyperboreus</i>	0.14	0.00	0.35	2.52	0.04	0.02	0.00	0.01
		Total <i>Calanus</i>	5.53	2.71	7.79	1.41	2.31	0.82	0.59	0.56
		Total zooplankton	6.72	4.57	6.92	1.03	4.09			

Table S3: Coefficient estimates with standard error for models explaining estimated dry weight (log dw) of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*. Optimal models have been selected by AIC values and backwards model selection. P-values are shown for each model term (temperature, season, depth and equipment), and r^2 for the models.

Model	Term	Estimate	Std error	p-value	r^2
log(<i>C. finmarchicus</i> , dw) ~ temperature + season + depth + equipment					0.38
	(Intercept)	-0.38	0.13		
	Temperature (continuous)	0.05	0.01	<0.001	
	Season			<0.001	
	spring	-0.39	0.07		
	summer	0.17	0.07		
	winter	-0.65	0.06		
	Depth (continuous)	0.0018	0.0002	<0.001	
	Equipment			<0.001	
	Juday	-0.9	0.2		
	MOCNESS	0.5	0.3		
	WP2	-0.01	0.13		
log(<i>C. glacialis</i> , dw) ~ temperature + season + depth + equipment					0.52
	(Intercept)	0.18	0.14		
	Temperature (continuous)	-0.22	0.01	<0.001	
	Season				
	spring	-0.78	0.08	<0.001	
	summer	-0.33	0.08	<0.001	
	winter	-0.57	0.06	<0.001	
	Depth (continuous)	0.0016	0.0002	<0.001	
	Equipment			0.01	
	Juday	-0.5	0.2		
	MOCNESS	-0.16	0.3		
	WP2	-0.44	0.14		
log(<i>C. hyperboreus</i> , dw) ~ temperature + season + depth + equipment					0.31
	(Intercept)	-0.71	0.13		
	Temperature (continuous)	-0.09	0.01	<0.001	
	Season			<0.001	
	spring	-0.18	0.07		
	summer	-0.02	0.08		
	winter	-0.37	0.06		
	Depth (continuous)	0.0024	0.0002		
	Equipment			<0.001	
	Juday	-0.69	0.19		
	MOCNESS	-0.07	0.3		
	WP2	-0.71	0.14		

Table S4: Biomass of *Calanus* species (g dw m⁻²) from the Barents Sea and other regions. The table shows mean dw, range of dw and standard deviation (SD) as presented in the study of reference. A ratio of 0.45 carbon content of total dw has been used when converting carbon weight to dw.

Area	Time	<i>Calanus finmarchicus</i>	<i>Calanus glacialis</i>	<i>Calanus hyperboreus</i>	Sum <i>Calanus</i>	Reference
Barents Sea						
Central 75-76°N	July (1987)	0.1-0.6	0.5-4.3	0.1	0.6-4.8	Tande (1991)
N Svalbard 79-82°N	July (1984)		4.3-4.7	1.7-2.9	6.4-7.2	Tande (1991)
Central 76-78°N	May (1997)	0.2-0.7	0.1-1.8	0-0.6	0.4-2.9	Hirche and Kosobokova (2003)
Central 76-78°N	June (1997)	0.2-0.7/5.5*	0.5-2.0	0.1-0.5	1.0-6.5	Hirche and Kosobokova (2003)
W and N Svalbard 77-82°N	May-Dec (2003, 2004)	1-8	0.5-29	0-2	0.5-30.6	Søreide <i>et al.</i> (2008)
Rijpfjorden 81°N			0.7-27			Daase <i>et al.</i> (2013)
Kongsfjorden			0.4-7.5			Daase <i>et al.</i> (2013)
Kongsfjorden	Sept (1997)	3.5	2	1.6	7.1	Scott <i>et al.</i> (2000)
Barents Sea, Western 10-20°E	June-July (2001-2009)	0.5-4.5	0.2-0.8	0.0-0.1		Carstensen <i>et al.</i> (2012)
Greenland Sea						
Fram Strait (MIZEX)	June-July (1984)	0.1-3.7	0-0.05	0.1-1.4	2.3** SD 1.9	Hirche <i>et al.</i> (1991)
Fram Strait (ARK V/2)	June (1988)	0.5-6	0-0.5	0.4-6	5.0** SD 2.5	Hirche <i>et al.</i> (1991)
Greenland Sea Gyre 73-78°N	Nov-Dec (1988)	1		5	6.4** SD 0.8	Hirche (1991)
Fram Strait	Sept (2006, 2007)				0.4-18	Svensen <i>et al.</i> (2011)
Greenland Sea 73.5-77.5°N	June (1999)	0.2-5		0.6-4.4	1.6-6	Møller <i>et al.</i> (2006)
Norwegian Sea						
Lofoten Basin 71-75°N	Nov-Dec (1988)				7.0-9.2**	Hirche (1991)
Station 'M'	March-June (1997)	1.7; 0.1-12.5				Hirche <i>et al.</i> (2001)
Lofoten Basin, Greenland Sea 69-81°N	June-July (2001-2009)	1.0-3.3	0.0-0.2	0.0-0.4		Carstensen <i>et al.</i> (2012)
Iceland Sea						
East Icelandic Current	April-June (1995)	0.8-1.4	<0.03	7-13	8-14	Asththorsson and Gislason (2003)
Baffin Bay						

Disco Bay	June-July (1996, 97)	ca 5	ca 5	ca 5	15	Madsen <i>et al.</i> (2001)
Disco Bay	April-May (2005)	2.5	0.4	0.4	3.4	Madsen <i>et al.</i> (2008)
Disco Bay			4.4-15.6			Daase <i>et al.</i> (2013)
Labrador Sea						
Labrador Sea	Spring (1996, 97, 2000)	0.3-4.6	0.0-0.7	0.2-3.7	0.7-7.2	Head <i>et al.</i> (2003)
Labrador Sea	Summer (1995, 98, 99)	0.6-8.1	0.0-1.4	0.1-2.5	2.8-8.6	Head <i>et al.</i> (2003)
Beaufort Sea						
Franklin Bay			0.1-3.3			Daase <i>et al.</i> (2013)
Amundsen Gulf			0.5-6			Daase <i>et al.</i> (2013)

*One high value in Atlantic water in the south

**Includes *Metridia* spp.

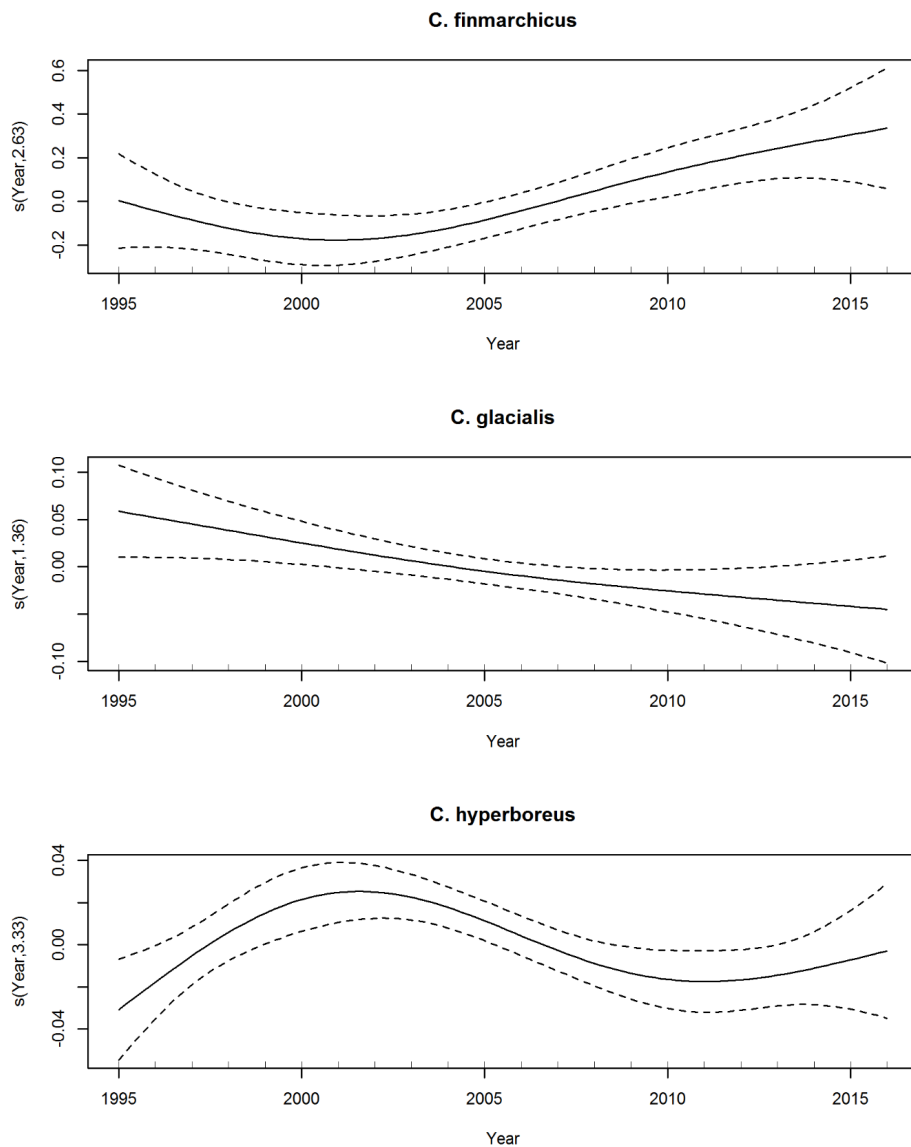


Figure S1: Output from GAM models on estimated proportion of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in the total mesozooplankton biomass in the western area of the Barents Sea, with year as explanatory variable. Models were run with a spline-based smoother using 4 degrees of freedom. $P = 0.003$, 0.04 and 0.002 for *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, and deviance explained = 10 %, 4.2 % and 12 % respectively. GAM models on changes in estimated biomass for the respective species showed similar trends, yet the model for *C. glacialis* was not significant on a 0.05 level ($p = 0.07$, see main text).

Length measurements of *Calanus finmarchicus* and *C. glacialis*

Length measurements on individuals of *C. finmarchicus* and *C. glacialis* stages CIV, CV and adult females were made from stored samples from one station at the Fugløya-Bear Island transect (73.5°N, 19°E) where both species are regularly present. Measurements were performed on June and August samples from 1997, 1998, 2004 and 2010. The length measurements were utilized with two different length-weight regressions from Hirche and Mumm (Hirche and Mumm, 1992) and Madsen et al. (2001), assuming a carbon content of 45 % of the individual dry mass (Postel *et al.*, 2000), to determine the expected weight distribution of these individuals. Results are presented in Tables S4 and S5 and Figures S2 and S3.

C. hyperboreus was not included due to few specimens in the samples.

Table S5: Measurements of prosome length (mean and SD in mm for n individuals) from individuals stored in formalin using samples from one station (73.5°N, 19°E) at the Fugløya-Bear Island transect in the Barents Sea. One-way ANOVA analyses with year as explanatory variable indicated a decrease in prosome length of stages CIV and CV *C. finmarchicus* between 1997 and 2010 ($p < 0.001$ for both stages and $r^2 = 0.16$ and 0.17 for CIV and CV, respectively). For *C. glacialis* a decline in prosome length was indicated for CV copepodites in 2004, though this was not statistically significant at the 0.05 level ($p = 0.07$).

Species	Stage	Measure	1997	1998	2004	2010
<i>Calanus finmarchicus</i>	CIV	Mean	2.04	-	1.94	1.92
		SD	0.10	-	0.12	0.13
		n	50	0	50	50
	CV	Mean	2.71	2.52	2.59	2.45
		SD	0.15	0.21	0.16	0.21
		n	50	101	50	50
	CVI female	Mean	2.68	-	2.79	-
		SD	0.17	-	0.19	-
		n	7	0	30	0
<i>Calanus glacialis</i>	CIV	Mean	2.36	-	2.36	2.32
		SD	0.11	-	0.05	0.04
		n	50	0	3	3
	CV	Mean	3.19	3.26	3.12	3.12
		SD	0.13	0.19	0.16	-
		n	50	101	26	1
	CVI female	Mean	3.56	-	-	-
		SD	0.00	-	-	-
		n	2	0	0	0

Table S6: Individual dry weight (dw, μg) of copepods and adult females employed for estimating species biomass in this study, and mean dw derived from new length measurements (Table S5) using length-weight regressions from Hirche and Mumm (1992) and Madsen et al. (2001).

Developmental stage		This study	Hirche and Mumm (1992)	Madsen et al. (2001)
<i>C. finmarchicus</i>	CIV	70	96	122
	CV	250	233	312
	females	235	305	414
<i>C. glacialis</i>	CV	600	502	700
	females	810	698	990

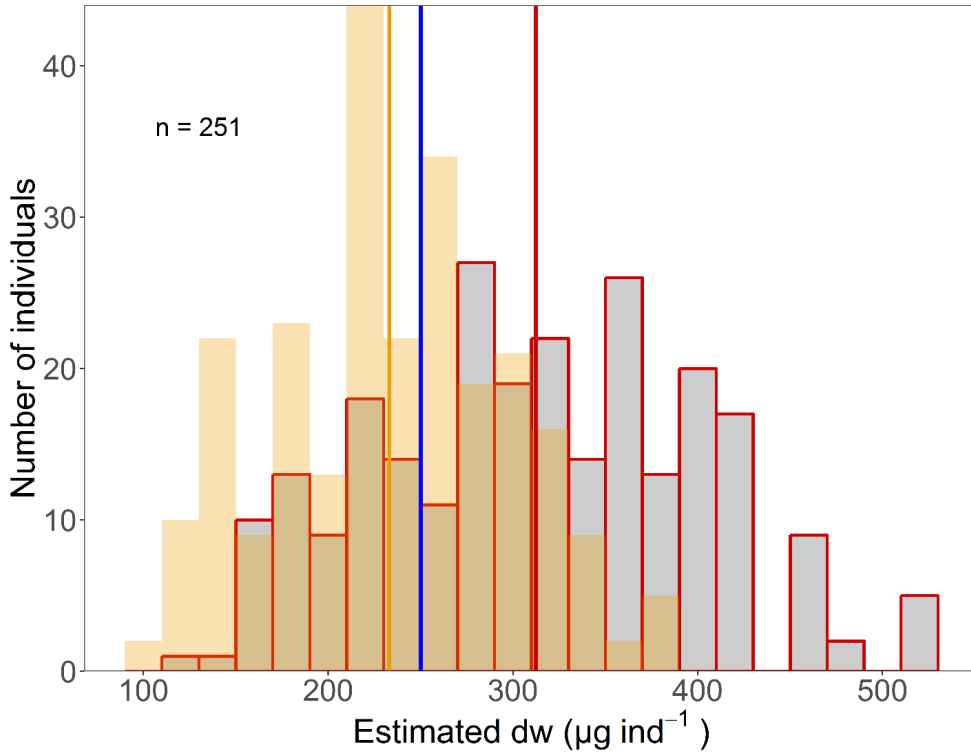


Figure S2: Individual dry weight of *Calanus finmarchicus* stage CV estimated from length measurements combined with length-weight regression equations from Hirche and Mumm (1992) (orange bars and mean in orange vertical line) and Madsen et al. (2001) (grey bars, red outline, mean in vertical red line). The blue vertical line shows the weight for stage CV employed in this study.

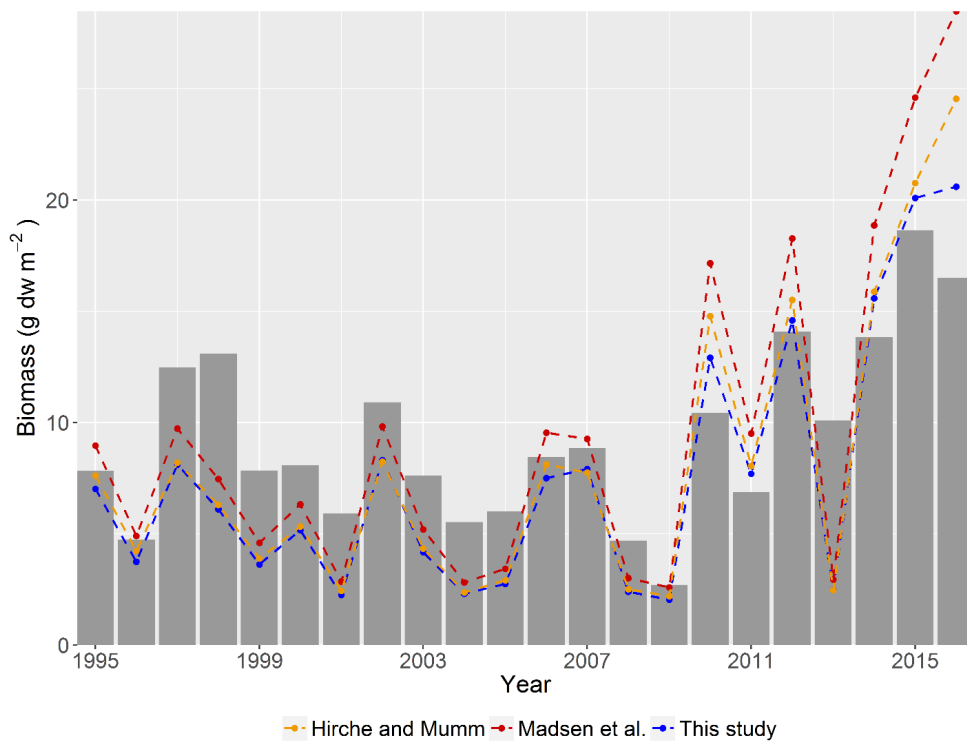


Figure S3: Observed mean June and August mesozooplankton biomass (grey bars) and mean estimated biomass of *C. finmarchicus* using three sets of weight data: weight-at-stage data employed in this study (blue), new weights of stage CIV to adults based on regression from Hirche and Mumm 1992 (orange) and new weights of CIV to adults based on regression from Madsen et al. 2001 (red). Mesozooplankton biomass and *C. finmarchicus* abundance data are from the western region of the Barents Sea.

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II

Caught in broad daylight: Topographic constraints of zooplankton depth distributions

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Abstract

For visual predators, sufficient light is critical for prey detection and capture. Because light decays exponentially with depth in aquatic systems, vertical movement has become a widespread strategy among zooplankton for avoiding visual predation. However, topographical features such as seamounts have been shown to block their descent, trapping them in illuminated waters with potential feeding benefits for visually searching fish. Here, we present an extensive and previously unpublished dataset on the vertical distribution of zooplankton in the topographically rugged Barents Sea, a continental shelf region hosting some of the largest fish stocks in the world. By modeling the ambient light exposure of zooplankton in relation to the bathymetry, we find support for a similar blockage mechanism. During daytime, zooplankton are exposed to four orders of magnitude more light above shallow banks than in the deeper water surrounding the banks. We show that zooplankton depth distributions are highly related to zooplankton size and that the bottom constrains the vertical distributions. Consequently, zooplankton remain in the planktivores' visual feeding habitat over the banks but not in deeper areas. Bottom topography and light absorbance are significant determinants of the seascape ecology across continental shelves with heterogeneous bathymetry.

Space is the stage for ecology. Spatial structures and gradients form the landscape where organisms compete, predate and reproduce. In terrestrial systems, the study of ecology with spatial structures and patterns is known as landscape ecology, while the concept of seascape ecology is still debated (Manderson 2016; Bell and Furman 2017; Manderson 2017). How do spatial gradients in the environment, such as fading light, seamounts, or bottom depth and topography, structure marine pelagic communities of small organisms drifting with the currents?

Interactions between vertically migrating pelagic species and ocean bathymetry may influence ecosystem structures. Truman et al. (2014) demonstrated that the diel vertical migrating (DVM) community is accessible to bottom feeding fish only at depths < 1000 m. Demersal fish that consume prey above the seafloor (benthopelagic feeders) therefore have a competitive advantage at greater depths and proliferate between 1000 and 1800 m. Interactions between the bathymetry and vertically

migrating prey may be important for pelagic feeding planktivores as well. Visual detection of individual prey is the common foraging mode in planktivorous fish (Eggers 1977), and the prey detection distance for a fish is sensitive to ambient light levels (Aksnes and Utne 1997). As light decreases exponentially in water, the vertical position of zooplankton prey is important for their foraging success. Zooplankton display a range of vertical migration strategies related to diurnal (Bollens and Frost 1991; Ohman and Romagnan 2016) and seasonal (Bandara et al. 2016) rhythms, which is an evolutionary adaptation to the trade-off between growth and survival in dynamic environments (Pearre 2003; Bandara et al. 2018). Zooplankton over shallow banks and shelves are prevented from migrating into deeper and darker waters, which increases their vulnerability to predation from fish. Advection of zooplankton onto seamounts and banks, where they are trapped and unable to seek safety in deep water, has been termed “the topographic blockage mechanism” (Isaacs and Schwartzlose 1965; Genin 2004) and is possibly an important driver of fish habitat choice.

Fish aggregation over bottom topographies such as seamounts, shelves, and banks can be linked to increased prey availability due to either enhanced productivity caused by upwelling of nutrients (Rogers 1994) or horizontal advection of resources from surrounding areas. Based on the topographic blockage mechanism, we hypothesize that the bathymetry

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influences foraging opportunities for fish that feed on vertically migrating zooplankton in the pelagic because of topographic constraints on zooplankton depth distributions. Previous studies have demonstrated topographic blockage of zooplankton performing DVM (reviewed in Genin [2004]), where individuals ascending to surface layers at night are advected onto shallow topographies that block their morning descent to deeper waters. Seasonal migrators such as *Calanus* spp., the key herbivores in North-Atlantic ecosystems (Melle et al. 2014), will also be blocked by the topography if occupying shallow areas in periods of diapause (e.g., Krumhansl et al. 2018). Survival of *Calanus* spp. during overwintering has earlier been related to access darkness for avoiding predation (Kaartvedt 1996; Dale et al. 1999).

Our study area, the Barents Sea, is a relatively deep shelf sea (bottom depth up to 500 m) situated on the Arctic continental shelf adjacent to the deep Norwegian Sea to the west. Atlantic water flows through the system from the shelf edge in the southwest to the northern Kara Sea and the Arctic Ocean in the northeast (Smedsrud et al. 2013). We use an extensive dataset on the vertical distribution of zooplankton in three size classes, to examine whether their depth distributions are constrained by the bathymetry and evaluate if this improves the foraging potential for visually searching planktivorous fish. Planktivorous fish are size selective (Brooks and Dodson 1965), and large-sized prey are easier to see (Eggers 1977; Aksnes and Giske 1993) and require deeper habitats to avoid visual predators (e.g., Ohman and Romagnan 2016). We therefore expect pronounced differences between the size classes and predict that the bathymetry limits the depth distribution particularly for the large zooplankton in our data. Water clarity alters the vertical light gradient, and we expect to find zooplankton deeper in clear relative to less transparent water (Dupont and Aksnes 2012; Ohman and Romagnan 2016). The ambient light exposure of prey is important for the foraging efficiency of planktivorous fish—and here we quantify zooplankton light exposure from vertical distributions, vertical light attenuation and the bathymetry.

Materials and methods

Data

The Barents Sea is a large marine ecosystem (1.6×10^6 km²) on the Arctic continental shelf and hosts economically and ecologically important fish stocks (Gjøsaeter 1998; Eriksen et al. 2017a). It is monitored extensively each year through a joint Norwegian/Russian monitoring program by the Institute of Marine Research (IMR) and Knipovich Polar Research Institute of Marine Fisheries and Oceanography (Eriksen et al. 2018). The annual ecosystem survey takes place in autumn and covers key physical and biological components of the ecosystem using different sampling equipment. Our study is based on zooplankton data from Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) sampling gear (Wiebe et al. 1985), with 1 m² opening and 180 μ m mesh size. The samples have

been collected at Norwegian vessels during ecosystem surveys in the period 1992–2016 and span day of year 214–280 (early August to early October). We also used salinity and chlorophyll *a* (Chl *a*) data from the same cruises and sampling stations as the zooplankton data (see below).

The MOCNESS samples zooplankton in up to eight depth strata in the water column. Samples have routinely been split in two, with one half used to determine dry weight biomass (g dw m⁻³) in three size fractions using mesh gauzes of 2000, 1000, and 180 μ m (Melle et al. 2004). Krill have been measured separately over the period and are not considered in this study, while amphipods and chaetognaths have been measured separately since 2008 and may comprise a smaller part of the > 2000 μ m size fraction in samples from before 2008. Copepods, particularly of the genus *Calanus*, dominate the mesozooplankton (> 0.2 mm) biomass in the Barents Sea (Aarflot et al. 2017) and likely comprise the larger part of the data analyzed here.

Zooplankton-weighted mean depth

Only samples covering > 75% of the water column were considered suitable for our purpose of determining zooplankton depth distributions and included in the analyses, and the upper and lower depth strata were extrapolated to the surface and bottom. Similar to Daase et al. (2008), we estimated the weighted mean depth (WMD, m) and the standard deviation (SD, m), which is a measure of the compactness, of the depth distribution (Manly 1977) for each sample and size fraction (j):

$$WMD_j = \sum_{i=1}^k \frac{\Delta Z_i b_{j,i} Z_{m,i}}{B_j} \quad (1)$$

$$SD_j = \sqrt{\sum_{i=1}^k \frac{\Delta Z_i b_{j,i} Z_{m,i}^2}{B_j} - WMD_j^2} \quad (2)$$

Here, ΔZ_i is the thickness (m) and $b_{j,i}$ the zooplankton biomass (g dw m⁻³) of size class *j* in stratum *i*, $Z_{m,i}$ is the stratum mean depth, *k* is the total number of strata sampled, and B_j is the depth integrated biomass (g dw m⁻²) of the size class ($\sum_{i=1}^k \Delta Z_i b_{j,i}$). The size classes will hereafter be denoted L, M, and S, referring to the large (> 2000 μ m), intermediate (1000–2000 μ m), and small (180–1000 μ m) size fraction. Surface irradiance was modeled with an algorithm from the HYbrid Coordinate Ocean model (HYCOM) (Bleck 2002) based on sampling time (day of year and hour at the onset of sampling) and latitude assuming 50% loss at and through the surface, and we sorted samples as day/night presuming day = surface irradiance > 1 μ mol m⁻² s⁻¹.

Light attenuation

Light absorption and scattering determine light attenuation and how deep surface irradiance penetrates the water column. In oceanic water, attenuation is largely influenced by the presence of algae (Morel and Maritorena 2001) and chromophoric dissolved organic matter (CDOM) (Bricaud et al. 1981). Many

Table 1. Results from regression analyses of daytime occurrences, with zooplankton WMD (WMD_j , m) and distribution compactness (SD_j , m) as functions of bottom depth (Z_b , m) and optical depth (K^{-1} , m). Both Z_b and K^{-1} were significant predictors for WMD_j ($p < 0.001$ and $p = 0.004$, respectively), but only Z_b was significant for SD_j ($p < 0.001$). The size classes ($j = L, M, \text{ and } S$) had significantly different slopes for WMD_j and SD_j as functions of Z_b ($p < 0.001$ for both), whereas slopes were not significantly different between the size classes for WMD_j as a function of K^{-1} (not shown). The table shows parameters with 95% confidence levels (CL), degrees of freedom (df), and variance explained (R^2). Thirteen percentage of the stations lacked Chl a and salinity measurements used to approximate K (hence different df in the two models), and there were missing values for the large, intermediate, and small size fraction in $n = 8, 2, \text{ and } 2$ samples, respectively.

Weighted mean depth ($WMD_j = a_j + b_j Z_b + c K^{-1}$)									
	a_j (intercept)	b_j (Z_b)	Lower CL	Upper CL	c (K^{-1})	Lower CL	Upper CL	df	R^2
Large (L)	-40.1	0.75	0.70	0.79	n.s.				
Intermediate (M)	-1.8	0.59	0.55	0.63	n.s.				
Small (S)	-2.7	0.40	0.36	0.44	n.s.				
All					1.13	0.38	1.88	1563	0.657
Distribution compactness ($SD_j = a_j + b_j Z_b + c K^{-1}$)									
Large (L)	-4.5	0.23	0.22	0.25	n.s.				
Intermediate (M)	-16.4	0.29	0.28	0.31	n.s.				
Small (S)	-10.9	0.32	0.31	0.34	n.s.				
All					n.s.	n.s.	n.s.	1794	0.663

n.s., not significant.

studies have shown that the CDOM concentration of marine waters is a strong function of the observed freshwater fraction or its salinity (reviewed by Nelson and Siegel 2013). This is particularly true for the Baltic Sea, the North Sea, and the Norwegian Coastal Water (NCW), which contain large amounts of CDOM of terrestrial origin (Højerslev et al. 1996; Stedmon et al. 2000; Kowalczyk et al. 2005; Aksnes 2015). NCW is transported into the Barents Sea with the Norwegian Coastal Current; and here, we have used data on Chl a and salinity from CTD casts at the MOCNESS stations, to approximate the water column light attenuation (K , m^{-1}) where the zooplankton was sampled (note that 13% of the stations lacked Chl a and salinity measurements).

Chl a has regularly been measured down to 100 m depth in the Barents Sea, though some samples had deeper measurements (Supporting Information Fig. S1). We used data from 10 m depth intervals between 0–50 m, 25 m intervals between 50–150 m, and additional 50 m intervals below 150 m when data were available. Chl a and salinity were interpolated between the depth intervals, and light attenuation was approximated down to the maximum depth where we had measurements for both variables. Few Chl a measurements below 100 m might have led to an underestimation of light attenuation at deeper stations.

Light attenuation by algae (K_{chl}) was here approximated for 440 nm wavelength, using the relationship of Morel and Mariorenza (2001):

$$K_{chl}(440) = 0.10963(Chl)^{0.67175} \quad (3)$$

Light attenuation by CDOM (K_{CDOM}) was estimated from the empirical relationship for nonchlorophyll light attenuation

in mixtures of North Atlantic Water and NCW given by Aksnes (2015):

$$K_{CDOM}(440) = 1.47 - 0.041S \quad (4)$$

where S is salinity. Total light attenuation (K) is the sum of Eqs. 3 and 4.

It is uncertain how well Eq. 4 relates to absorption by CDOM in the Barents Sea, as the freshwater component in this water also has other origins (melting of sea ice) than the water masses studied by Aksnes (2015). We therefore tested the effect of both total K and K_{chl} as predictors for the zooplankton WMD (see Statistics section below).

Statistics

Our main focus was samples collected during daylight ($n = 604$), when fish are able to detect their prey by vision. Resembling Dupont and Aksnes (2012), we used linear regression techniques to evaluate the WMD for zooplankton size class j as a function of bottom depth (Z_b) and optical depth (K^{-1}) at the sampling station:

$$WMD_j = a_j + b_j Z_b + c_j K^{-1} \quad (5)$$

We used ANCOVA to estimate the coefficients a_j , b_j , and c_j and ANOVA to test whether the coefficients were significantly different between the size classes. Taking SD_j instead of WMD_j as response variable, we also applied Eq. 5 to assess variation in the compactness of zooplankton distributions with bottom depth and optical depth.

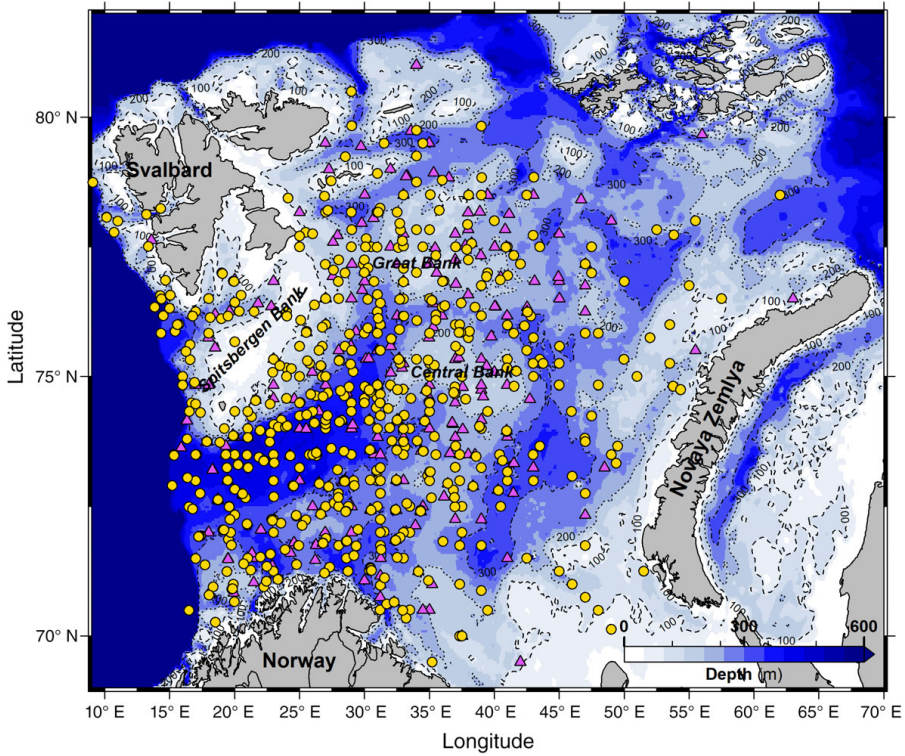


Fig. 1. Barents Sea study area and distribution of samples from MOCNESS sampling gear, providing data on the vertical distribution of zooplankton in the period 1992–2016. The map shows samples collected during daylight (yellow, $n = 604$) and at night (pink, $n = 258$), based on our definition of day vs. night described in Materials and Methods section. Bathymetry data from the ETOPO1 database (1 -min resolution) are plotted on a darkening blue scale for increasing bottom depth. Major banks with depth < 200 m are labeled in the map.

In addition, we analyzed the complete dataset (i.e., including samples collected at night, $n = 258$) to check for a diel migration pattern in the data, or if WMD changed between day and night. These analyses were run individually for each size class, using day/night (1) as categorical covariate:

$$WMD_{j,1} = a_{j,1} + b_{j,1}Z_b \quad (6)$$

All analyses and figures were made in the statistical software package R version 3.4.0 (R Core Team 2016).

Expectations from topographic constraints of daytime occurrences

We hypothesized that zooplankton have deep daytime distributions to avoid depths where planktivorous fish can forage efficiently by sight and that the bathymetry limits their preferred depth distribution without a bottom constraint. This implies the expectation of a positive statistical

effect of bottom depth on the weighted mean zooplankton depth. Given that larger zooplankton need to go deeper than smaller zooplankton to reduce their visibility to fish, we expected a significant interaction between Z_b and j and that $b_L > b_M > b_S$. Note that if all zooplankton biomass is caught in the deepest stratum, WMD_j is equal to the mean depth Z_m of that stratum (Eq. 1) rather than to the bottom depth Z_b , so the coefficient b_j of Eq. 5 becomes less than 1. Therefore, the closer b_j is to 1, the stronger the effect of Z_b on WMD_j . Less transparent water (high K) allow zooplankton to remain closer to the surface at the same light exposure (Ohman and Romagnan 2016). We therefore expected the WMD to be deeper in clear water and to find a positive effect of optical depth (K^{-1}) on WMD_j (c_j of Eq. 5 larger than 0). Yet, if distributions are limited by the bathymetry, the effect of K should be small in areas where the zooplankton are forced to occupy depths with unfavorable light levels despite low water clarity.

Table 2. Results from linear regressions evaluating WMD_j and SD_j as functions of Z_b in day and night samples ($l = \text{day or night}$), j indicates size class (L, M, and S). The table shows parameters with 95% confidence levels (CL), degrees of freedom (df), and variance explained (R^2).

Weighted mean depth: $WMD_{j,l} = a_{j,l} + b_{j,l}Z_b$							
		a_j (intercept)	b_j (Z_b)	Lower CL	Upper CL	df	R^2
Large (L)	Day	-29.8	0.73	0.69	0.77	850*	0.69
	Night	-40.5	0.75	0.68	0.80		
Intermediate (M) [†]	Day	20.9	0.55	0.51	0.59	856 [‡]	0.56
	Night	-13.7	0.66	0.60	0.73		
Small (S) [‡]	Day	18.8	0.36	0.32	0.40	856 [‡]	0.41
	Night	-17.1	0.52	0.45	0.58		
Distribution compactness: $SD_{j,l} = a_{j,l} + b_{j,l}Z_b$							
		a_j (intercept)	b_j (Z_b)	Lower CL	Upper CL	df	R^2
Large (L) [§]	Day	-4.5	0.23	0.21	0.25	850*	0.53
	Night	-7.7	0.27	0.24	0.3		
Intermediate (M)	Day	-16.4	0.29	0.28	0.31	856 [‡]	0.63
	Night	-15.1	0.31	0.28	0.34		
Small (S)	Day	-10.9	0.32	0.31	0.34	856 [‡]	0.77
	Night	-15.1	0.35	0.33	0.37		

* Missing values in eight samples.

[†] Significant difference in slopes for day and night ($p < 0.01$).

[‡] Missing values in two samples.

[§] Significant difference in slopes for day and night ($p = 0.02$).

Results

Bottom constrains zooplankton daytime depth distributions

Bottom depth had a significant effect on the zooplankton WMD ($p < 0.001$), and slopes (b_j) were different between the size classes ($p < 0.001$). The slopes confirmed our prior expectation of $b_L > b_M > b_S$ (Table 1), that is, that larger zooplankton are more constrained by topography than smaller zooplankton. Large zooplankton resided primarily close to the bottom, with a strong effect of bottom depth on WMD_L ($b_L = 0.75$; see Table 1; Fig. 2a). Including only samples collected after the change in sampling procedures in 2008 (see *Data* above) did not change this finding. Intermediate-sized zooplankton ($j = M$) also had the weight of their distribution close to the bottom in a large fraction of the observations (Fig. 2a) and a strong effect of bottom depth on WMD_M ($b_M = 0.59$). The small size class ($j = S$) had the weight of their distribution closer to the surface (Fig. 2a), although distributions were deeper in deeper areas also for this size class ($b_S = 0.40$). The vertical extension of the zooplankton distributions (as given by SD_j) increased with bottom depth ($p < 0.001$), that is, distributions were more compact in areas where the bathymetry was limiting the depth distributions. Slopes were significantly different between the size classes ($p < 0.001$), and the small size class had the strongest statistical effect of bottom depth on SD (Table 1).

Large, intermediate, and small zooplankton above deep topographies experienced several orders of magnitude reduction in light exposure compared to zooplankton at shallow

banks (Fig. 2b). In deep regions, large zooplankton had about 10,000 times lower light exposure than small zooplankton. The ecological consequence of this difference in light exposure is that a hypothetical fish can visually detect a large prey at about 20 cm distance at 100 m, but hardly at all below 300 m (Fig. 2c). The prey detection distance is the radius of the visual sphere and consequently scales to the power of two in terms of how much water a fish can scan for prey per time unit (see Supporting Information) (Eggers 1977). The prey encounter rate for the fish is therefore about 25 (proportional to 5^2) and 400 (proportional to 20^2) times larger for the small and large zooplankton, respectively, above (100 m) and off a bank edge (300 m) for any given prey concentration at the WMD of the zooplankton distributions.

Water clarity is a second-order factor in the Barents Sea

The optical depth, given as the reciprocal water column light attenuation (K^{-1}), had a significant, positive effect on the zooplankton WMD ($p = 0.004$), that is, the zooplankton had deeper distributions in clear water, but it did not significantly affect distribution compactness (SD) (Table 1). The effect of K^{-1} (c) was not significantly different between the size classes (j), although only the small size class had in fact a confidence interval for c excluding zero. We therefore ran individual analyses for the WMD of each size class (Eq. 5) and discovered that while K^{-1} had a significant effect on the WMD for the small size class in all areas ($p < 0.001$), it only affected the WMD for the large size class in areas > 300 m ($p = 0.03$).

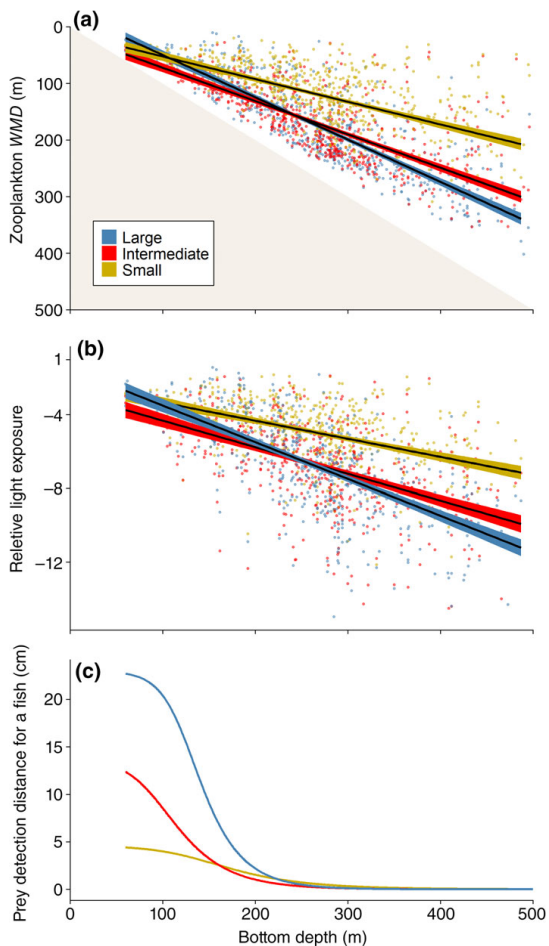


Fig. 2. (a) Estimated WMD (WMD_j) for daytime occurrences of large ($> 2000 \mu\text{m}$), intermediate ($1000\text{--}2000 \mu\text{m}$), and small ($180\text{--}1000 \mu\text{m}$) zooplankton in the Barents Sea, and linear models with 95% confidence bands of WMD_j as a function of bottom depth and light attenuation (K^{-1}) (Table 1), j indicates size class. Predictions have been plotted using the mean K of all samples (0.08 m^{-1}). Beige area illustrates the bottom depth. (b) Deeper distributed zooplankton achieve several orders of magnitude reduction in light exposure relative to the surface irradiance. Relative light exposure was here estimated for the WMD_j based on mean K at the sampling station: $\text{Exp}(-K \times WMD_j)$. Note that light exposure is plotted on a \log_{10} scale. Lines are linear regressions with 95% confidence bands. (c) Approximated prey detection distance for a fish at the predicted depth of the zooplankton size class from the linear models described in (a). Reaction distance has here been approximated for a 13 cm fish foraging on prey with body lengths of 5, 3, and 1 mm, based on Aksnes and Utne (1997). We used a light attenuation coefficient of 0.08 m^{-1} (mean K for the Barents Sea dataset). All parameters and equations are provided in the Supporting Information (“Elaboration on fish reaction distance” and Table S1).

Moreover, we found no significant effect of water clarity on the WMD for the intermediate size class, both in the total dataset and in samples from deeper areas, when examined individually. The effect of water clarity on WMD_L only in deeper areas implies that large zooplankton are forced to occupy depths with suboptimal light levels regardless of water clarity in areas $< 300 \text{ m}$, in line with our prior expectations. Using only K_{chl}^{-1} instead of K^{-1} ($K_{\text{chl}}^{-1} + K_{\text{CDOM}}^{-1}$), we found a significant effect of water clarity on the WMD (all sizes) only in areas $> 300 \text{ m}$.

Overall, light attenuation had a second-order effect on the WMD of the zooplankton distributions, which we believe is partly due to low variation in the approximated K from our data on Chl a and salinity (Supporting Information Fig. S2). Including K did, however, improve the explanatory power (R^2) of the statistical model compared to a simpler model with only bottom depth and size as predictors (models compared with ANOVA, $p = 0.003$).

Zooplankton biomass depth profiles

Vertical profiles of mean zooplankton biomass (g dw m^{-3}) by depth confirmed that large zooplankton had the bulk of their biomass close to the bottom, particularly in areas $> 200 \text{ m}$ (Fig. 3). Intermediate sizes also had a large part of their biomass close to the bottom, although in areas $> 200 \text{ m}$, they displayed a bimodal distribution pattern with more biomass in surface waters and low biomass between 50 and 200 m. This bimodality was most pronounced in areas with 400–500 m depth, which covers the western entrance where Atlantic water flows into the Barents Sea (Fig. 1). The intermediate size class had the largest variation in sampled biomass, both in the surface and deeper waters (shown as 95% confidence intervals in Fig. 3). Small zooplankton had greater biomass in surface waters (0–50 m), also showing tendencies of a bimodal vertical distribution in areas $> 200 \text{ m}$. Zooplankton appeared to be more evenly spread throughout the water column in areas $< 200 \text{ m}$.

Night-time occurrences indicate overwintering and inverse DVM

For large zooplankton, we found a similar, strong effect of bottom depth on WMD_L during both day and night (Table 2), and b_L was not significantly different in day vs. night samples. This indicates that the majority in this size class had ceased feeding in surface waters and migrated downward for overwintering (samples were from mid-August to mid-October). Bottom depth had a stronger effect on the spread in distributions (SD_L) in night-time samples ($b_{L,\text{day}} = 0.23$ vs. $b_{L,\text{night}} = 0.27$, $p = 0.02$), that is, distributions were more compact (closer to the bottom) during the day.

Both intermediate and small sizes had significantly different slopes (b_j) for day and night ($p < 0.01$), with deeper distributions at night than during the day (Table 2). This suggests an inverse diel vertical migration (DVM) behavior; however,

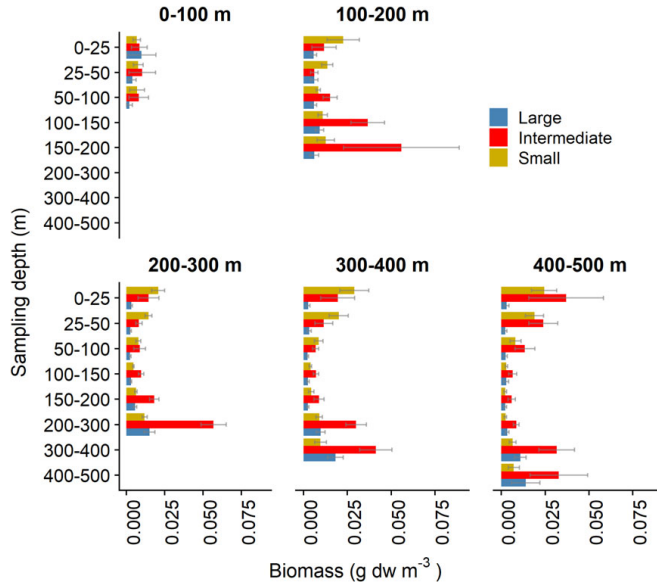


Fig. 3. Vertical biomass profiles (average of all stations, samples collected by day) for the three sizes of zooplankton, panel titles specifies bottom depth at the sampling station. Samples have been sorted according to the mean strata depth (y -axis, Z_m), and the figure shows mean biomass (g dw m^{-3}) with 95% confidence intervals ($\pm 1.96 \times \text{SEM}$). Small zooplankton were largely caught in the surface waters in all areas, whereas the intermediate and large size fraction had greater biomass closer to the bottom. Intermediate zooplankton constituted the largest biomass of the three and showed a bimodal distribution pattern in deeper areas (> 200 m).

the difference was not very pronounced ($b_M = 0.55$ for day vs. 0.66 for night, and $b_S = 0.36$ for day vs. 0.52 for night), making it difficult to draw any firm conclusions. It can also suggest that distributions are more spread out through the water column at night, yet the spread in the distributions (SD) was not significantly different between day and night samples (Table 2; see also Supporting Information Fig. S3). We cannot exclude that this is also due to a sampling bias, with more night-time samples collected later in the period when there is fewer hours of daylight and when more zooplankton likely have migrated out of the surface for overwintering.

Note that coefficients for $b_{j,\text{day}}$ in Table 2 are slightly different than b_j in Table 1, as analyses shown in Table 1 include the effect of K and were run on a smaller dataset (13% of the samples lacked data for approximating K).

Discussion

The Barents Sea is a continental shelf with a varied topography consisting of banks with trenches in between. It is also an important fishery area supporting some of the world's largest fish stocks (Eriksen et al. 2017a). Our results provide observational evidence for topographic constraints of zooplankton vertical distributions in this fish-rich continental shelf ecosystem. The uniqueness of our dataset stems from the magnitude

of samples, covering the large and varied bathymetry of the Barents Sea seascape (Fig. 1). Topographic constraints limit the depth distribution for large and intermediate-sized zooplankton in particular, resulting in increased light exposure at the banks. Consequently, planktivores presumably have higher probability of detecting zooplankton prey in areas with bottom depth < 200 m (Fig. 2).

The blockage mechanism has previously been shown for seamounts (e.g., Isaacs and Schwartzlose 1965; Genin et al. 1994) and shelf breaks (Simard and Mackas 1989; Robinson and Goómez-Gutiérrez 1998), and parallels can be drawn with depth constraints on *Daphnia* populations by hypolimnetic anoxia in freshwater lakes (Sakwińska and Dawidowicz 2005). Advection is key in the blockage mechanism; with no replenishment of zooplankton by advection, it is likely that the zooplankton standing stocks over banks are quickly predated due to lack of refuge from visual foraging. Genin et al. (1994) observed patches devoid of zooplankton (gaps) formed on a daily basis over a seamount in California and attributed this to predation by planktivores on topographically blocked zooplankton. Lower biomass of zooplankton in areas shallower than 100 m in our study may have been an effect of predation (Fig. 3). The strength of the blockage mechanism in terms of providing foraging opportunities for visually feeding fish would in general depend on the topographic

configuration and the exchange of water and plankton between deep and shallow waters (Genin 2004). Variation in advection of zooplankton over shallow topographies will create additional variation in the food availability and foraging success for the fish. The major banks in the Barents Sea, for example, the Central Bank, Great Bank, and Spitsbergen Bank (see Fig. 1), are large structures (100–200 km) with complex hydrography and circulation features associated with the topographically steered oceanographic polar front (Ingvaldsen and Loeng 2009). We have merged data from a large ecosystem with both Arctic and Atlantic characteristics (e.g., Johannesen et al. 2012b), and there can be spatial variation that we have not unveiled. Studies combining hydrodynamic and particle-tracking models (e.g., Harms et al. 2000) will be useful to further identify important feeding grounds where there is both topographic blockage and zooplankton replenishment by advection.

Results from our study are likely transferrable to other regions with a rugged bathymetry. The topographic blockage mechanism has been suggested to sustain fish populations above steep oceanic topographies like seamounts and shelf breaks (Isaacs and Schwartzlose 1965; Mauchline and Gordon 1991; Genin et al. 1994; Seki and Somerton 1994; Fock et al. 2002), and large remains of dead copepods (carcasses) indicate elevated predation over these topographies (Haurv et al. 1995). Topographic blockage of zooplankton may also have contributed to denser capelin concentrations at banks than over deeper troughs in the central Gulf of Alaska (McGowan et al. 2018). In the North Sea, predation on herring has been identified as a major driver of *Calanus finmarchicus* mortality (Papworth et al. 2016), and topographic blockage resulting in increased visibility is a likely explanation for the low abundance of *C. finmarchicus* during winter. The stock is replenished in spring by *C. finmarchicus* advected with Norwegian Sea deep water through the Faroe-Shetland Channel (Heath et al. 1999). Reduced deep-water inflow is thus suggested to explain the long-term (1950–present) decline in abundance (Heath et al. 1999), with a negative effect on the recruitment of cod (Beaugrand and Kirby 2010) and also potentially on the growth rate of planktivorous fish (van Deurs et al. 2015).

The type of migration pattern exhibited by zooplankton will determine if their depth distribution limits fish in its search for prey. Shallow topographies may, for instance, be more important for fish during autumn and winter, if their prey here is unable to seek deeper waters for overwintering. Transport of *Calanus* from the deep basins of the Norwegian Sea onto the Barents Sea shelf as well as the Norwegian Shelf (Samuelsen et al. 2009; Opdal and Vikebø 2015) is in some respects a part of the topographic blockage mechanism on a seasonal basis (although it is rarely called so in the literature). In our autumn dataset from the Barents Sea, *C. finmarchicus* has for the most part entered the overwintering dormant state (Hirche 1996) or is descending to overwintering depths which in the adjacent Norwegian Sea is below 500 m (Edwardsen et al. 2006). Our data suggest that *C. finmarchicus* and other

overwintering species are seeking the deeper part of the water column in concert with the deepening water depth. Zooplankton can also display daily migration patterns, although it is debated whether DVM is present in Arctic zooplankton during summer (e.g., Blachowiak-Samolyk et al. 2006; Berge et al. 2009).

Capelin (*Mallotus villosus*) is a key planktivore in the Barents Sea ecosystem (Gjøsæter et al. 2009) and exerts a significant top-down control on zooplankton in the central and northern areas where the major banks are found (Fig. 1) (Stige et al. 2014). Capelin can possibly consume all the zooplankton biomass in the upper, illuminated part of the water column in a matter of days when the seasonally migrating “capelin front” moves into a new and previously unpredated area (Hassel et al. 1991). Baleen whales (minke whale *Balaenoptera acutorostrata*, fin whale *Balaenoptera physalus*, and humpback whale *Megaptera novaeangliae*), which forage on both zooplankton and pelagic fish, were found to remain at banks in the northern Barents Sea even in years with low capelin abundance, instead of migrating southward to feed on abundant herring (*Clupea harengus*) (Skern-Mauritzen et al. 2011). Atlantic cod (*Gadus morhua*), a key predator on capelin, is also largely associated with shallow areas of the Barents Sea (Johannesen et al. 2012aa). For capelin, these areas therefore represent not only potentially increased prey availability but also higher risk of predation for capelin itself. Due to this trade-off, it is not evident that there is more planktivorous fish in shallow areas in the Barents Sea although their prey are more visible there.

Conclusion

Exponential decay of light in water means that zooplankton can reduce their light exposure considerably by shifting their vertical position by only tens of meters (Fig. 2b). Over a seascape varying in bottom depth from 100 to 500 m, the shallower bathymetry force zooplankton into more illuminated habitats and increase the feeding potential for planktivorous fish. For fish feeding on *Calanus* and other seasonal migrators, the bathymetry effectively prevents prey from deep descends for safer overwintering. This is likely to affect fish distributions and an important factor for pelagic predator-prey interactions and seascape ecology.

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Conflict of Interest

None declared.

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The following supplementary material accompanies the article:

Caught in broad daylight: topographic constraints on zooplankton depth distributions

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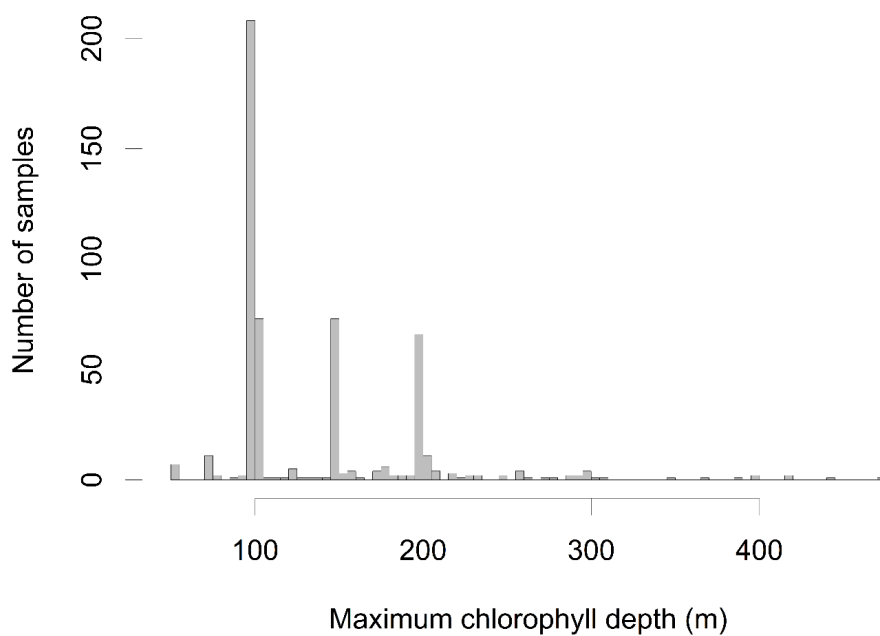
Supplementary figures

Figure S1: Maximum depth down to which chlorophyll *a* has been sampled in our dataset of daytime samples from the Barents Sea. This defines the maximum depth to which light attenuation (K) has been approximated for the stations with zooplankton data.

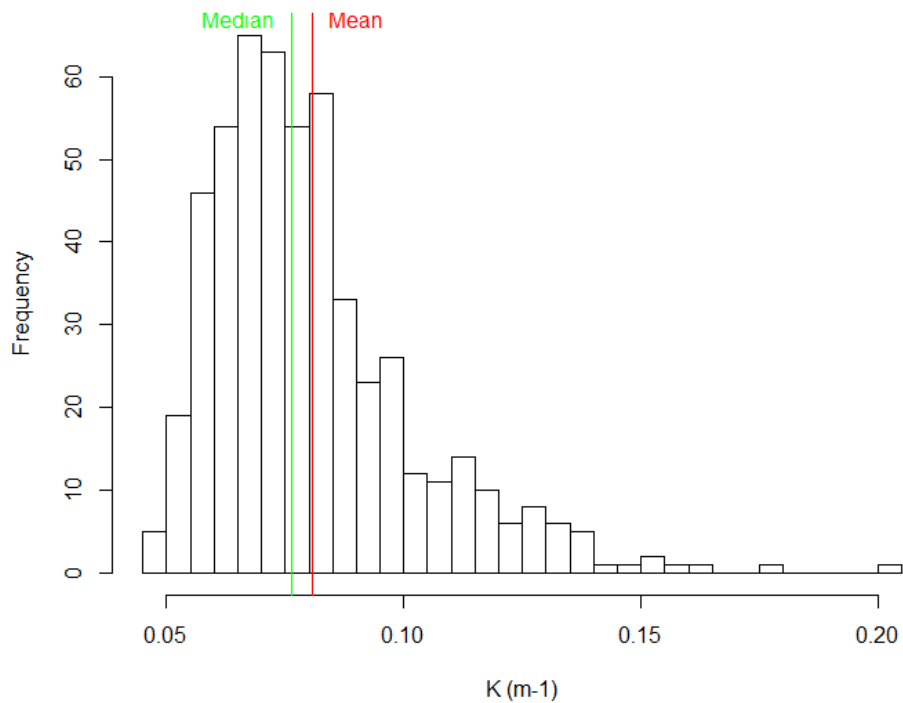


Figure S2: Frequency distribution of the approximated K (m^{-1}) used to examine the relationship between zooplankton weighted mean depth and optical depth (K^{-1}).

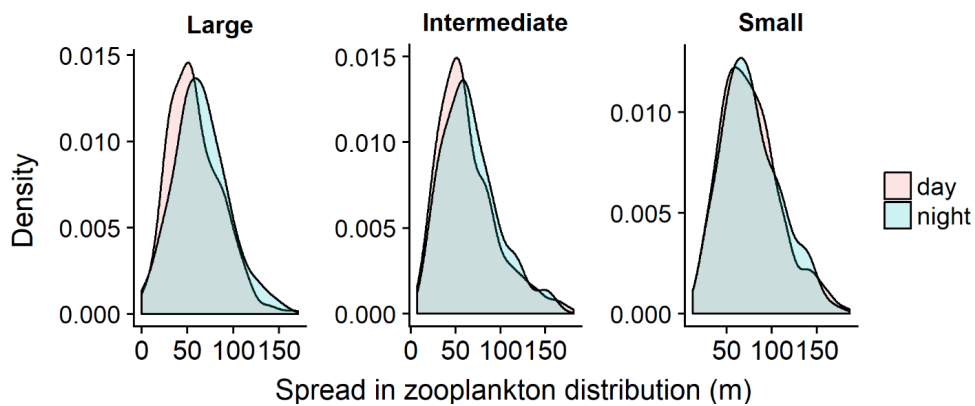


Figure S3: Spread in zooplankton distributions estimated from samples taken during daylight and at night, plotted as a kernel density estimate from all samples (y-axis). Panel titles denotes the large ($>2000 \mu\text{m}$), intermediate ($1000\text{-}2000 \mu\text{m}$) and small ($180\text{-}1000 \mu\text{m}$) size fractions.

Elaboration on fish reaction distance

A theoretical model of a visual feeding fish (Aksnes and Giske 1993; Aksnes and Utne 1997) was used to illustrate how the prey detection distance for a fish changes with prey size and vertical position in the water column. In the model, the distance at which the fish will detect a zooplankton (reaction distance, R) is a function of prey size (image area, A) and contrast against the background (C), visual capabilities of the fish (eye sensitivity, E , and adaptation to specific light levels, k_l), and ambient light (I). Here, we used the approximation for R given in Huse and Fiksen (2010):

$$R = \sqrt{C \times A \times E \times \frac{I}{(k_l + I)}}$$

This is a reasonable approximation for small prey, low light levels or clear water (low turbidity). Parameters used to estimate R (main text Fig. 2c) are given in Table S1. R is the radius of the visual sphere, hence scales to the power of two in terms of how much water a fish can scan for prey (clearance rate, β) per time unit (Eggers 1977):

$$\beta = \pi R^2 V$$

where V is the fish' swimming velocity (m s^{-1}).

Supplementary table

Table S1: Parameters employed for approximating the prey detection distance (R) for a fish (main text Fig. 2c).

Model component	Symbol	Description	Value	Unit
Fish	BL	Body length	0.13	m
	E	Eye sensitivity [†]	$BL^2/9 \times 10^{-7}$	
	k_I	Light satiation (half saturation coefficient for R to I)	1	$\mu\text{mol m}^{-2} \text{s}^{-1}$
Large zooplankton	P_L	Prey length	0.005	m
	P_W	Prey width	$P_L/2$	m
Intermediate zooplankton	P_L	Prey length	0.003	m
	P_W	Prey width	$P_L/2$	m
Small zooplankton	P_L	Prey length	0.001	m
	P_W	Prey width	$P_L/2$	m
Zooplankton	C	Contrast against the background [‡]	0.3	dimensionless
Light	A	Image area [§]	$P_L \times P_W \times 0.75$	m^2
	I_s	Surface irradiance	200	$\mu\text{mol m}^{-2} \text{s}^{-1}$
	K	Diffuse attenuation coefficient	0.08	m^{-1}
Depth, large size fraction	I	Ambient light	$I_s \exp(-K \times WMD)$	$\mu\text{mol m}^{-2} \text{s}^{-1}$
	WMD	Predicted weighted mean depth (Eq. 5/Table 1 in main text)	$WMD = -40.1 + 0.75Z_b + 14.9^{\parallel}$	m
	WMD	Predicted weighted mean depth	$WMD = -1.8 + 0.59Z_b + 14.9^{\parallel}$	m
Depth, intermediate size fraction	WMD	Predicted weighted mean depth	$WMD = -2.7 + 0.40Z_b + 14.9$	m

[†] Here used as a constant for fish length, see (Aksnes and Utne 1997)

[‡] Same for both prey sizes, see Utne-Palm (1999)

[§] Small, elongated prey

^{||} Z_b is bottom depth, here modelled in the range of our data (60–500 m). 14.9 is the effect of mean K (0.08 m^{-1}) on the WMD .

Supplementary references – modelling fish reaction distance

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