# Spatial scales of benthic ecosystems in the sub-Arctic Lofoten-Vesterålen region

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A thesis for the degree of
Philosophiae Doctor (PhD)

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# Preface

This thesis is submitted in fulfillment of the requirements for the degree of Philosophiae Doctor (PhD) at the Faculty of Biosciences and Aquacuture (FBA), Nord University. The presented original research was performed as part of the ARCTOS LoVe MarinEco project, made possible through the support of Statoil.

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Marc J. Silberberger

Bodø, June 8, 2017

# Acknowledgements

Finally, I want to thank my parents, siblings and friends for your unlimited support and all the great times we had over the years. I have decided not to name anyone here, since I would definitely forget someone, and I believe you know that I am very thankful for having you in my life.

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**Paper II**    Silberberger MJ, Renaud PE, Espinasse B, Reiss H. (2016) Spatial and temporal structure of the meroplankton community in a sub-Arctic shelf system. Mar Ecol Prog Ser 555:79-93

**Paper III**    Silberberger MJ, Renaud PE, Kroencke I, Reiss H. Food web structure on the northern European continental shelf. Submitted

# Abstract

Benthic habitats provide a variety of ecosystem services, including food production, carbon sequestration, or nutrient cycling. To protect these services for future generations, benthic communities and the ecological processes related to them need to receive the appropriate attention in an area-based management. Hence, knowledge of relevant spatial scales for such ecological processes and benthic communities is indispensable. Identifying these relevant spatial scales, however, is not trivial, since a combined effect of multiple biotic and abiotic environmental drivers, which vary on multiple spatial scales, are involved in the structuring of benthic ecosystems. Above all, large knowledge gaps exist about spatial scales of benthic communities and ecosystem functioning in remote regions. One such region, the sub-Arctic Lofoten-Vesterålen region is commercially and ecologically particularly valuable, with supra-regional implications for the Norwegian Sea and the Barents Sea ecosystems. Therefore, the overall objective of this dissertation was to study the structure of benthic communities and identify patterns and scales important for the functioning of the benthic ecosystem in the Lofoten-Vesterålen region.

The general spatial patterns identified in this study showed that the benthic community structure strongly reflects the boundary of Atlantic (warm) and Arctic (cold) water masses, which is situated approximately at 800 m depth in the Lofoten-Vesterålen region. On smaller spatial scales, however, epifauna and infauna communities display different spatial patterns. For the infauna, sediment characteristics play an important role in structuring of the community. The epifauna community largely reflects the geomorphological landscapes in the region. Within these landscapes, epifauna shows a spatial structure that can be partly attributed to water mass properties, but the largest part of this structure is not related to any of the observed environmental drivers, such as water mass properties, sediment characteristics or primary production and vertical flux.

Planktonic larval stages play an important role for the spatial distribution of benthic organisms, as they enable larvae to disperse over large distances. In the Lofoten-Vesterålen region, the species diversity of such larval stages is higher than in regions further north. The larval community follows a seasonal development, with three distinct assemblages associated with the seasons: winter, spring, and summer. Species abundance and diversity during winter is low, with higher values in spring, and maximum abundances in summer. Particle-tracking simulations suggest that the source populations of the spring community are situated along the coast south of the sampling region, while the summer community originates primarily on the shelf. During both seasons, spring and summer, larvae are transported primarily northward toward Andfjord and adjacent shelf regions. This spatially restricted dispersal highlights the importance of local populations for the resilience of benthic communities in the Lofoten-Vesterålen region.

Despite distinct benthic communities on different spatial scales, food-web structure suggests high functional similarity between a fjord and an open shelf habitat in the Lofoten-Vesterålen region. Pelagic primary production was identified as the dominant carbon source. Two well separated trophic pathways, benthic and pelagic, transfer this carbon to several top predator fish species. *Gadus morhua* and *Polachius virens* relied on the pelagic pathway, while *Microstomus kitt* had a high reliance on benthic affinity prey. With regard to the number of top predator fish species, the Lofoten-Vesterålen region differs strongly from the North Sea, where *G. morhua* acts as the only top predator fish species. The Lofoten-Vesterålen food web is likely more resilient towards high fishing pressure compared to the North Sea ecosystem.

In summary, benthic ecosystem functioning in the Lofoten-Vesterålen region is tied to the separated Atlantic and Arctic water associated communities. This separation is maintained by the different temperature preference of the adults and by the retention of larval stages on the continental shelf. A considerable habitat connectivity and a preserved food-web structure characterize the local ecosystem on the continental shelf. The work in this thesis illustrates the multiscale nature of benthic ecosystems and identifies environmental variables that can be used to better assess benthic habitats in

new areas with similar environmental settings, which is indispensable knowledge for a successful ecosystem-based management of marine systems.

# 1   Introduction

Marine ecosystems provide a variety of ecosystem services, including food production, carbon sequestration, regulation of climate and atmosphere, nutrient cycling, generation of tourism income, marine biodiversity, and many more (Costanza et al., 2014, Lau, 2013, Millennium Ecosystem Assessment, 2005, Palumbi et al., 2009), of which most were not considered in marine ecosystem management until the late 1970s (Larkin, 1996). Marine ecosystem management was mainly restricted to documenting the catch of individual commercial species and defining quotas on their use to maximize the economic profit. This approach did not account for biological units and led to frequent mismatches between management units and genetic population structure (Reiss et al., 2009). Since the early 1980s, a paradigm change in the scientific community towards the acknowledgement of more complex ecosystem structure and functioning has taken place (Larkin, 1996, Pikitch et al., 2004). Today, the importance of healthy ecosystems has been widely recognized and ecosystem-based management has become the paradigm of environmental decision makers (Christensen et al., 1996, McLeod et al., 2005, Pikitch et al., 2004). Unfortunately, an effective ecosystem-based management is very often difficult, if not impossible, due to the lack of required data and understanding of marine ecosystem functioning as the basis for most ecosystem services (Kaufman et al., 2004, Stelzenmüller et al., 2013). These knowledge gaps concern particularly the no-use components of marine ecosystems, including benthic communities, early life stages, and baseline data for all ecosystem components in pristine ecosystems (*i.e.* without any human impact). In addition, only limited knowledge exists about ecological processes (biogeochemical cycle, energy flow and community dynamics), environmental drivers behind these processes, and the importance of individual faunal components and processes for the resilience of marine ecosystems (Kaufman et al., 2004, Norkko et al., 2013, Stelzenmüller et al., 2013, Woodin et al., 2016). Especially the role of seafloor habitats is often not appropriately accounted for in environmental models and management decisions, due to the limited understanding of these habitats, although the importance of them has been recognized in the light of the biodiversity crisis, climate

change, and marine ecosystem services (Smith et al., 2000, Snelgrove et al., 2014, Woodin et al., 2016).

## 1.1  Benthic communities

The benthos comprises the communities of all organisms living in direct association with the seafloor. Globally, benthic habitats cover more than twice the area of the earth's total land mass and accordingly, benthic communities contribute substantially to marine ecological processes, on local, regional, and global scales. Benthos affects (i) water column processes and trophic transfer by assimilation, decomposition, and burial of particulate and dissolved organic matter, (ii) biogeochemical cycling, (iii) pollutant accumulation and transformation, and (iv) sediment stability and transport (Snelgrove, 1997). Benthic ecosystem functioning and conservation of the previously mentioned services, however, are dependent on the benthic biodiversity (Danovaro et al., 2008, Naeem et al., 1994), which is likely to change in the future (Hale et al., 2011, Sax and Gaines, 2003, Widdicombe and Spicer, 2008).

Accordingly, benthic diversity should be assessed on all relevant spatial scales and management decisions need to be directed to safeguard this diversity and the associated ecosystem services. Unfortunately, this is practically impossible due to the high effort that is needed to collect data on benthic community composition. For example, MAREANO (Marine AREA database for NOrwegian coast and sea areas), an extensive program to map the Norwegian sea floor, executes a sampling density of approximately 2 stations and 10 video transects per 1000 km$^2$ (Buhl-Mortensen et al., 2015) at a total cost for biological, geological, and chemical mapping of approximately 230.000 USD per 1000 km$^2$. This means that approximately 7 km video recordings are used to describe the megafaunal community, approximately 800 m$^2$ sampling area represent epifauna and hyperfauna, and only 1 m$^2$ is used to represent the infauna community of 1000 km$^2$ seafloor. Although these data are invaluable to the scientific community, they fall short of describing the total spatial structure of the benthos, and say very little about rates of critical processes the benthic ecosystem performs.

Furthermore, processing of physical samples is time-consuming, leading to community data of physical samples being not integrated in reporting and accordingly in management decisions (Degnbol et al., 2016). Due to such high costs, slow work flow, and limitation to broad spatial scales, an effective ecosystem-based management is dependent on easily measurable environmental surrogates of benthic community structure.

In contrast to animals in the water column, benthic fauna is rather sedentary and constantly exposed to the prevailing environment. Therefore, the distribution of benthic communities is predominantly reflecting the physical environment at a fixed location. In particular, variation in hydrology, substrate type, turbidity, water currents, or hydrostatic pressure have been identified to be important environmental drivers of benthic community structure (Ellingsen, 2002, Tait and Dipper, 1998).

Even though the physical environment is the main driver of benthic community structure, biological factors like predation, competition for resources, or dispersal processes, can play important roles in determining the spatial distribution of benthic communities (Palmer et al., 1996, Sih et al., 1985, Virnstein, 1977).

**Benthic reproduction and dispersal**

The majority of benthic organisms are sedentary during their adult life and spatial dispersion is largely limited to the early life stages. As a consequence, benthic invertebrates have evolved a variety of life history strategies to enable local and regional dispersal of their offspring and to ensure that they can settle in a suitable habitat (Scheltema, 1986, Thorson, 1950, Vance, 1973). The reproductive strategies fall in one of two main categories: (i) direct development and (ii) indirect development (Fig. 1).

Direct development implies that juveniles are hatching from eggs as functionally similar smaller copies of the adults, without their reproductive capabilities. Such direct development occurs with variable extent of parental care, including the deposition of egg-capsules, release of juveniles directly after hatching, or the carrying of juveniles until
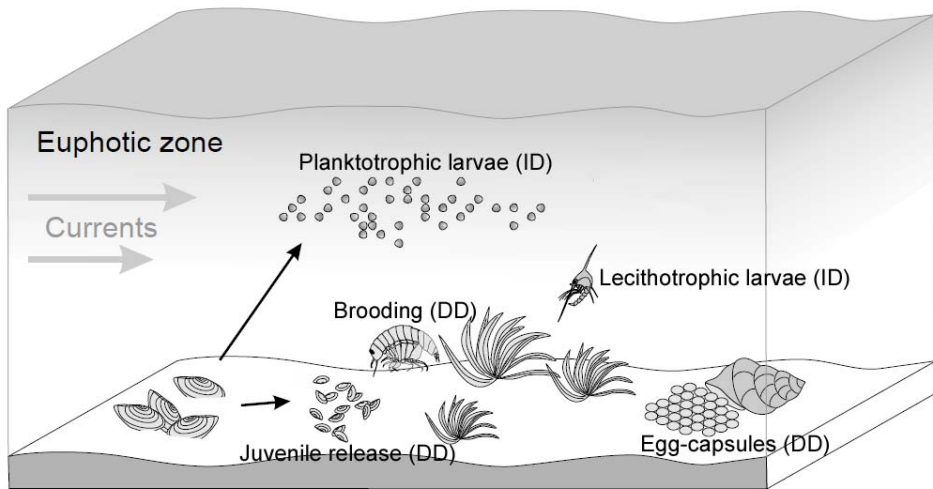
**Figure 1** Reproductive strategies of benthic invertebrates. Generalized modes of direct development (DD) and indirect development (ID) are depicted. Slightly modified after Fetzer (2004)

they reach a certain size (Fetzer, 2004, Levinton, 2009). However, all forms of direct development imply a high investment per offspring, which is generally well invested since the adults ensure that the juveniles encounter a suitable habitat by releasing them into their own habitat. By definition, this strategy results in a comparatively limited dispersal, potentially leading to a low (re-)colonization of newly available habitats, high competition for space and resources between adults and their own offspring, and greater likelihood for speciation due to limited gene exchange with other populations (Jablonski and Lutz, 1983, Levinton, 2009).

Indirect development involves some form of planktonic larval stage that differs considerably in form and function from adults of the same species. These larvae are collectively known as meroplankton and allow for long-distance dispersal and increased connectivity among benthic populations (Levin, 2006, Levinton, 2009). At the same time, such a long dispersal bears the risk that the prevailing currents might transport the larvae away from favorable settlement locations and exposes them to a high predation pressure in the plankton (Pechenik, 1999). Accordingly many benthic species have adapted their spawning to the local hydrology (*e.g.* seasonal spawning, spawning according to the tidal cycle), ensuring the highest chances for the larvae to encounter favorable benthic habitats. Benefits of this reproductive strategy include greater access

to food in the productive upper water column, reduced inbreeding, reduced intra- and interspecific competition, and avoidance of predation by abundant benthic omnivores (Palumbi, 2003, Pechenik, 1999). Meroplankton shows a strong intra- and inter-specific variability in the duration of the planktonic phase (hours to several weeks) according to their feeding mode (lecithotrophic or planktotrophic), water temperature, and food availability (for planktotrophic larvae) (Hadfield and Strathmann, 1996, O'Connor et al., 2007). Lecithotrophy describes a form of nutrition that relies completely on reserves from the yolk. In contrast, planktotrophic larvae rely on food in the water column. In practice, these two extreme feeding-modes are rather seldom and most species possess a combination of both, displaying an often strong intra-specific plasticity depending on food availability (Hadfield and Strathmann, 1996).

The majority of benthic invertebrates reproduce *via* some form of planktonic larvae (Levinton, 2009). However, early studies have shown that the importance of lecithotrophy and direct development increases with latitude and in the deep sea (Mileikovsky, 1971, Thorson, 1950). This traditional view has been put into perspective for coastal and shelf waters at high latitudes after recent studies have reported abundant and diverse meroplankton communities for long periods of the year (Fetzer, 2004, Kuklinski et al., 2013, Stanwell-Smith et al., 1999, Stübner et al., 2016). Until today, the connection between latitude and the benthic life cycle has not been fully resolved.

Only limited information exists on seasonality of meroplankton communities and how the seasonality differs across climate zones. In general, the length of the period with abundant meroplankton decreases strongly with increasing latitude (*e.g.* from 10 months in northern Spain (Weidberg et al., 2013) to 4-5 months in Svalbard (Kuklinski et al., 2013, Stübner et al., 2016)), but distinct knowledge gaps remain on how such seasonal patterns vary on smaller spatial scales within the same climate zone and whether knowledge from coastal regions can be directly transferred to the open continental shelf. Furthermore, consequences of the seasonal succession of the meroplankton community on the dispersal pathways of individual components of the community are largely unknown. This lack of knowledge contrasts the influence of

meroplankton dispersal on the spatial structure of benthic communities and the ecosystem services connected to these communities.

**Spatial patterns of benthic communities**

Population connectivity and spatial patterns of benthic communities are tightly linked to pre-settlement processes, like predation, dispersal pathways, and larval behavior (Thorson, 1950, Todd, 1998). Population connectivity is known to play a fundamental role for population, metapopulation, and community dynamics and structure, as well as for the resilience of benthic ecosystems in response to natural and anthropogenic disturbances, including climate change (Botsford et al., 2001, Hastings and Harrison, 1994, Kirby et al., 2008). However, the larval-dispersal component of benthic population connectivity is poorly understood and accordingly it is seldom appropriately addressed in conservation and resource-management (Cowen et al., 2007).

Although larval supply is the prerequisite for any post-settlement processes, there is strong evidence that settlement (*e.g.* encounter of suitable settlement habitat) and post-settlement processes (*e.g.* benthic predation, food limitation, post-settlement transport, abiotic stress) play a more important role for spatial patterns of benthic communities than pre-settlement processes (Olafsson et al., 1994, Todd, 1998). This implies that benthic communities reflect the local benthic environment and accordingly, knowledge of relevant environmental drivers allows for prediction of spatial patterns of benthic communities. However, due to the complex species-environment relationships within benthic communities (*i.e.* multiple species – multiple environmental drivers), patterns are evident on multiple spatial scales in these communities and therefore relevant environmental drivers need to be identified for each spatial scale (Cottenie, 2005, Hughes et al., 2005, Levin, 1992).

Marine landscapes, sediment characteristics, and water mass properties have frequently been identified as best predictors of benthic community structure (Buhl-Mortensen et al., 2012, Cochrane et al., 2009, McBreen et al., 2008, Reiss et al., 2010),

and accordingly geophysical habitat classifications based on these environmental variables are often used to define spatial management units (Davies et al., 2004, Greene et al., 1999, Roff et al., 2003). Only few studies have compared whether spatial patterns and according environmental drivers are applicable for different components of the benthic community (*e.g.* epifauna vs. infauna) (Buhl-Mortensen et al., 2012, Reiss et al., 2010), and hardly any knowledge exists whether such a correlation is valid across multiple spatial scales of benthic community structure. Particularly the scarcity of studies considering multiple spatial scales within one ecosystem has been pointed out as a main obstacle for a knowledge-based management (Buhl-Mortensen et al., 2012, Tews et al., 2004, Williams et al., 2010).

**Benthic food-web structure**

A food web is an important ecological concept that describes trophic interactions within a community (Hui, 2012, Smith and Smith, 2012), which can be used to study how energy is transferred from primary producers to higher trophic levels and help to understand bioaccumulation or biomagnification of persistent contaminants (Hobson et al., 2002, Muir et al., 1995). Food webs illustrate direct (predator-prey) and indirect (trophic cascades) species interactions, allowing for the identification of keystone species with an important role for the functioning and the resilience of the ecosystem (Smith and Smith, 2012), thereby facilitating an effective management of marine resources. Studies of food-web structure can be used to understand bottom-up (food availability) and top-down (predation pressure) processes in a community (Hui, 2012, Smith and Smith, 2012). These processes are a key to achieving a sustainable management of marine systems, since they need to be addressed differently. In general, top-down processes can be regulated directly in the form of fishing quota. Bottom-up processes are more difficult to address, since they are impacted indirectly by human activities (*e.g.* nutrient runoff from land, climate change).

Direct observations of feeding are almost impossible in aquatic habitats and indirect methods have to be used to identify the diet of an organism. The traditional approach

identifies undigested parts of the prey in feces or stomach contents, but can only provide a snapshot of the diet, does not integrate over a longer time scale (Gaston and Noble, 1985) and is biased towards slowly digestible or even indigestible prey items. Furthermore, diet studies are very time-consuming and accordingly knowledge of trophic interactions in aquatic systems is often limited to some commercially important species at the top of the food chain. Over the last decades, however, the enhanced application of stable isotope analysis and fatty-acid trophic-marker analysis has led to enhanced understanding of trophic interactions and energy flow through aquatic food webs (Iverson, 2009, Iverson et al., 2004, Post, 2002, Vander Zanden and Fetzer, 2007). Both methods can be used to trace carbon flow through the whole food web and to determine the relative importance of different carbon sources (primary producers) for individual organisms (Dalsgaard et al., 2003, Fry and Sherr, 1984). In addition, stable isotope analysis allows to infer the trophic positions of the organisms (Hobson et al., 1995, Post, 2002). This can reveal the detailed structure of a food web and the key species or trophic groups within an ecosystem can be identified (Dunne et al., 2002, Sokołowski et al., 2012).

Marine benthic primary production can be exceptionally high in coastal regions, but is negligible for the vast majority of benthic habitats that do not receive any considerable photosynthetic active radiation (Gattuso et al., 2006, Tait and Dipper, 1998). Therefore, the majority of benthic communities are ultimately dependent on energy export from the productive upper water column. On the other hand, eventually most organic carbon in the oceans will sink to the sea floor in the form of marine snow, fecal pellets, or as larger carcasses. Accordingly, organic material, energy and nutrients accumulate on the sea floor over time and the pelagic zone depends on the benthic communities for the decomposition of detritus, nutrient cycling and as food source for higher trophic levels. Thereby benthic communities sustain high standing stocks of commercially important species. This interdependence of benthic and pelagic communities (Fig. 2), the so called benthic-pelagic coupling, is an essential aspect in the functioning of all marine ecosystems (Graf, 1989, Griffiths et al., 2017).
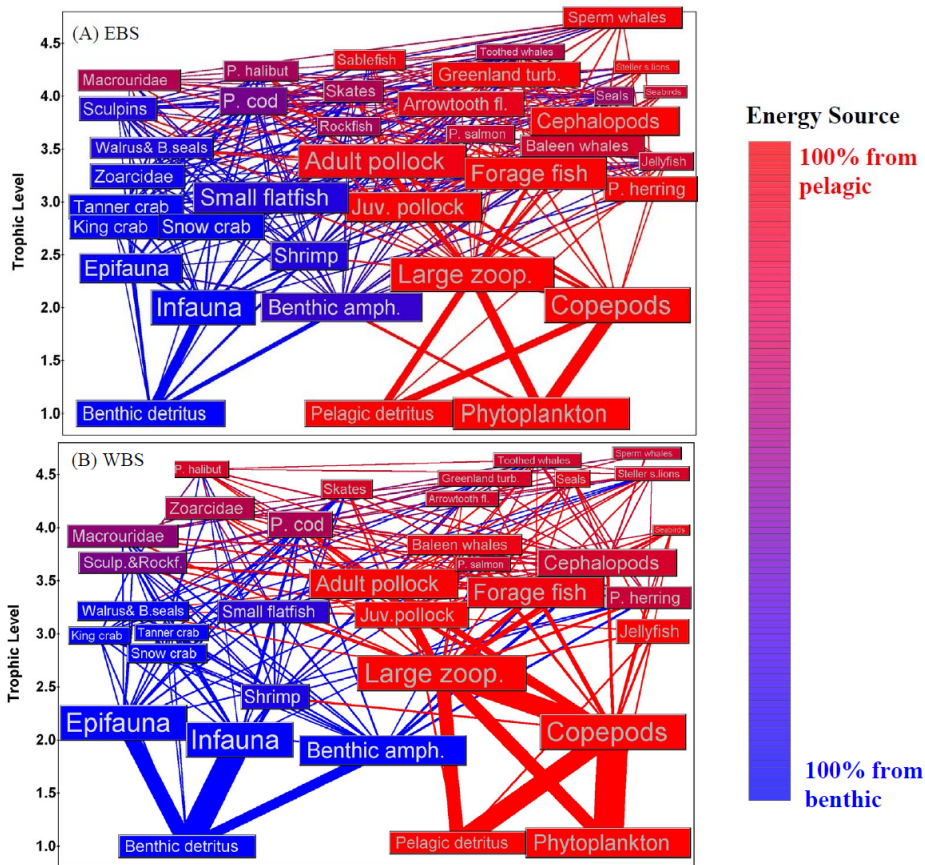
**Figure 2** Examples of marine food webs from (A) the eastern Bering Sea shelf and (B) the western Bering Sea shelf. Box and text size is proportional to log(biomass) of each compartment, while the area of each connection link is proportional to the volume of flow. Color indicate the proportion of energy flow deriving from pelagic (red) and benthic sources (blue). Reproduced from Aydin et al. (2002)

Food-web structure and benthic-pelagic coupling can differ between climate zones, between ecosystems (Aydin et al., 2002), but also on smaller scales between habitats of the same ecosystem (Le Loc'h et al., 2008, McCann et al., 2005). Accordingly, knowledge of spatial variation of food-web structure, benthic-pelagic coupling, and the communities sustained by these food webs are keys to the achievement of sustainable management of marine ecosystems.

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## 1.2 The Lofoten-Vesterålen region

The Lofoten-Vesterålen archipelago in northern Norway is located north of the Arctic Circle. It is separated from the Norwegian mainland by Vestfjorden in the South and Andfjorden in the North (Fig. 3). The region has been identified as commercially and ecologically particularly valuable, with supra-regional implications for the Norwegian Sea and the Barents Sea ecosystems (Olsen and von Quillfeldt, 2003).
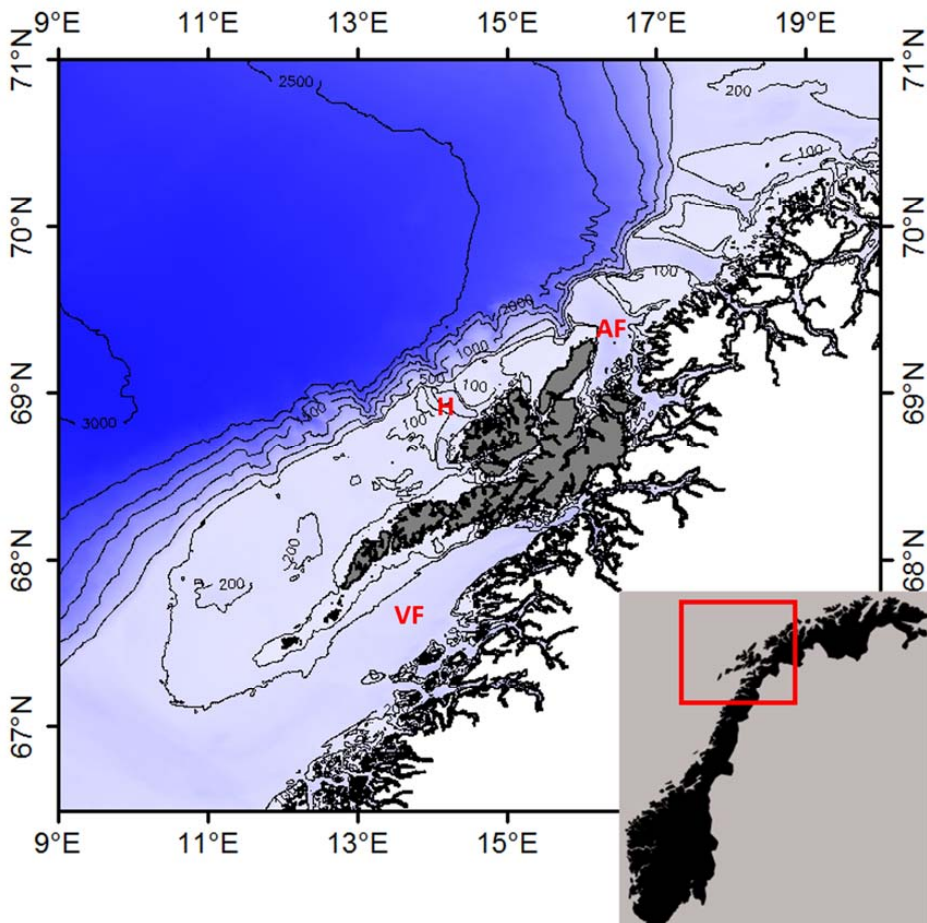


**Figure 3** Map of the Lofoten-Vesterålen region with bathymetry indicated by blue gradient. Bathymetric isobaths drawn at 100 m, 200 m and for every 500 m depth. Lofoten and Vesterålen islands are colored grey. Andfjorden (AF), Vestfjorden (VF), and the focus area Hola (H) are indicated. Inset: location of the study area in Norway

**Physical environment**

The sub-Arctic Lofoten-Vesterålen region is one of the geologically most diverse marine regions in Norway (Thorsnes et al., 2009). The continental shelf is particularly narrow in the Lofoten-Vesterålen region, including the narrowest part of the Norwegian shelf between Andøya and Bleiksdjupet (shelf width < 10 km). The region is characterized by diverse submarine landscapes (Fig. 4). On the shelf, shallow banks with mixed substrate are separated from each other by cross shelf marine valleys with sediments consisting mainly of sand and gravel. From the continental shelf, the seabed slopes down to the Norwegian Sea deep sea plain over a relatively short distance, with the steepest slope offshore the Vesterålen islands (> 5°). The slope is frequently transected by marine canyons (Rise et al., 2013).

Two northward flowing currents characterize the oceanographic conditions on the continental shelf (Gascard et al., 2004, Hansen and Østerhus, 2000). The low salinity
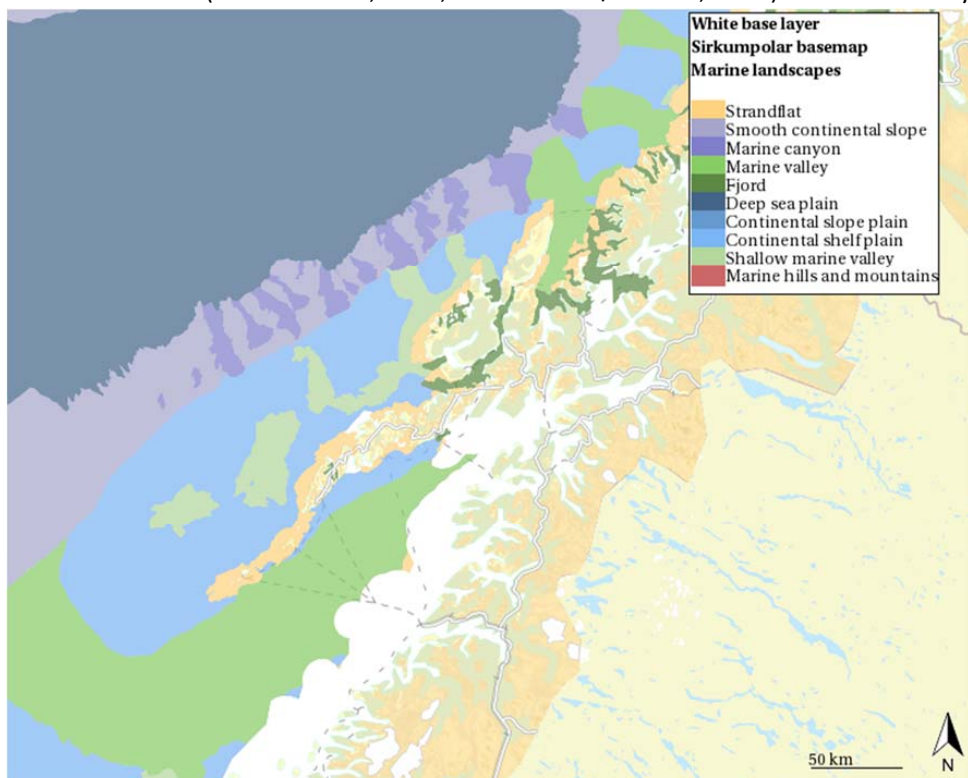


**Figure 4** Marine landscapes in the Lofoten-Vesterålen region. Created from the map service at www.mareano.no

water of the Norwegian coastal current overlies the high salinity water of the Norwegian Atlantic current like a wedge, with the greatest depth of the layer along the coast (Fig. 5). The strength, width, and depth of the Norwegian coastal current varies over a year as it is partly driven by run-off from land. The offshore region is characterized by 3 distinct water masses (Hansen and Østerhus, 2000). The warm and high saline water of the Norwegian Atlantic current (minimum temperatures over 0.5°C, salinity over 35) extends down to approximately 800 m depth. A layer of cold Norwegian Sea Arctic intermediate water (temperature range from -0.5 to 0.5°C; salinity range: 34.87 – 34.9), up to 500 m thick, is situated below the Norwegian Atlantic current, which in turn overlays the Norwegian Sea deep water (temperature below -0.5°C; salinity 34.91).

The warm water masses of the Norwegian Atlantic current are responsible for the Lofoten-Vesterålen region being permanently ice-free, which is atypical for many
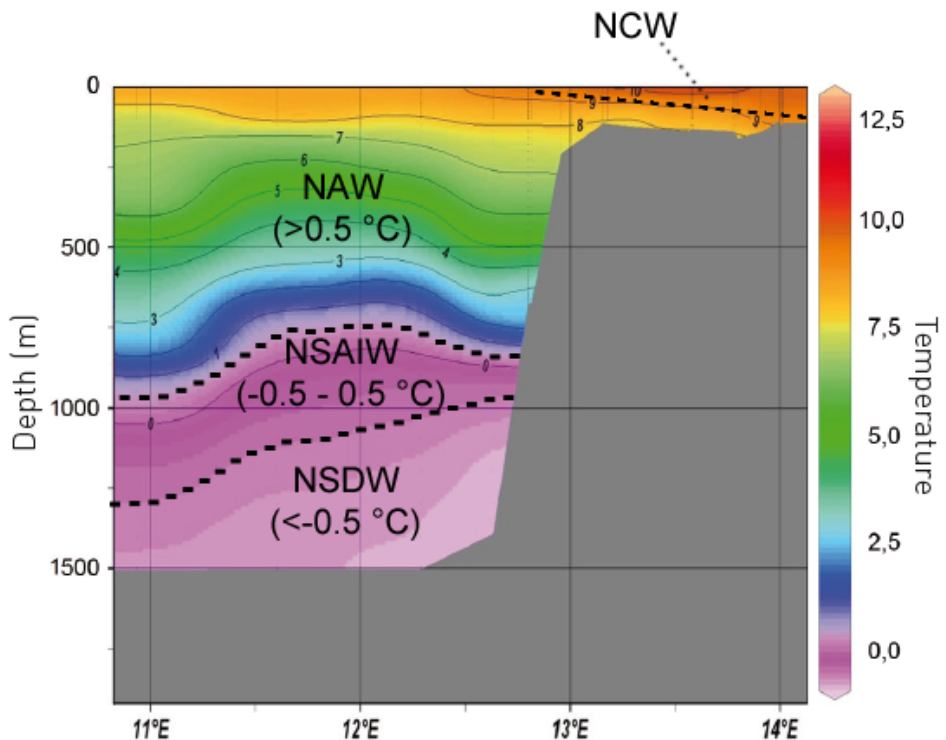


**Figure 5** Example of a temperature-depth profile in the Lofoten-Vesterålen region. Position of the local water masses is indicated. NCW = Norwegian coastal water; NAW = Norwegian Atlantic water; NSAIW = Norwegian Sea Arctic intermediate water; NSDP = Norwegian Sea deep water. Modified after Buhl-Mortensen et al. (2015)

locations at such high latitudes. Nonetheless, due to its location north off the Arctic Circle, the region experiences a pronounced seasonality, especially with regard to day length (polar night vs. midnight sun).

The Hola glacial trough, a shallow marine valley on the continental shelf off Vesterålen was the main focus area for this dissertation (Fig. 3). It has a north-northwest—south-southeast orientation and lies between the two banks Eggagrunnen and Vesterålsgrunnen. It is known for its strong and complex bottom currents, which generally flow towards the coast along Eggagrunnen and towards the shelf break along Vesterålsgrunnen (Fig. 6). During a tidal cycle, short lived local eddies form and disintegrate again within Hola. These complex bottom currents are responsible for four large sandwave fields and favor a high number of coral reefs (>330) (Bøe et al., 2016, Bøe et al., 2009, Frederiksen et al., 1992). Hola has two basins (depth 200 – 270 m), which are separated by a gentle moraine ridge in the center of the trough (10 – 35 m off the bottom). A second moraine ridge crosses Hola in the outer part.
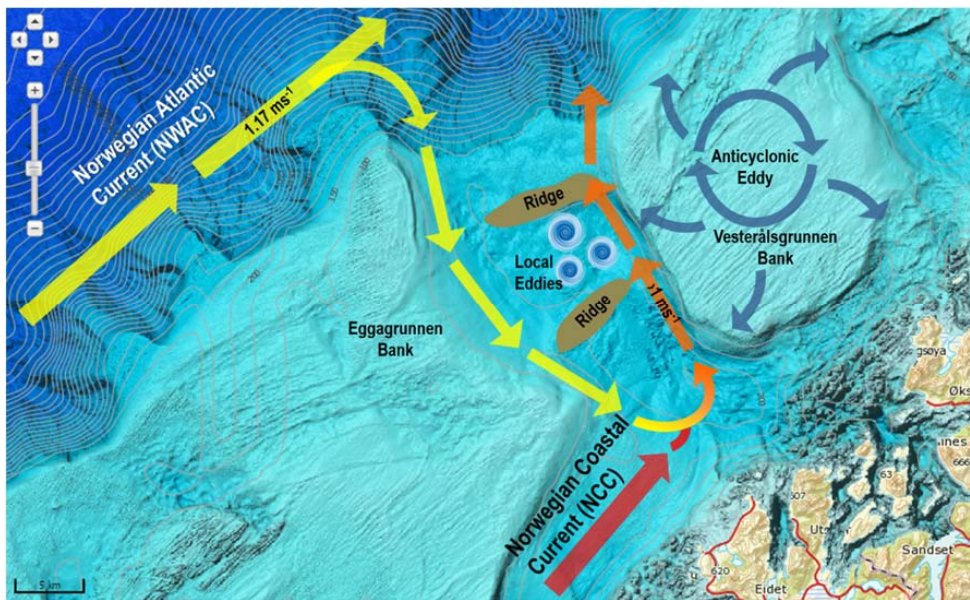


**Figure 6** Conceptual model of the bottom currents in the Hola area based on Bøe et al. (2009). The Norwegian Atlantic current enters the Hola trough flowing towards the coast along the southwestern margin (in yellow). Close to the coast it joins the Norwegian coastal current (in red) and due to the anticyclonic gire on Vesterålsgrunnen a current in a northwestern direction along the slope of Vesterålsbanken is created (in orange). In the central part of the trough a complex group of eddies is created and changes with tidal cycles and wind patterns. Background bathymetric map source: MAREANO. Slightly modified after Jordà Molina (2015)

**The Ecosystem**

The annual pelagic primary production is generally high in the Lofoten-Vesterålen region, with the maximum production associated with the Norwegian Coastal current over the upper continental slope (Norwegian Coastal current production: 80-120 gC m$^{-2}$ yr$^{-1}$ vs. mean Norwegian Sea production: 79 gC m$^{-2}$ y$^{-1}$ (Skjoldal, 2004, Skogen et al., 2007)). Due to strong seasonal variations in sunlight and temperature, primary production follows a distinct seasonal pattern. Typically, the spring bloom begins during April and high production lasts through May and June (Wassmann et al., 2010). The productive season usually ends with a weak autumn bloom in September.

The zooplankton community in the Lofoten-Vesterålen region is commonly dominated by copepods (*Calanus* spp., *Oithona* spp., *Pseudocalanus* spp.), appendicularians (*e.g. Oikopleura* spp.), and hydrozoans (Basedow et al., 2006). As in most parts of the north Atlantic and Arctic Oceans, *Calanus* spp. is the key zooplankton species in the Lofoten-Vesterålen region and plays an important role as food for higher trophic levels (Basedow et al., 2006, Espinasse et al., 2017, Melle et al., 2014). It is believed that *Calanus finmarchicus* is the dominating *Calanus* species in the region, but recent discoveries of general misidentification of *Calanus* species has created some uncertainty about the species identity (Gabrielsen et al., 2012). The *Calanus* life cycle is well adapted to the seasonal pattern of primary production and the succession of nauplii and copepodite stages can be followed throughout May and June (Basedow et al., 2006). Besides studies on *Calanus*, little is known about the ecology of plankton communities in the Lofoten-Vesterålen region. This holds true for planktonic larvae of benthic invertebrates in particular, and it is completely unknown if larvae of benthic invertebrates are a common feature of the local zooplankton community, if they occur at the same time as the peak abundance of holoplankton, and if they might compete with them for resources.

The Lofoten-Vesterålen region is known for its large sea-bird colonies, high numbers of marine mammals, and large fish stocks (Anker-Nilssen, 2006, Føyn et al., 2002). In addition, it is a main spawning ground for several commercial fish species, including the

Northeast Arctic cod and the Norwegian spring spawning herring (Føyn et al., 2002). Relatively little is known about the trophic interactions that sustain such high stocks, and only the diet composition of few species is known. For example, the Norwegian spring spawning herring feeds predominantly on the local zooplankton (Dalpadado et al., 2000), while being itself the major prey item of cod and killer whales (Michalsen et al., 2008, Similä et al., 1996). The Northeast Arctic cod has adapted its spawning such that the hatched larvae encounter the abundant *Calanus* nauplii when they start feeding. The overall food-web structure and the role of benthos as a link to higher trophic levels, however, have not been investigated.

Overall, only limited knowledge about benthic communities and benthic ecosystem functioning in the Lofoten-Vesterålen region exists today. Video recordings have shown that diverse megafaunal communities are associated with different submarine landscapes (Fig. 7) (Buhl-Mortensen et al., 2012, Mortensen et al., 2009). Such a broad-scale video analysis, however, is restricted to large animals at the sediment surface and excludes infauna. Information about the small- and meso-scale distribution of benthic communities and the corresponding environmental drivers in the Lofoten-Vesterålen region is lacking completely. This knowledge is indispensable for knowledge-based management, as it allows to address the multiscale spatial heterogeneity of benthic communities (Williams et al., 2010). Buhl-Mortensen et al. (2012) also studied benthos on a smaller scale for the Tromsøflaket, a shelf area further north of the Lofoten-Vesterålen region. They reported an increased abundance, diversity and biomass for all faunal groups with increased habitat heterogeneity. These results in connection with the diversity of submarine landscapes (Thorsnes et al., 2009), high abundances of cold water coral and sponge reefs, and the high small-scale habitat heterogeneity (Bøe et al., 2009) indicate that the benthic communities might be particularly diverse in the Lofoten-Vesterålen region.
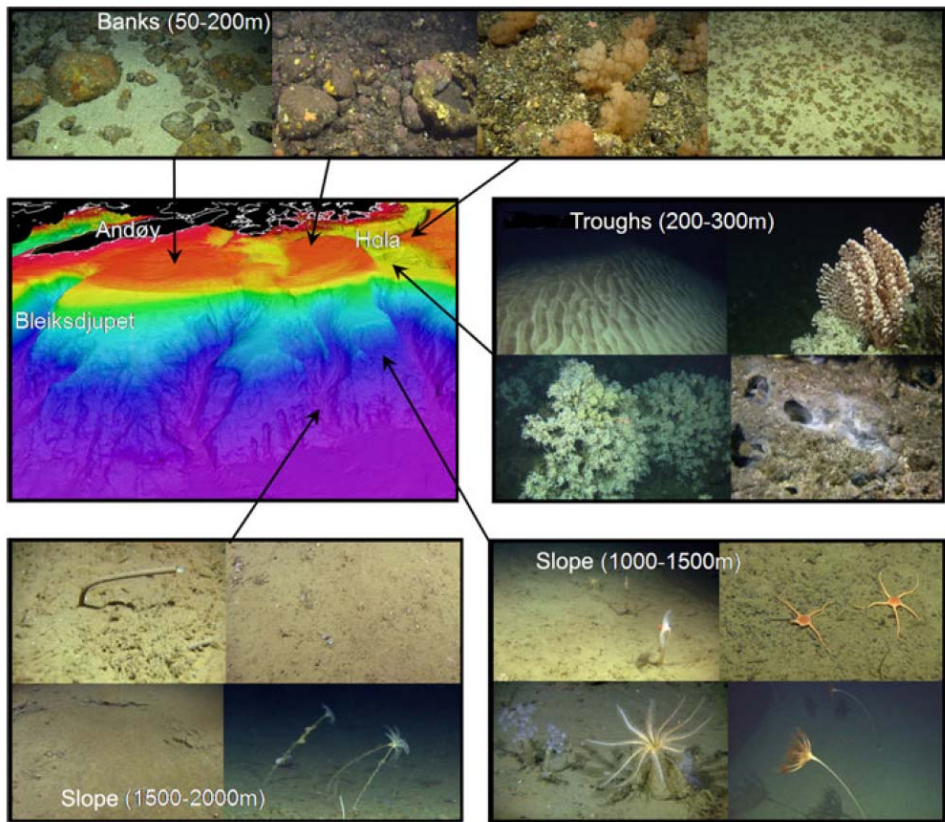
**Figure 7** Example of habitats and landscapes with some dominant megafaunal species in the Lofoten-Vesterålen region. Reproduced from Buhl-Mortensen et al. (2015)

## Human impact and exploitation

While it is among the most pristine marine regions in Europe, the Lofoten-Vesterålen region is also known to feature an overall extremely valuable marine environment (Aanesen et al., 2010). The values directly related to the marine environment include tourism, nutrient cycling, and huge populations of seabirds (Aanesen et al., 2010, Anker-Nilssen, 2006). It is well known as an important nursery habitat and main spawning ground for the Northeast Arctic cod stock (ICES, 2005, Nordeide, 1998) and several other commercially used fish species (Føyn et al., 2002, Misund and Olsen, 2013). The total annual landings of Northeast Arctic cod exceeded 700.000t since 2011 (ICES, 2016) and

accordingly, a regionally important fishing industry depends on the sustainable use of the local resources and ecosystems.

In addition to traditional economic and cultural ecosystem services, the potential of this region for petroleum development has been explored for the past decades, resulting in a controversy within the Norwegian society. Supporters of the opening of the region to petroleum exploitation argue that the probability of an accident is very small, while the opponents support the point of view that the negative outcomes of a possible accident will be disproportionately greater than in other regions, like the North Sea (Boland, 2012). Furthermore, fisheries biologists predicted that petroleum activities will reduce the catch of fisherman and make areas with installations unsuitable spawning grounds for a long time (Boland, 2012). In 2006, the Integrated Management Plan for the Marine Environment of the Barents Sea—Lofoten area was released (Norwegian Ministry of the Environment, 2006, 2011) and the importance of the Lofoten-Vesterålen marine system was furthermore reflected in the high priority of this region within the MAREANO program. Under the management plan, hydrocarbon resources in the Lofoten-Vesterålen region were kept closed, but explorative seismic activity was allowed (Boland, 2012). Eventually, the Norwegian petroleum and oil minister stated clearly that the resources offshore Lofoten and Vesterålen (estimated 1.3 billion barrel oil) must come into play after 2017.

While the previously mentioned human impacts are directly manageable (endogenic pressures), the region is also strongly impacted by exogenic pressures, of which the causes cannot be controlled by spatial management (Elliott, 2011). The most prominent exogenic pressure is the ongoing climate change, to which management can only respond. Temperate species are extending their range northward and establishing themselves in the Lofoten-Vesterålen region, while other species with a southern distribution limit in the Lofoten-Vesterålen region might decline in the future (Poloczanska et al., 2016, Renaud et al., 2015b, Stenevik and Sundby, 2007, Weinert et al., 2016). However, management will only be able to respond to such shifts in species distributions if they can be detected. Therefore, a better understanding of

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environmental drivers of benthic communities and a regular monitoring of the communities is necessary.

# 2 Main objectives

In connection to the establishment of an ecosystem-based management plan for the Lofoten-Vesterålen region, large knowledge gaps regarding spatial scales of benthic community structure, habitat connectivity, and the functioning of the benthic ecosystem became obvious, and therefore the overall objective of this dissertation was to study the structure of benthic communities and identify patterns and scales important for the benthic ecosystem functioning in the Lofoten-Vesterålen region. Specifically, the aims were to:

- **Paper I**: Identify and compare spatial patterns of epi- and infauna communities in the Lofoten-Vesterålen region on multiple spatial scales and to identify characteristic species and environmental drivers that have a high importance in structuring the benthic community, thereby assessing whether epifauna and infauna community are influenced by the same environmental drivers.

- **Paper II**: Describe the spatial and temporal distribution of meroplankton in relation to large-scale benthic habitats and water mass properties and to evaluate the importance of the spatial and temporal variability of environmental variables in structuring the meroplankton community. In addition, possible source and settlement locations of the sampled meroplankton should be identified.

- **Paper III**: Compare sub-Arctic (Lofoten-Vesterålen) and temperate (North Sea) food webs of shelf seas and identify structural differences among the study systems and evaluate whether the food web structure in Lofoten-Vesterålen could favor community shifts similar to shifts already observed in the North Sea.

# 3 General discussion

## 3.1 Main Contributions

One major aim of marine ecology is a better understanding of processes that produce and maintain benthic biodiversity and ecosystem functioning (Cowen et al., 2007, Cowen et al., 2006, Gambi et al., 2014, Levin, 1992, Zeppilli et al., 2016). One central challenge in achieving this goal is the problem of pattern and scale, *i.e.* the interrelation of environmental drivers, biodiversity, and ecological processes and how it varies across a range of spatial, temporal, and organizational scales (Harte et al., 2005, Levin, 1992). In addition to the scientific interest, a particular need for knowledge about the multiple spatial scales in benthic ecosystems exists, since successful ecosystem-based management depends on spatially defined management units (Buhl-Mortensen et al., 2012, Stelzenmüller et al., 2013). Accordingly, the overall objective of this thesis was to study the structure of benthic communities and identify patterns and scales important for the benthic ecosystem functioning in the Lofoten-Vesterålen region. My key findings were:

- **Scales of benthic community structure (paper I):**
  Benthic community structure strongly reflects the boundary of warm-Atlantic and cold-Arctic water masses (≈800 m depth). Besides this dominant broad-scale structure, epifauna and infauna display different spatial patterns. Sediment characteristics play an important role in structuring the infauna community on meso- and fine-scales, while the epifauna community reflects local geomorphological landscapes. Within these landscapes, epifauna shows a spatial structure that can be partly attributed to water mass properties, but the largest part of this structure could not be attributed to any of the included environmental drivers. This difference in epifauna and infauna spatial structure on part of the investigated spatial scale indicates the importance of integration of multi-scale–multi-component approaches in the benthic habitat classification to secure an ecosystem-based management.

- **Spatio-temporal structure of sub-Arctic meroplankton (paper II):**

  The meroplankton community in the Lofoten-Vesterålen region displays a higher species diversity than in regions further north, but does not match the diversity in temperate regions. Three characteristic meroplankton assemblages are associated with the seasons: spring, summer, and winter. Abundance and diversity during winter was low, increased over the spring, and reached maximum abundances for most taxa in summer. Particle-tracking simulations suggest that offshore transport is negligible and virtually all larvae are retained on the continental shelf. Larvae of the spring and summer assemblage originated from the Lofoten-Vesterålen coast and shelf, respectively. Dispersal pathways suggest Andfjord and adjacent shelf regions as primary settlement locations for both seasons. This high local settlement indicates a high importance of the meroplankton community for the resilience of local benthic assemblages.

- **Food web structure on the European shelf (paper III):**

  In general, food-web structure suggests high functional similarity between Hola and a close-by fjord. Phytoplankton was identified as the major primary producer in both habitats, while macroalgae only played a role as carbon source for two echinoid species in the fjord. Both food webs were characterized by well separated benthic and pelagic trophic pathways. The Lofoten-Vesterålen food webs support a high number of top predator fish species, which is a clear difference to food webs in the North Sea, where *Gadus morhua* is the single top predator. This is likely the reason that the southern North Sea experienced a mesopredator release, following a collapse of the local cod stocks. In the Lofoten-Vesterålen region, the top predators *G. morhua* and *Polachius virens* relied on the pelagic pathway, while *Microstomus kitt* had a high reliance on benthic affinity prey. Due to the combined top-down control of several species and the separate benthic and pelagic trophic pathways, the Lofoten-Vesterålen food web is likely more resilient towards high fishing pressure than the North Sea ecosystem.

## 3.2 Environmental drivers of benthic community structure

Ecosystem-based management as the key to conservation of ecosystem services is fundamentally dependent on knowledge of structure and interrelationship of benthic communities and their underlying environmental drivers (Reiss et al., 2010, Stelzenmüller et al., 2013). On broad scales, hydrographic variables, in particular bottom temperature, are common drivers of benthic communities (*e.g.* Cochrane et al., 2009, Reiss et al., 2010). Similarly, the boundary between Atlantic (warm) and Arctic (cold) water masses was identified as the main driver of broad-scale structure in the Lofoten-Vesterålen region across all components of the benthic community (**paper I**, Buhl-Mortensen et al., 2012). As the temperature drops by over 5°C across the permanent pycnocline, there can be little doubt that physiological temperature preferences play an important role in shaping these distinct communities (**paper I**, Hutchins, 1947). In addition to temperature, it is likely that food limitations due to a low vertical flux of organic material across the pycnocline contribute to the clear separation of benthic communities at this broad scale (**paper I**, Smith et al., 2008, Thiel, 1979). A third aspect that strengthens the separation of the communities is the dispersal pathways of meroplankton in the Lofoten-Vesterålen region. Larvae are retained over the shelf (**paper II**, Mileikovsky, 1968) and accordingly larval transport from the Atlantic to the Arctic water masses is low. All three factors, temperature, food limitation, and oceanic flow, individually are sufficient drivers of benthic community structure (Gaylord and Gaines, 2000, Thiel, 1979). In the Lofoten-Vesterålen region, however, all three factors follow the same broad-scale pattern (**papers I** and **II**) and accordingly the separation between the Atlantic-water and Arctic-water community can be considered particularly strong.

Apart from the predominant broad-scale community structure according to the prevailing water masses, structure in epifauna and infauna communities in the Lofoten-Vesterålen region reflect different environmental drivers across all studied spatial scales (**paper I**). Marine landscape elements are an often used approach to define spatial units in an ecosystem-based management approach (Roff et al., 2003, Zajac, 2008) and have

also been introduced for the Lofoten-Vesterålen region based on megafauna (Buhl-Mortensen et al., 2012, Mortensen et al., 2009). **Paper I** suggests that this spatial structure can be extended to the whole epifauna community. For the infauna, however, sediment characteristic and bottom type are drivers of spatial structure, which are varying within individual landscapes and between landscape elements of the same type. Furthermore, bottom types are not limited to a single landscape type. Such a relation between bottom type and infauna community has frequently been observed in studies of infauna communities (e.g. McBreen et al., 2008, Schratzberger et al., 2006, Van Hoey et al., 2004) and can be expected as it reflects the immediate habitat of the infauna community. As epifauna is living on the seafloor, the bottom type comprises also an important aspect of its habitat, but its role in structuring the community seems generally lower than for the infauna (**paper I**, Schratzberger et al., 2006). Due to their life mode, epifauna is exposed to a number of potential drivers that can significantly impact their spatial distribution. Both, selective feeding by visual predators (Russ, 1980) or local bottom currents (Bøe et al., 2009, Frederiksen et al., 1992, Smith et al., 2006), are factors that might explain the meso- and fine-scale spatial structure observed in **paper I**.

## 3.3   Larval dispersal and benthic ecosystem resilience

The planktonic larvae of benthic invertebrates on the Lofoten-Vesterålen shelf could be assigned to 65 distinct taxa (**paper II**), which seems relatively low in comparison to the total number of benthic species known from the region (**paper I**). However, the importance of planktonic larvae in benthic reproduction should be considered import, since the taxonomic resolution of benthic invertebrates was not comparable to the meroplankton (*e.g.* only 5 distinct morphotypes for bivalves) and the collection method with a 200 μm mesh size is insufficient to collect species with small larvae. In contrast, a similar year round study in the sub-Arctic Porsangerfjord with similar taxonomic resolution and a comparable mesh size of 180 μm found a considerable lower number of meroplankton taxa (n = 41) (Michelsen et al., 2017). It remains, however, unclear whether the higher number of meroplankton taxa on the Lofoten-Vesterålen shelf is

reflecting a higher importance of reproduction *via* planktonic larvae in the region or if it reflects a general higher benthic diversity at the source localities.

In general, meroplankton abundance declines drastically towards the center of the Norwegian Sea, although some individuals can be found over 500 miles offshore (Mileikovsky, 1968). According to Thorson (1950), it is questionable whether reproduction *via* planktotrophic larvae could be very successful in a stable deep sea environment, like the cold water benthic community below the pycnocline (**paper I**), where asynchronous year-round reproductions is presumably most common (Rokop, 1974). Planktotrophic larvae in a region with seasonal primary production are dependent on well-timed larval release, so that they encounter food in the water column. Normally, the larval release is triggered by a food impulse to the parental population (Crisp and Spencer, 1958). Other possible triggers are increasing water temperatures or light periods. However, water temperatures are constant in the deep community (**paper I**), light does not penetrate to this depth and the food impulse in the deep Norwegian Sea occurs in late summer or autumn (von Bodungen et al., 1995). Accordingly a mismatch between meroplankton and food availability would be the consequence. However, the most common species in the cold water community (**paper I**), oweniids (infauna), sipunculans (infauna), or the brittle star *Ophiocten gracilis* (epifauna) are generally known to reproduce *via* long lasting planktonic larval stages (Bhaud, 1998, Gage and Tyler, 1981, Young et al., 2002), although direct development is also known from some sipunculans.

On the continental shelf, the meroplankton community follows a clear seasonal succession from a cirriped and ophiuroid dominated spring community to a more abundant and diverse summer community (**paper II**). Such a seasonal succession is known from sub-Arctic fjords, although the period with abundant meroplankton decreases with increasing latitude (Kuklinski et al., 2013, Michelsen et al., 2017, Stübner et al., 2016). Spring communities show strong similarities along the whole European coast from Spain to Svalbard. However, it appears that the benthic species reproducing in the autumn (especially prosobranch gastropods) are limited by shorter seasons at high latitudes (**paper II**, Clarke, 1992, Fetzer and Arntz, 2008, Thorson, 1946).

Benthic populations can be sustained by local recruitment (closed) or by immigrants, commonly in the form of larvae, from other populations (open) (Cowen and Sponaugle, 2009, Pinsky et al., 2012). This habitat connectivity is essential for the resilience of benthic ecosystems and according to theory, the openness of benthic populations varies according to the spacing between suitable habitat patches and the potential dispersal distance of the larvae (Pinsky et al., 2012). Consequently, the broad-scale community structure associated with the Atlantic and Arctic water masses in the Lofoten-Vesterålen region should be considered closed communities, since larval exchange seems to be virtually absent (**paper I** and **II**). On the continental shelf, meroplankton dispersal pathways (**paper II**) indicate a potential for considerable habitat connectivity between habitat patches identified in **paper I**. According to studies of population genetics, however, connectivity estimates based on pelagic larval duration and hydrodynamics are often overestimating habitat connectivity (Hellberg et al., 2002, Weersing and Toonen, 2009). Accordingly, the potential for high habitat connectivity in the Lofoten-Vesterålen region should be interpreted conservatively and not as a general high resilience of the benthic ecosystems. Furthermore, ecosystem resilience is not solely related to recruitment processes, but also to food web robustness, a measure of the capacity of a food web to buffer against the loss of a single species (Dunne et al., 2002, Yen et al., 2016). Thus, benthic ecosystem functioning and its resilience may depend on the structure of the regional food web *i.e.* the connectivity among trophic components and their functional diversity. (Duffy, 2009, Dunne et al., 2002, Hooper et al., 2005, Yen et al., 2016).

## 3.4   Spatial aspects of food-web structure

Food-web structure showed little differences between the open shelf (Hola) and a fjord (Malnesfjord) in the Lofoten-Vesterålen region (**paper III**). The primary carbon source appears to be the pelagic primary production which fuels separate benthic and pelagic trophic pathways, supporting different top predator fish species (**paper III**). According to theory, such a compartmentalized food web is more resistant to

disturbances, as the compartmentalization limits the impacts of a disturbance within a single compartment, minimizing the effect on the other compartments (Krause et al., 2003). At the same time, such food webs are highly interconnected within the compartments, making them more resilient towards extinctions of individual species than food webs without compartments, which have often longer food chains and fewer trophic links (Vermaat et al., 2009, Yen et al., 2016). For example, North Sea food webs do not have such a distinct compartmentalization and a single top-predator (cod) at the end of a slightly elongated food chain (**paper III**). This food-web structure might have promoted a release of mesopredatory fish after the cod fisheries collapsed in the southern North Sea (**paper III**, Daan et al., 2005, Ehrich et al., 2007, van Hal et al., 2010). According to the differences in food-web structure between the Lofoten-Vesterålen region and the North Sea, it is unlikely that the collapse of an individual fish population could have a similar impact on the whole ecosystem in the Lofoten-Vesterålen region.

Hola and Malnesfjord represent contrasting habitats and accordingly it is likely that the general food-web structure, observed in both locations, is typical for the Lofoten-Vesterålen shelf (**paper III**). However, this food-web structure cannot be extended to the food web associated with the Arctic water communities below 800 m depth for various reasons: (i) Differences in community composition (**paper I**, Buhl-Mortensen et al., 2012) are often reflecting functional differences (Danovaro et al., 2008, Naeem et al., 1994), (ii) low overall carbon flux (**paper I**), with sporadically large food falls (*e.g.* fish carcasses) require a functionally different food-web structure at greater depth (Rowe and Pariente, 1992).

Both, the benthic and pelagic trophic pathways, relied on pelagic primary production as main carbon source (**paper III**), even in Malnesfjord, where a higher importance of macroalgal derived carbon could be expected. Within Malnesfjord, only two species were collected that possibly made use of macroalgae (**paper III**). This differs clearly from other high-latitude Norwegian fjords, where macroalgae were shown to contribute considerably as carbon source to the food web (Nilsen et al., 2008, Renaud et al., 2015a). Although **paper III** suggests that no universal high importance of macroalgae for fjord food webs exists, it should be avoided to make any assumptions about the generality of

this observation for fjords in the Lofoten-Vesterålen region, without further investigation of the local fjord ecosystems.

# 4 Conclusion and further perspectives

Spatial patterns of benthic ecosystems and ecosystem functioning are effectively the result of complex interrelations of ecological processes. This complexity can be overwhelming, leaving the question 'Where to begin?' one of the hardest to answer (Schmitz, 2010). It is therefore illusory to fully resolve the interrelation of environmental drivers and the communities on a regional scale completely within the framework of a PhD project, since most studies raise an equal number of questions as they answer. Nonetheless, the work in this thesis depicts a significant progress identifying relevant scales of benthic ecosystems in the Lofoten-Vesterålen region. The original research in this thesis has shown that:

- Prevailing water masses are the main broad-scale driver of benthic community structure, separating the Lofoten-Vesterålen region in two distinct benthic ecosystems associated with Atlantic and Arctic water masses, respectively.
- Spatial patterns on other scales are not universally valid for all components of the benthic community. Epifauna and infauna community correspond with geomorphological landscapes and bottom type, respectively.
- The meroplankton community in the Lofoten-Vesterålen region displays a relatively high species diversity and a distinct seasonal succession.
- Dispersal pathways suggests a high importance of local populations for the resilience of benthic communities in the Lofoten-Vesterålen region.
- Food-web structure suggests high functional similarity between shelf and fjord habitat, with well separated benthic and pelagic trophic pathways.
- The Lofoten-Vesterålen region is likely more resilient towards a high fishing pressure in comparison to the North Sea.

Ultimately, this new knowledge needs to be incorporated in the area-based management of the Lofoten-Vesterålen region. Furthermore it is important that future research builds upon this knowledge and fills knowledge gaps that were revealed in this dissertation. Future research should address:

- Whether the meso- and small-scale spatial structure of the benthic community and its environmental drivers in Hola (**paper I**) can be transferred to other marine valleys and possibly to other landscape elements.

- The broad-scale community structure in **paper I** has demonstrated that the food-web structure on the continental shelf (**paper III**) cannot be extended towards the deep community. Accordingly, future research should identify the food-web structure of the Arctic water associated benthic community.

- As a future goal for an efficient ecosystem-based management of the Lofoten-Vesterålen region, an ecosystem model for the region would allow to explore management policy options, evaluate the placement and impact of marine protected areas, or test ecosystem theories on resilience, stability and regime shifts (Heymans et al., 2016).

- The importance of direct development and lecithotrophic larvae with short planktonic duration in the recruitment of benthos and for the resilience of benthic ecosystems needs to be addressed.

- Furthermore, future studies should focus on larvae and dispersal of the abundant ecosystem engineers in the Lofoten-Vesterålen region, like the cold-water coral *Lophelia pertusa* or sponges, which were not encounter in **paper II** and are poorly studied in general.

- Population genetics should be used to link the identified dispersal pathways in **paper II** to population connectivity in the Lofoten-Vesterålen region.

- In the meroplankton community, the dominating species showed a considerable growth during a long planktonic period (**paper II**, *e.g.* Amphinomidae: > 20,000 ind. m$^{-2}$). From an energetic perspective, the importance of the active carbon transport from the pelagic to the benthic zone, when larvae settle, should be evaluated, since this life stage and their role in ecological processes are generally not integrated in ecosystem models.

Studying all these processes, which are important for the ecosystem functioning and an effective management of the Lofoten-Vesterålen region, is a tedious task and therefore, ecosystem-based management is often regarded as a threat for immediate

economic growth and opposed by parts of the society. However, knowledge about these aspects of ecosystem functioning and the corresponding ability to better estimate the potential impact of human activities on this valuable ecosystem is invaluable to society. I hope the knowledge that was produced in the course of this project will be successfully implemented in the area-based management of the Lofoten-Vesterålen region and that future research will further build on this knowledge.

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Paper I

1    **Running head**: Scales of benthic community structure

2

# 3    Spatial patterns in sub-Arctic benthos: multiscale
# 4    analysis reveals structural differences between epi-
# 5    and infauna

6

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## Abstract

An important goal for ecosystem-based management is to protect marine habitats and their associated fauna, thus, understanding the spatial structure and interrelationships of benthic communities and their underlying environmental drivers is of great importance. The benthic community off the Lofoten-Vesterålen islands was studied on multiple spatial scales, using the MEM (moran's eigenvector maps) framework to identify spatial structure in broad-scale (100s of km), meso-scale (20 km), and small-scale (1.5 km) epifauna and infauna community data sets. A combination of eigenvector-based multivariate analyses and variation partitioning was used to identify characteristic species and environmental drivers that have a high importance in structuring the benthic community. Community structure of both components, epifauna and infauna, strongly reflected the boundary of warm-Atlantic (> 0.5°C) and cold-Arctic water masses (< 0.5°C), which coincides approximately with the 800 m isobath in the Lofoten-Vesterålen region. Apart from this dominant broad-scale structure, epifauna and infauna displayed different spatial patterns. Sediment characteristics played an important role in structuring the infauna community on meso- and fine-scales. The epifauna community was well reflected by the local geomorphological landscapes, and within these landscapes, the epifauna displayed a spatial structure that could for the most part not be attributed to any of the included environmental drivers.

**Keywords:** Lofoten-Vesterålen region, multivariate multiscale spatial analysis, epifauna, infauna, spatial scales, environmental drivers

## Introduction

Marine systems provide a variety of services to humans, including the production of food, carbon sequestration, or the generation of tourism income (de Groot et al., 2012, Palumbi et al., 2009). These services have been degrading globally due to anthropogenic pressures, and safeguarding marine ecosystems and their services for future generations is one of marine ecosystem management's greatest challenges (Costanza et al., 2014). This has been widely acknowledged by political decision makers, and ecosystem-based management has become the central paradigm of marine legislation (e.g. European Commission, 2000, Norwegian Ministry of the Environment, 2006). Management at this scale, however, is often hampered due to lack of knowledge about ecological baselines, ecosystem functioning and relevant spatial scales (Miller et al., 2014, Reiss et al., 2009, Roff and Taylor, 2000). Due to the lack of detailed biological data, the use of geophysical habitat classification has become an important tool to define management units in marine conservation (Davies et al., 2004, Greene et al., 1999, Roff et al., 2003), and marine landscapes, sediment characteristics, and water mass properties have frequently been used to define spatial units in studies of benthic communities (Buhl-Mortensen et al., 2012, Cochrane et al., 2009, McBreen et al., 2008, Reiss et al., 2010).

Benthic organisms inhabit the seafloor and their communities are fundamental for the functioning of most marine systems. They are important for the decomposition of organic material, nutrient cycling, and as a food source for higher trophic levels. In contrast to animals in the water column, benthic fauna is rather sedentary and, therefore, constantly exposed to the local physical environment. This makes benthic communities an interesting subject for environmental studies and an ideal component for ecosystem monitoring (Gray and Elliott, 2009, Pearson and Rosenberg, 1978). However, the study of benthic communities is often difficult and most studies are limited in which part of the community they can capture and which spatial scale they can assess. Comparative sampling of benthic communities is challenging due to the variety of niches in benthic ecosystems (above and below the surface). Thus, a multitude of sampling gears is necessary to adequately sample all components of the benthic community. Furthermore, benthic communities are known to exhibit patterns on multiple spatial scales and no single natural spatial scale should be used to study or monitor them (Cottenie, 2005, Hughes et al., 2005, Levin, 1992).

The sub-Arctic Lofoten-Vesterålen region, the southern limit of the Lofoten-Barents Sea ecosystem, is among the most pristine marine regions in Europe. It has a very diverse submarine landscape (Thorsnes et al., 2009), which forms diverse habitats for the

associated benthic megafauna communities, including high numbers of cold-water coral reefs and other vulnerable habitats (Buhl-Mortensen et al., 2012, Mortensen et al., 2009, Norwegian Ministry of the Environment, 2011). The area is the spawning ground of several economically and ecologically important fish stocks and sustains regionally important fisheries (Føyn et al., 2002, Misund and Olsen, 2013). Beside fisheries, human value creation from this marine system is mainly limited to tourism, but the exploitation of this area will certainly increase over the next years particularly if the area is opened to hydrocarbon exploitation as expected (Hjermann et al., 2007, Misund and Olsen, 2013). In addition to increased direct human impact, it is predicted that sub-Arctic regions will be impacted particularly strongly by ongoing climate change (Burrows et al., 2011, Doney et al., 2012). In this context, species with a more southern distribution will extend their range to the north and enter the Lofoten-Vesterålen region, while species living at their southern distribution limit will disappear (Renaud et al., 2015, Weinert et al., 2016). Despite the importance of the Lofoten-Vesterålen region in terms of fisheries, impending hydrocarbon development, and potential climate change impacts, there is limited knowledge about the spatial distribution of benthic communities here today. Recent video recordings have shown that diverse megafaunal communities primarily reflect local water mass distribution, and distinct megafaunal communities are associated with different submarine landscapes (Buhl-Mortensen et al., 2012, Mortensen et al., 2009). Particularly the shelf, with an alternating pattern of shallow banks and deep troughs, encompasses a wide range of habitats (Mortensen et al., 2009). This large-scale video analysis is restricted to large animals at the sediment surface and excludes infauna and smaller epifauna. In addition, information about the fine- and meso-scale distribution of benthic communities in the Lofoten-Vesterålen region is lacking completely. On a shelf area north of the Lofoten-Vesterålen region, abundance, diversity and biomass for all faunal groups increased with increasing habitat heterogeneity (Buhl-Mortensen et al., 2012) and accordingly particularly diverse benthic communities can be expected in the Lofoten-Vesterålen region.

In this study, we present the first comparative inventory of epifaunal and infaunal benthic communities in the Lofoten-Vesterålen region, covering habitats from shallow banks to the deep sea. The main objectives were to (i) identify and compare the spatial patterns of benthic communities (epifauna and infauna) in the Lofoten-Vesterålen region on three different spatial scales and (ii) identify characteristic species and environmental drivers that have a high importance in structuring the benthic community.

## Methods

### Study area

The Lofoten-Vesterålen region, an area of approximately 26,000 km$^2$ off the counties Nordland and Troms in northern Norway, comprised our study domain (Fig. 1). The region is influenced by four main water masses with a typical vertical distribution (Buhl-Mortensen et al., 2012, Hansen and Østerhus, 2000): (1) The low-saline Norwegian coastal water of the northward flowing Norwegian coastal current (coastal surface waters, maximum depth decreases with distance from coast), (2) the warm and saline Norwegian Atlantic water of the northward flowing Norwegian Atlantic current (maximum depth: 500-600 m), (3) the Norwegian Sea Arctic intermediate water (-0.5 to 0.5°C; maximum depth: ≈1300 m), and (4) the Norwegian Sea deep water (-1.1 to -0.5°C). The topography of the region is particularly diverse (Buhl-Mortensen et al., 2012, Norwegian Ministry of the Environment, 2011). On the shelf, shallow banks (depth <100 m) are separated by frequent cross shelf trenches (depth 200-500 m). Similarly, the continental slope, which is sloping down to the deep sea plain of the Norwegian Sea (depth ≈3000 m), is frequently cut through by deep marine canyons.

### Sampling and sample processing

Infauna and epifauna samples were collected at various spatial scales with van Veen grabs (64 stations) and beam trawls (56 stations), respectively. Broad-scale sampling (Fig. 2a) covered the whole study area and included samples from all marine landscapes in the study area. These samples were collected as part of the MAREANO program (Marine AREA database for NOrwegian coast and sea areas) from 2007-2009 (Ringvold et al., 2015). More detailed meso-scale (1-10s km) and small-scale (100s m) sampling in 2014 and 2015 focused on Hola (Fig. 2b), a shallow marine valley off the coast of Vesterålen with a diverse seabed structure and complex bottom currents (Bøe et al., 2009). It is separated by a 10-35 m high moraine ridge into an inner and an outer part. Samples were collected along a cross-shelf transect through Hola and from an intensively sampled box (1 × 1 nm) in the center of Hola. The box was located in the outer part of Hola, with a part of the box extending on the moraine ridge.

Infauna samples (n=134) were collected at 64 stations (1 – 5 replicates per station) with van Veen grabs of three sizes (0.1 m$^2$, 0.2 m$^2$, 0.25 m$^2$). Infaunal samples were washed over a 1 mm sieve prior to fixation with 4% formaldehyde and the fauna was identified to the lowest possible taxonomic level and standardized to 1 m$^2$.

158     Epifauna samples were collected at 56 stations without replication. Sampling was
159 conducted with beam trawls (2 m opening, bottom chain, 20 mm mesh, 4 mm cod end).
160 The towing time was 5 min at a speed of 1 knot, after the beam trawl made contact with
161 the sea bed. Epifaunal samples were washed over a 5 mm sieve prior to fixation with 4%
162 formaldehyde, and later identified to the lowest possible taxonomic level and
163 standardized to 100 m$^2$.
164
165     Taxon names follow the World Register of Marine Species (WoRMS Editorial Board,
166 2017).
167

## Data preparation

### Community data

172     Colonial organisms were excluded from infauna data prior to the analysis. In addition
173 to colonial organisms, pelagic fish and infauna were excluded from epifauna data.
174 Infauna and epifauna data were analyzed separately for the sampled spatial scales.
175 Infauna data were split in three sets: broad scale (MAREANO samples), meso scale (Hola
176 transect), and fine scale (Hola box). Epifauna data were only split in two sets, due to the
177 lower number of samples from Hola: broad scale (MAREANO samples) and meso scale
178 (Hola transect + box). A Hellinger transformation was performed on all five faunal
179 datasets to allow for the use of Euclidean-based ordination methods (PCA and RDA)
180 (Legendre and Gallagher, 2001).

### Environmental data

184     We included four sets of environmental variables in the analysis of the community
185 data sets: (i) water mass properties, including monthly average bottom temperature and
186 salinity, (ii) productivity, including the annual pelagic primary production and the vertical
187 flux to the sediment, (iii) sediment type according to the classification of the Geological
188 Survey of Norway, (iv) marine landscapes according to the categorization of MAREANO
189 (Holte et al., 2015). Water mass properties and productivity were extracted from the
190 numerical ocean model SINMOD ([www.sintef.no/SINMOD](www.sintef.no/SINMOD)).
191     SINMOD is a nested, coupled 3D hydrodynamic-ecological-biogeochemical model
192 system that is well established for oceanographic and ecosystem studies along the
193 Norwegian coast and in the Barents Sea (See Slagstad and McClimans (2005) and
194 Wassmann et al. (2006) for more detailed model descriptions). The ecosystem module
195 is formulated in an Eulerian framework and includes state variables for nutrients ($NO_3$,
196 $NH_4$, Si), the bacterial loop, heterotrophic nanoflagellates, diatoms and flagellates,

ciliates and mesozooplankton as well as detritus. The hydrodynamical model provides temperature and salinity fields in addition to water currents. SINMOD is established for the Norwegian coast with a spatial resolution of 800 m horizontally. Vertically a total of 36 layers are used with thickness from 3 m in the surface and gradually increasing in thickness towards the bottom. Open boundary conditions are obtained by running the SINMOD in several steps starting with a 20 km resolution grid covering the Nordic and Arctic seas and then nest to 4 km and 800 m (*e.g.* Broch et al., 2013). The model uses tidal forcing (8 components), freshwater run-off and atmospheric forcing (Era-Interim). The model gives a statistically good representation of the currents and hydrographic conditions in the Lofoten region (Anon, 2011).

For the meso- and fine-scale data analysis, marine landscapes were not included, since all sampling was conducted in the same shallow marine valley. In addition, we did not include water mass properties and productivity in the fine-scale analysis, since the spatial variation was too small to be considered meaningful considering the grid size of the model.

Gravel-, sand-, and mud-content were added to the meso-scale sediment characteristics for the infauna analysis.

**Spatial predictor MEMs (Moran eigenvector maps)**

We used the MEM framework after Dray et al. (2006) to detect and describe spatial structure in this study. The strength of MEMs lies in their capability of presenting complex spatial structures (Griffith and Peres-Neto, 2006), and they are among the most powerful tools to identify spatial structure in communities (Peres-Neto and Legendre, 2010). The MEM framework has two main assets: (i) for a sampling design with $n$ samples, a set of $n$-1 linearly independent spatial variables is produced, which can be used individually or combined in spatial modelling. (ii) MEMs are extracted in order of decreasing eigenvalues. Therefore, the first extracted MEMs are associated with high positive eigenvalues and high positive autocorrelation and can be used to describe global structures (Dray et al., 2006). Later extracted MEMs are associated with negative eigenvalues and negative autocorrelation and can be used to describe local structures.

One important aspect for the construction of MEMs is the selection of a suitable neighbor matrix, *i.e.* defining suitable criteria whether sampling locations are considered to be spatial neighbors (Dray et al., 2006). Therefore, we explored five neighbor matrices: (i) Delaunay triangulation (ii) Gabriel graph, (iii) relative neighborhood graph, (iv) minimum spanning tree, and (v) distance criterion with tested maximum distances

236   between the longest edge of the minimum spanning tree and the range of a multivariate
237   variogram (Dray et al., 2006, Legendre and Legendre, 2012). We used function f1 to
238   create different edge weighting matrices for each neighbor matrix.
239

240   $$f_1 = 1 - \left(\frac{d_{ij}}{\max(d_{ij})}\right)^{\alpha}$$

241

242   With $d_{ij}$ being the distance between sampling locations $i$ and $j$ and $\max(d_{ij})$ being the
243   maximum distance between sampling locations connected in the according neighbor
244   matrix. We selected 19 different values for α to explore linear (α = 1), concave down (2
245   ≤ α ≤ 10, α ∈ **Z**), and concave-up (α = 1 / β; 2 ≤ β ≤ 10, β ∈ **Z**) weighting. We constructed
246   sets of MEMs for each combination of neighbor matrix and spatial weighing matrix and
247   selected the best combination according to the lowest corrected Akaike information
248   criterion (AIC$_C$) (Dray et al., 2006). The characteristics of the selected combinations are
249   shown in Table 1 and all respective MEMs are shown in Supplement 1.
250

251   **Statistical analysis**
252

253   Each community dataset was subject of an individual analysis, comprising three parts:
254

255   **Main patterns in the community data**
256

257   Principal component analysis (PCA) was used to identify general (spatial) patterns in
258   the Hellinger transformed community data. We used Pearson's product-moment
259   correlation to test for correlation between individual PCA axes and both species number
260   and total abundance.
261

262   We created a scalogram for each of the main axes by projecting the sites scores onto
263   the spatial predictor MEMs (Dray et al., 2012). This decomposes the variance of the axis
264   on the individual MEMs, ranked from the broadest to the finest. A permutation test
265   (9999 repetitions) was used to test if the observed $R^2$ of each MEM was significantly
266   larger than values obtained in the absence of a spatial pattern, allowing us to identify
267   the relevant spatial scales underlying the structure depicted by the individual axes.
268

269   **Variation partitioning**
270

271   We partitioned the variation in the community data on all sets of environmental
272   variables and one set of spatial predictor MEMs with a significant positive spatial
273   autocorrelation, using adjusted $R^2$ in redundancy analysis (RDA). There were two

274 reasons for restriction to MEMs with positive spatial autocorrelation: (i) no considerable
275 spatial structure associated with any MEMs with negative eigenvalues was observed in
276 the PCAs. (ii) Variation partitioning on $n$ sets of predictor variables leads to $n^2-1$ non-
277 overlapping components (Økland, 2003), making calculations and interpretation very
278 tedious for $n > 5$. To avoid artificial inflation of the explained variation, we performed a
279 forward selection procedure for each set of predictor variables, using redundancy
280 analysis (RDA) and a double stop criterion (Blanchet et al., 2008).
281
282 **Constrained and residual patterns in the community**
283
284    We used RDA and partial residual analysis (PRA) to identify variation in the community
285 data that was related (RDA) or unrelated (PRA) to selected sets of environmental
286 variables. The selection of the sets was based on the results of the variation partitioning.
287 Scalograms were produced for the RDA and PRA axis to identify relevant spatial scales.
288
289    All statistical analysis were run in R version 3.3.2 (R Core Team, 2016), making use of
290 the adespatial (Dray et al., 2017), ade4 (Dray and Dufour, 2007), and vegan packages
291 (Oksanen et al., 2016).
292

## Results

### Physical environment

Temperature and salinity reflected the individual water masses at the sampling locations with a permanent pycnocline between 500 and 800 m depth. Bottom temperatures never dropped below 6°C above the pycnocline and was never as warm as 1°C below it. The salinity showed little variation below the pycnocline (range: 34.92-34.99), with virtually no variation throughout the season. Within and above the pycnocline, salinity varied throughout the season, exceeding 35 for some time of the year. On the continental shelf, an increasing number of months with low salinity (<34.9) were apparent with decreasing distance to shore and decreasing depth.

Annual pelagic primary production in the study area ranged from 117 to 178 g C $m^{-2}$ $yr^{-1}$. Highest production occurred along the shelf break over the continental slope. However, this difference in production had little influence on the amount of carbon reaching the seafloor, which mainly reflects bottom depth at the sampling location (Fig. 3).

### Faunal communities

Infauna and epifauna were assigned to a total of 795 and 721 taxa, respectively. After removal of not representatively sampled taxa, we registered 753 infauna taxa (533 identified to species level) and 496 epifauna taxa (346 identified to species level) in the analysis (Supplement 2).

### Broad scale

For both epifauna and infauna, the first axis of the PCA reflected a separation of cold water communities (below the pycnocline, positive (black) values) and warm water communities (within and above the pycnocline, negative (white) values) (Fig. 4). For the epifauna, the axis showed a significant negative correlation with species number, while we observed a significant positive correlation with total abundance for the infauna (Table 2). In both cases, the community below the pycnocline was numerically dominated by few individual taxa. In 10 out of 18 epifauna samples below the pycnocline, the most abundant taxon in each sample accounted for over 50% of all individuals (range: 18.7-76.9%). Within and above the pycnocline, only 1 out of 28 samples had a single taxon accounting for 50% of the individuals and 21 of the samples had the most abundant taxon accounting for less than 30%. Typical dominating taxa

332   below the pycnocline were *Ophiocten gracilis*, *Thelepus cincinnatus*, or Actiniaria. Within
333   and above the pycnocline, *Munida sarsi*, *Ophiactis abyssicola*, and *Nothria hyperborea*
334   were among the species that frequently dominated individual samples. For the infauna,
335   17 out of 32 samples from cold waters were dominated (>40% of all individuals) by a
336   single taxon (range: 17.1-82.7%), typically *Galathowenia fragilis*, *Thyasira equalis*, or
337   sipunculans. Within and above the pycnocline, the most abundant taxon accounted for
338   less than 20% of the total number of individuals (range: 5.7-45.7%) in 52 out of 65
339   samples. The polychaetes *Aonides paucibranchiata*, *Spiophanes wigleyi*, and *Pista bansei*
340   were frequently among the most abundant taxa in these samples.
341
342      The according scalograms showed that the first PCA axis was mainly structured on the
343   broadest scales for infauna (significant MEMs in order of decreasing $R^2$: 4, 5, 6, 1) and
344   epifauna (significant MEMs: 4, 1) (compare with Supplement 1 for spatial structure
345   behind the individual MEMs). For the infauna, some underlying spatial structure was
346   indicated at finer scales, corresponding to MEMs 18, 10, and 16.
347
348      The second PCA axis differed between epifauna and infauna. For the epifauna, it
349   described a week spatial structure corresponding to MEMs 1, 2, 12, and 17, separating
350   the area outside the Lofoten and Vesterålen islands from the area north of it and from
351   the deepest locations (> 1500 m depth). This axis was largely driven by the absence of
352   Actiniaria outside the Lofoten and Vesterålen islands. For the infauna, the second axis
353   displayed a more complex broad-scale pattern (MEMs 1-7), clearly separating a few
354   locations with high abundances of the sipunculid *Onchnesoma steenstrupii steenstrupii*
355   in the marine valleys in the north of the study region from the rest of the study area.
356   The samples from these regions changed gradually along a narrow range of the second
357   PCA axis, with increasing importance of several of the most common polychaete species
358   in the study region (e.g. *Galathowenia fragilis*, *Aonides paucibranchiata*, *Spiophanes
359   wigleyi*, *Pista bansei*, *Glycera capitata*).
360
361   **Meso scale**
362
363      The main structure in the epifauna community in Hola was associated with the
364   broadest spatial scales (PCA axis 1 with MEM 1; PCA axis 2 with MEM 2) (Fig. 5 a). Axis 1
365   separated the epifauna into inshore and offshore communities, and interestingly
366   separating the communities within the fine-scale sampling box. The community in the
367   outer part was best characterized by the presence of the polychaete *Nothria
368   hyperborea*, which was rare in the inner part. PCA axis 2 separated the samples from the
369   fine-scale box from the samples of the meso-scale sampling. The brachiopod

*Macandrevia cranium* was absent from all but one epifauna sample in the box, but was common in the other parts of Hola.

PCA axis 1 for the infauna community was also associated with a broad spatial scale (MEM 1). However, it described a somewhat different pattern, separating the samples from the three deepest stations (over 230 m depth) in the inner part of Hola from the locations shallower than 230 m. The second axis described a more complex spatial pattern on a smaller scale, associated with MEMs 4, 3, and 5 (Fig. 5b).

**Fine scale**

Within the fine-scale sampling box, the infauna was distinct between an eastern and a western part (PCA axis 1; MEM 2) (Fig. 5c). The samples in the eastern part typically contained *Heteromastus filiformis* and *Macandrevia cranium*, while the western part was characterized by high abundances of *Aonides paucibranchiata*, *Exogone verugera*, and Edwardsiidae. The second axis mainly identified samples with high abundances of the polychaete genus *Polycirrus* in the western part of the box and showed no particular spatial structure associated with any MEM.

The importance of *M. cranium* in the eastern part seems to contradict the epifauna results, where this species was only found in one sample within the box. Due to the lower sample number, however, the epifauna data did not cover the box as good as the infauna data and especially the eastern part of the box is not well represented in the epifauna. However, the epifauna sample containing *M. cranium* was the most eastern sample and therefore epifauna and infauna results reflect a similar pattern with regard to this species.

**Environmental drivers**

Forward selection of spatial and environmental variables showed that all sets of explanatory variables explained significant variation on all spatial scales for infauna and on the broad-scale epifauna (Supplement 3). For the meso-scale epifauna data, only water-mass properties and the spatial predictors explained significant variation.

Subsequent variation-partitioning showed that water-mass properties and marine landscapes were the best predictors for the epifauna community on the broad scale (Fig. 6). Water mass properties accounted for 65% and marine landscapes for 56% of the total variation explained (TVE) by all environmental and spatial predictors (adj.$R^2$ = 0.28). The fraction of TVE accounted for exclusively by water mass properties (24%) and exclusively

409    by marine landscapes (13%) were not related to any spatial structure. The variation
410    explained by both water mass properties and marine landscapes was accounted for by
411    the spatial predictors. On the meso-scale, however, almost the complete TVE (adj.$R^2$ =
412    0.23) was explained by spatial variables (94%). A part of this structure could be explained
413    by the hydrography, but the majority of this structure was not explained by any
414    environmental variables in this study.
415
416    For the infauna, the variation partitioning revealed different results. The TVE (adj.$R^2$ =
417    0.55) was particularly large on the broad-scale and almost completely accounted for by
418    the spatial predictors (94%). Water mass properties were the set of environmental
419    variables that accounted for the largest part of the variation in the broad-scale infauna
420    data (70% of the TVE). The role of sediment characteristics in structuring the infauna
421    increased from the broad-scale towards meso- and fine-scales (Fig. 6). As for the broad-
422    scale, almost the complete TVE was accounted for by the spatial predictors for meso-
423    scale (92%) and fine-scale infauna (88%).
424

## Environmentally structured community

### Broad-scale epifauna – marine landscapes

429    An RDA of the broad-scale epifauna data with marine landscapes as predictors,
430    produced axis 1 and 2 (Fig. 7), resembling the first two axis of the PCA. The first axis
431    (projecting 50% of the total inertia of the RDA) separated the shelf landscapes
432    (continental shelf plain, shallow marine valley, marine valley) from the deeper
433    landscapes (smooth continental slope, marine canyon, deep sea plain). Generally this
434    reflected the first PCA axis very well, but the shallowest stations on the continental slope
435    (above the pycnocline) are placed differently in the two ordinations. The second axis
436    (projecting 19% of the total inertia of the RDA) separated the deep sea plain and the
437    marine valleys from the other four landscapes. The species loading showed that mainly
438    the same species were responsible for shaping PCA and RDA axis.
439

### Broad-scale infauna – structure not explained by water mass properties

442    An RDA of the broad-scale infauna data with water mass properties as predictor
443    produced virtually the same first two axes as the PCA (RDA not shown). Excluding this
444    structure from the total explained variation, a PRA (Fig. 7) identified some structure on
445    finer spatial scales (axis 1: MEMs 15, 22, 23, 26, 28, 33, 37, 38; axis 2: MEMs 11, 14, 20,
446    24, 32, 37, 39). The first axis mainly separated between locations with a high importance
447    of either *Galathowenia fragilis* or Sipuncula. Since these taxa were particularly

important at the deeper locations below the pycnocline, the absolute site scores of PRA axis 1 were higher for these locations. The second axis was largely driven by the bivalve *Thyasira equalis* on the one side and the polychaete genus *Paraonis* on the other side.

**Meso-scale epifauna – exclusive spatial structure**

The exclusively spatially structured part of the meso-scale epifauna described a similar spatial pattern as the PCA for the first axis, but differed considerably for the second axis (Fig. 8). Together, both axes projected the complete inertia of the exclusive spatial structure (Axis 1: 70%, axis 2: 30%). While axis 1 was shaped mainly by the same species as in the PCA, the second axis separated between samples with high abundances of *Eunice pennata*, *Gracilechinus acutus*, and *Nothria hyperborea* from samples with high abundances of *Parastichopus tremulus*, *Anapagurus laevis*, and the caridean shrips *Pandalina brevirostris*, *Dichelopandalus bonnieri*, and *Crangon allmanni*.

**Meso-scale infauna – sediment**

The RDA of meso-scale infauna with sediment as predictor (Fig. 8) differed from the pattern in the PCA, but contained a separation of the deepest stations on axis 1. In contrast to the PCA, where the three deepest stations were separated, only the two deepest stations (depth: >250m) were clearly separated in the RDA. The same species played a role in shaping the first axis in both ordinations, but the importance of the polychaete *Amythasides macroglossus* was much smaller in the RDA than in the PCA. The second RDA axis described a spatial pattern according to MEMs 2, 3, and 4 and was largely shaped by *A. macroglossus*.

**Fine-scale infauna – sediment**

For the fine scale, only one RDA axis was extracted (Fig. 8), reflecting all the structure explained by the sediment, since it contained a single variable with only 2 different bottom types. Nonetheless, the spatial pattern and the species behind the axis reflected the first PCA axis very well.

## Discussion

We report a high number of benthic species for the Lofoten-Vesterålen region. The number of species in this study exceeded, for example, the numbers reported from the North Sea for both epifauna (Lofoten-Vesterålen: 346 vs. North Sea: 280) and infauna (Lofoten-Vesterålen: 533 vs. North Sea: 489) (Reiss et al., 2010). The number of infauna species in the Lofoten-Vesterålen region also exceeded the diversity known from each of five similar sized study regions along the Norwegian continental shelf (range: 177-477) (Ellingsen and Gray, 2002). However, while covering areas of similar or larger scales, all comparable studies were limited to the continental shelf and the higher number of species in the Lofoten-Vesterålen region is reflecting the particular diverse geomorphology (Thorsnes et al., 2009) and the wide depth range sampled in our study.

The patterns of community structure that we observed on the broadest scales for both studied faunal components matched the pattern described for benthic megafauna (Buhl-Mortensen et al., 2012). Like Buhl-Mortensen et al. (2012), we identified the prevailing hydrography as the main driver of the benthic communities on a broad-scale in the Lofoten-Vesterålen region, thereby separating the benthos into deep (depth > 800 m)- and shallow (depth < 800 m)-water communities. This conserved structure observed in all benthic components in the Lofoten-Vesterålen region suggests that the permanent pycnocline should be considered a boundary of two adjacent biogeographical units (Gray, 2000). Hydrography has often been shown to be the main environmental driver of broad-scale patterns in benthic communities, including the shelf seas north (Barents Sea) and south (North Sea) of the Norwegian coast (Cochrane et al., 2009, Reiss et al., 2010). Hydrological regimes in the North Sea or Barents Sea expand over large geographic regions (100s km). In contrast, the prevailing hydrography in the Lofoten-Vesterålen region varies on local scales (10s km) due to the heterogeneous geology and the narrow shelf, and accordingly smaller scales have to be selected to address aspects of biogeographic scales in Lofoten-Vesterålen benthos.

Community shifts associated with shifts in hydrological regimes have been attributed, among others, to physiological temperature preference (Hutchins, 1947) or to restricted larval dispersal across hydrological boundaries (Gaylord and Gaines, 2000). It is likely that both mechanisms contribute to the separation of the deep and shallow communities in the Lofoten-Vesterålen region: (1) Temperature decreased by approximately 5°C across the pycnocline, a difference that has physiological limitations for a high number of species (Longhurst, 2007). (2) Pelagic larvae of benthic invertebrates are retained within the Atlantic water on the continental shelf in the study

region, and onshore-offshore transport is virtually absent (Mileikovsky, 1968, Silberberger et al., 2016).

In the broad-scale data set, we observed an overall reduced number of epifaunal and infaunal taxa in the deep community compared to the shallow community (Epifauna: 135 vs. 363; Infauna: 189 vs. 586). Admittedly, the number of samples taken below the pycnocline was considerably lower than in the shallower community (Epifauna: 18 vs. 28; Infauna: 32 vs. 65) and therefore the absolute difference in species numbers needs to be considered an overestimate. However, the relation between sampling effort and discovered number of species is not linear and the chance of finding a new species declines fast after the first samples, as only rare species remain to be found (Colwell et al., 2004, Soberón and Llorente, 1993). Accordingly the number of taxa associated with the cold water masses has to be considerably lower than the taxa associated with the warm water masses. This is in agreement with the known maximum of megafaunal taxa between 200 and 700 m in the region (Buhl-Mortensen et al., 2012). This reduction of benthic species richness at such a shallow depth (800 m) contradicts the traditional paradigm that the number of benthic species increases to its maximum at a depth of 2000 m, below which it declines (Sanders, 1968). However, several studies have shown that there is no global pattern how benthic diversity varies with depth and that the local depth associated environmental gradients are structuring the benthic community and not depth *per se* (Gray, 2001, Gray et al., 1997, Renaud et al., 2009, Wlodarska-Kowalczuk et al., 2004).

Furthermore, we observed a greatly increased dominance of a few abundant taxa in the community below the pycnocline for both, epifauna and infauna community. This result corresponds with the significant negative correlation between depth and evenness of megafauna in the Lofoten-Vesterålen region (Buhl-Mortensen et al., 2012), but was somehow unexpected as evenness is considered generally high in the deep-sea benthos of the North Atlantic (Rex et al., 2000) and no correlation between depth and evenness has been found in previous studies that considered macrofauna (Wlodarska-Kowalczuk et al., 2004).

Hydrography, in particular the bottom temperature, was identified to explain some spatial structure on a cross-shelf scale for both, epifauna and infauna (meso-scale data). Across the shelf, the temperature changed gradually and no distinct cline was observed for any of the selected months. This generally week gradient reflects the relatively strong influence of the Norwegian coastal current at the coast and the increasing influence of the Norwegian Atlantic current with distance from shore (Gascard et al., 2004). However, on this scale, hydrography cannot be considered the dominant driver

558 of the benthic communities, what becomes evident in the differing community structure
559 of epifauna and infauna.
560

561    Apart from the community structure according to the prevailing water masses,
562 different spatial patterns for epifauna and infauna were identified in the broad-scale
563 data set, reflecting marine landscapes and bottom types, respectively. Marine landscape
564 elements are frequently applied to define spatial units in an ecosystem-based
565 management approach (Roff et al., 2003, Zajac, 2008) and have also been introduced
566 for the Lofoten-Vesterålen region based on spatial patterns in the megafauna
567 community (Buhl-Mortensen et al., 2012, Mortensen et al., 2009). Our results suggest
568 that this classification can be extended to the whole epifauna community, but fails to
569 represent the infauna community. Bottom types, as driver of infaunal community
570 structure, vary considerably within individual landscape elements, but then each bottom
571 type is also found across multiple landscape classes (Buhl-Mortensen et al., 2012).
572 Accordingly, area-based management needs to account for this discrepancy between
573 spatial patterns of epifauna and infauna.
574

575    Bottom type and sediment characteristic were identified as important drivers of
576 spatial structure of the infauna across all spatial scales, but only played an insignificant
577 role for the epifauna. Bottom type and sediment characteristics are commonly identified
578 as predictors for infauna communities (*e.g.* McBreen et al., 2008, Schratzberger et al.,
579 2006, Van Hoey et al., 2004) and can be expected as it reflects the immediate habitat of
580 the infauna community. For the epifauna, which is living on the seafloor, the bottom
581 type comprises also an important aspect of its habitat, but its role in structuring the
582 community seems generally lower than for the infauna (Schratzberger et al., 2006). Due
583 to the observed epifauna community structure in the Lofoten-Vesterålen region, at least
584 two environmental drivers, which were not included in this study, must have a strong
585 influence on the epifauna community: (i) a driver varying with the marine landscapes
586 and (ii) a driver that varies within individual landscape elements. Since this spatial
587 structure is only present in the epifauna community, but not in the infauna community,
588 it is likely that these drivers are somehow related to the exposed life style of epifauna.
589 One possible driver, on the scale of marine landscapes, could be related to the spatial
590 distribution of visual predators (Russ, 1980), or to the ability of these predators to
591 encounter food within the different landscapes. The marine landscapes differ
592 considerably in depth, and therefore the ambient light intensity could reduce the ability
593 of predators to find their prey. Within landscapes it is likely that the local bottom
594 currents have a strong impact on the epifauna community structure (Bøe et al., 2009,
595 Frederiksen et al., 1992, Smith et al., 2006). Complex current systems, like the one found
596 in Hola, have the ability to create small-scale habitats, dislocate epifauna, and create a
597 high local supply with fresh or re-suspended organic material.

598

599   In this study, samples for the meso- and fine-scale communities were sampled within
600   a shallow marine valley. Since marine landscapes were poor predictors for the infauna
601   community in the broad-scale data set, it is likely that the identified meso- and small-
602   scale environmental drivers, water mass properties and sediment, are also important
603   environmental variables for the infauna in other marine landscapes. For the epifauna,
604   however, the communities differed between landscape elements. Therefore, it is
605   questionable whether the structuring mechanisms can be the same in the different
606   landscapes.

607

608   The fine-scale infauna community data revealed a very clear spatial pattern,
609   associated with the bottom types in the sampling box. The sampling approach using
610   single grab samples at 14 sites, as proposed by van Son et al. (2016), captured the spatial
611   structure in the community very well. This pattern would have been very difficult to
612   identify with a similar effort using a traditional sampling approach (5 stations with 3
613   replicates). Indisbutably, a single sample at each site reduces the chance to have rare
614   species represented in the sample and the species richness at each individual sampling
615   site is better represented with several replicates. However, the species richness at a
616   single point is seldom the interest of research and management, but rather the species
617   richness in a specific study region or management unit. For this purpose, a many-sites,
618   one-sample strategy is able to recover more species in total, because species are likely
619   to show up at other sites with similar environmental conditions (Aarnio et al., 2011, van
620   Son et al., 2016). Accordingly, we believe that the meso- and broad-scale infauna
621   sampling in this study could have benefitted from such a sampling approach, since we
622   would expect a better capturing of the spatial gradients and a better recovery of the
623   species richness in the study region.

624

625   In conclusion, our study has given an insight into spatial scales and relevant
626   environmental drivers for benthic communities in the Lofoten-Vesterålen region. The
627   deep cold-water benthic communities below the permanent pycnocline in the Lofoten-
628   Vesterålen region differ distinctly from shallow communities associated with Atlantic
629   water (this study, Buhl-Mortensen et al., 2012) and appear to be almost two isolated
630   systems since larval transport between these systems seems to be negligible
631   (Silberberger et al., 2016). Our results suggest that the applied marine landscape
632   classification could be used to define management units for the epifaunal component,
633   but are not transferable to the infauna, which is mainly reflecting the bottom type,
634   impartial of the marine landscapes they belong to. On smaller spatial scales, sediment
635   characteristics play an important role in structuring the infauna community, while the
636   majority of the spatial structure in the epifauna could not be explained by the included
637   environmental variables. Future studies should address whether the structuring

638    mechanisms at the meso- and fine-scale apply only to Hola or if they are transferable to
639    other marine valleys and other marine landscapes. Furthermore, we advocate the
640    adoption of a sampling approach of many sites and one-sample for studies of general
641    community patterns and spatial structure of infauna, as it allows for the identification
642    of more detailed spatial patterns without increasing the number of samples or the
643    sample processing.

## Acknowledgements

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840    explanatory variables. *J Veg Sci,* 14**:** 693-700. DOI 10.1111/j.1654-1103.2003.tb02201.x
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**Tables**

846  Table 1 Spatial weighing matrices selected by the data-driven selection procedure for all
847  5 data sets

| Scale | Epifauna | | Infauna | | |
|---|---|---|---|---|---|
| | Broad | Meso | Broad | Meso | Fine |
| $AIC_C$ | -8.49 | -4.15 | -32.15 | -12.04 | -7.36 |
| connectivity criterion | distance-based | minimum spanning tree | distance based | distance based | distance based |
| maximum distance (m) | 174.609 | 9536 | 43.045 | 6898 | 1250 |
| α used in the weighing function f1 | 1 | 1 | 1/7 | 1/10 | 2 |

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850 **Table 2** Correlation between PCA axis and total abundance per sample and number of
851 taxa per sample

| Community | Spatial scale | PCA axis | Abundance | Number of taxa |
|---|---|---|---|---|
| Epifauna | Broad | 1 | 0.273 | -0.457** |
| | | 2 | 0.157 | 0.196 |
| | Meso | 1 | 0.082 | -0.087 |
| | | 2 | 0.694* | 0.914*** |
| Infauna | Broad | 1 | 0.363*** | -0.124 |
| | | 2 | -0.127 | -0.562*** |
| | Meso | 1 | 0.422* | 0.257 |
| | | 2 | 0.417* | 0.579** |
| | Fine | 1 | 0.642* | 0.885*** |
| | | 2 | -0.251 | -0.152 |

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## Figures legends

**Figure 1**. Map of the study region, red bathymetric isobaths indicate approximate separation of the dominating water masses: Norwegian Atlantic water (NAW), Norwegian Sea Arctic intermediate water (NSAIW), and Norwegian Sea deep water (NSDP). Inset top: location of the study area in Norway, indicated by a red rectangle.

**Figure 2**. Sampling plan. Epifauna stations indicated by blue squares. Infauna stations indicated by red circles. a) Broad-scale sampling, location of Hola (meso- and fine-scale sampling) indicated by black dotted rectangle. b) Meso- and fine-scale sampling plan. Fine-scale sampling box indicated by black dotted rectangle.

**Figure 3**. Marine landscapes, vertical flux, average annual bottom temperature, and average annual bottom salinity for all epifauna and infauna sampling locations. Values presented on the grey-scales are cut-off values between the individual levels.

**Figure 4**. Results of the principle component analysis (PCA) of the broad-scale data sets for a) epifauna and b) infauna. PC scores for axis 1 and 2 are indicated for each sample on the map by black and white squares. Fraction of projected inertia (PI) for each axis is shown. Scalograms indicate the portion of variance explained by each MEM. MEMs identified as significant are indicated by an asterisk. Species loadings of 20 taxa (10 most positive and 10 most negative) for each axis are shown on the right of the according maps. Taxa abbreviations according to supplement 2.

**Figure 5**. Results of the principle component analysis (PCA) of the a) meso-scale epifauna data set, b) meso-scale infauna data set, and c) fine-scale infauna data set. PC scores for axis 1 and 2 are indicated for each sample on the map by black and white squares. Fraction of projected inertia (PI) for each axis is shown. Scalograms indicate the portion of variance explained by each MEM. MEMs identified as significant are indicated by an asterisk. Species loadings of 20 taxa (10 most positive and 10 most negative) for each axis are shown on the right of the according maps. Taxa abbreviations according to supplement 2.

**Figure 6**. Variation partitioning results of all spatial scales of the infauna (top) and epifauna (bottom). Arrow width indicates the explained variation (adj.$R^2$ value) of the according combination of sets of explanatory variables. Arrows were drawn in decreasing order of adj.$R^2$ until 80% of the total variation explained (TVE) by all sets of explanatory variables were depicted (note: Arrows in the figure do not add up to the TVE, because of that). Variation that is explained by several environmental predictors is

893    indicated by arrows originating from boxes surrounding the relevant environmental
894    variables. Arrows indicating spatial structure (*i.e.* structure explained by the MEMs) are
895    intercepted by the central box and have a dashed outline below this box.
896
897    **Figure 7**. Results of a) redundancy analysis (RDA) of broad-scale epifauna data with
898    marine landscapes as predictors and b) residual analysis (PRA) of broad-scale infauna
899    data depicting the part of the total variation explained that was not explained by water
900    mass properties. Axis scores for axis 1 and 2 are indicated for each sample on the map
901    by black and white squares. Scalograms indicate the portion of variance explained by
902    each MEM. MEMs identified as significant are indicated by an asterisk. Species loadings
903    of 20 taxa (10 most positive and 10 most negative) for each axis are shown on the right
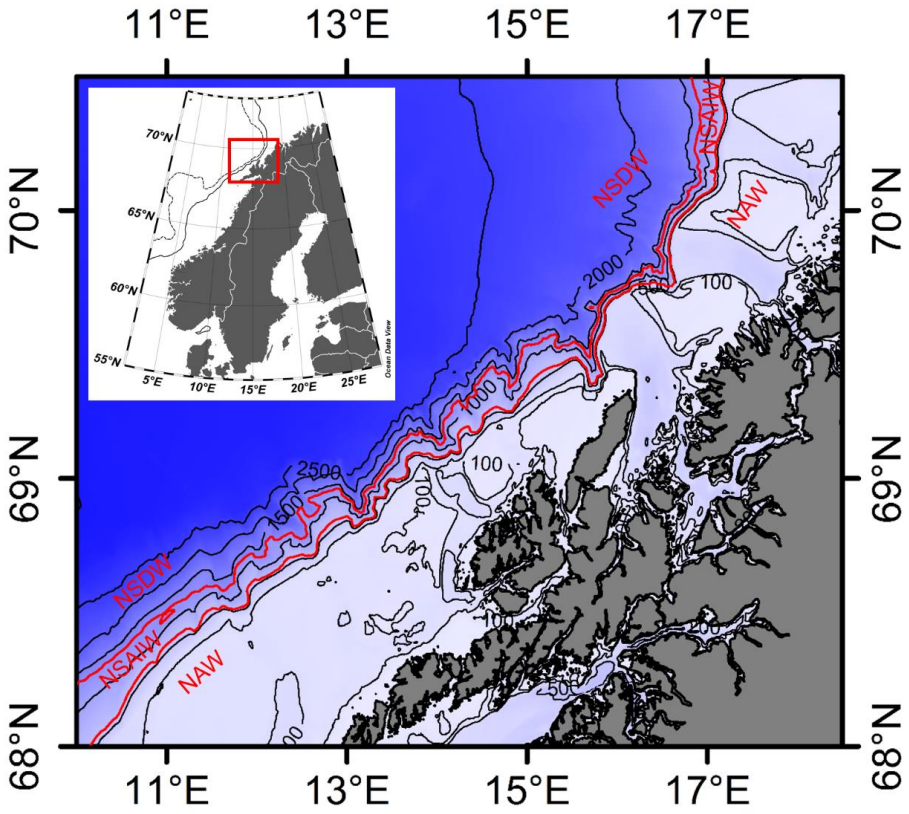904    of the according maps. Taxa abbreviations according to supplement 2.
905
906    **Figure 8**. Results of a) redundancy analysis (RDA) of meso-scale epifauna data depicting
907    the spatial structure not explained by other environmental variables, b) RDA of meso-
908    scale infauna data with sediment characteristics as predictors, and c) RDA of fine-scale
909    infauna data with sediment characteristics as predictors. Axis scores for axis 1 and 2 are
910    indicated for each sample on the map by black and white squares. Scalograms indicate
911    the portion of variance explained by each MEM. MEMs identified as significant are
912    indicated by an asterisk. Species loadings of 20 taxa (10 most positive and 10 most
913    negative) for each axis are shown on the right of the according maps. Taxa abbreviations
914    according to supplement 2. Only 1 axis extracted for c), since only one variable was used
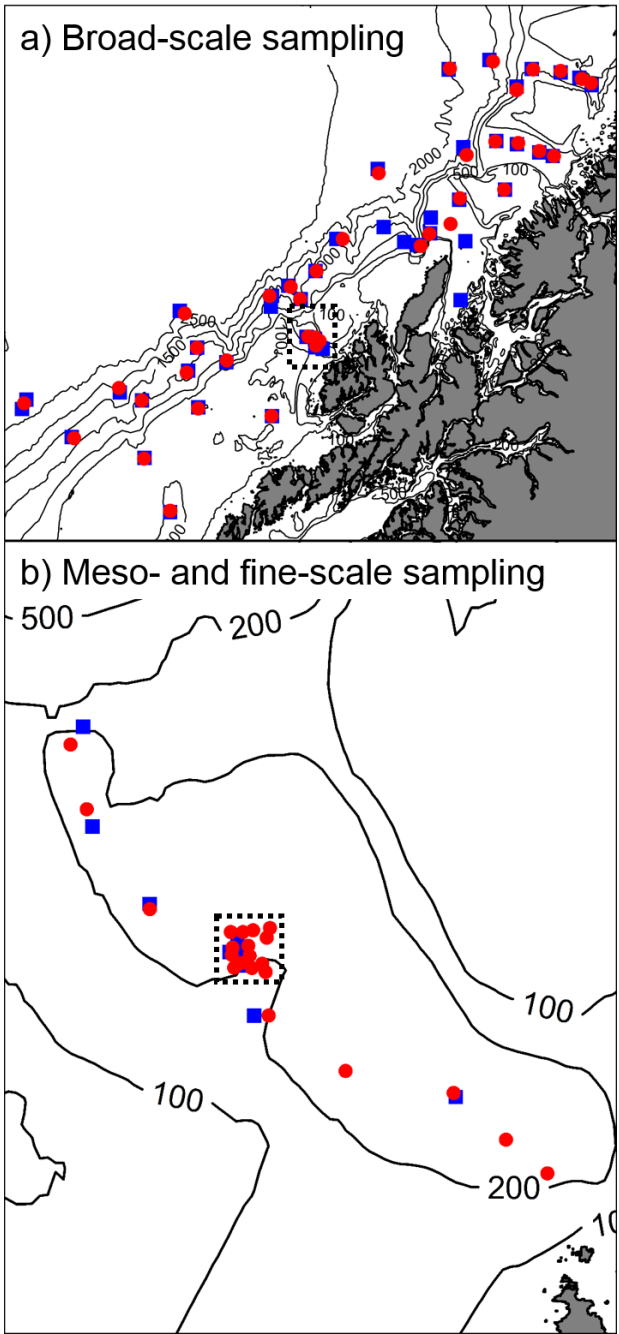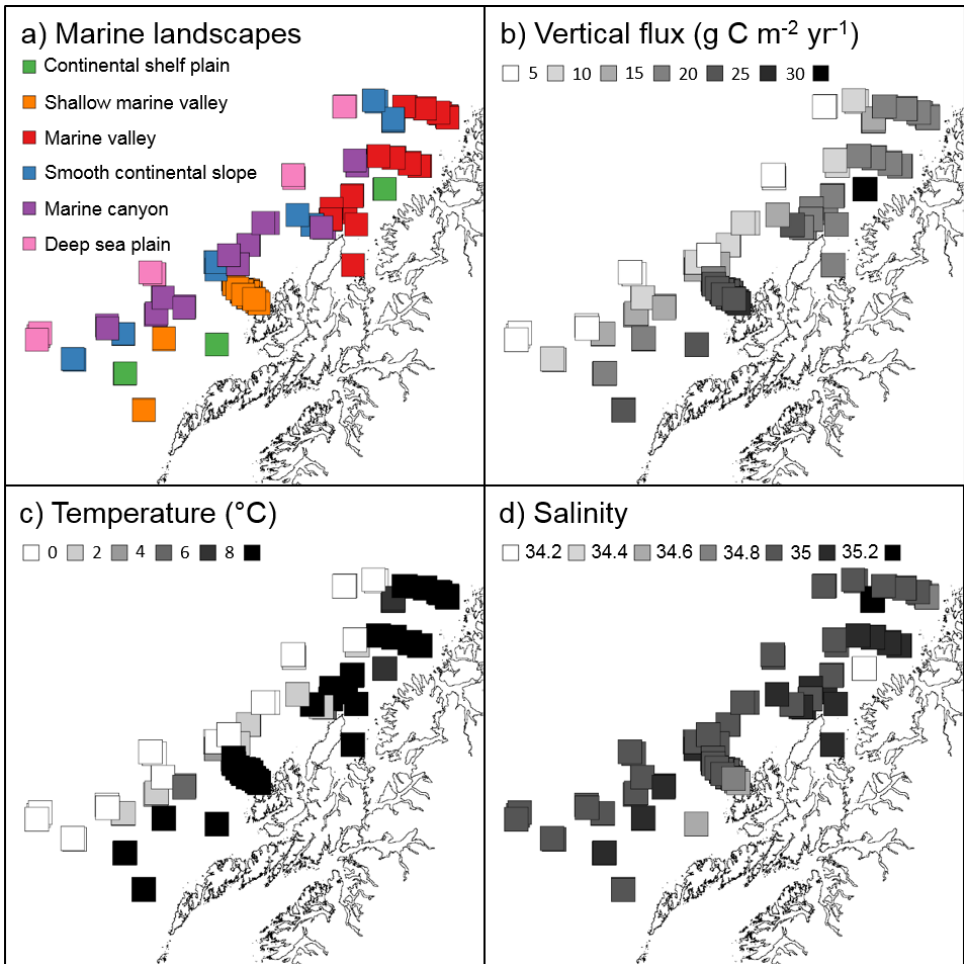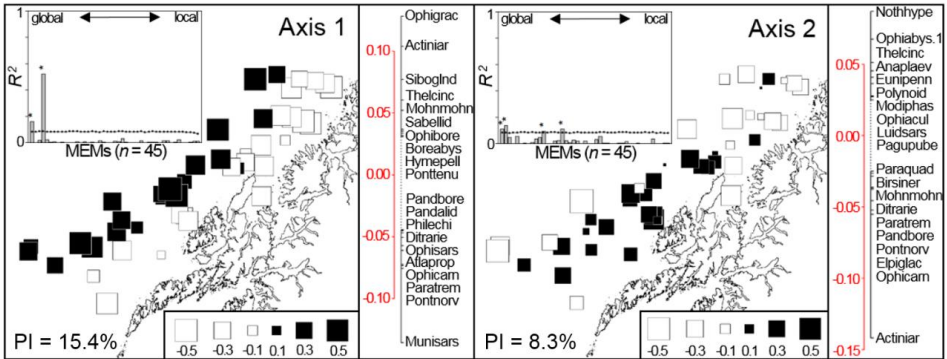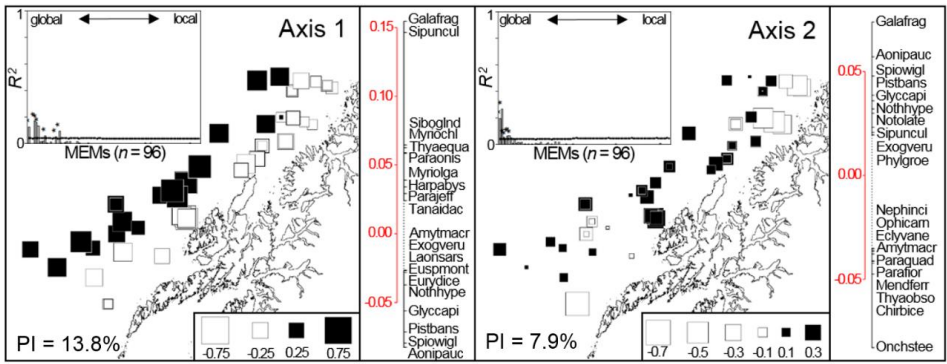915    as predictor.
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918    **Fig. 1**
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922    **Fig. 2**

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a) Broad-scale sampling

b) Meso- and fine-scale sampling

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925 **Fig. 3**

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**Fig. 4**

a) Epifauna

b) Infauna

**Fig. 5**



a) Epifauna (meso-scale)
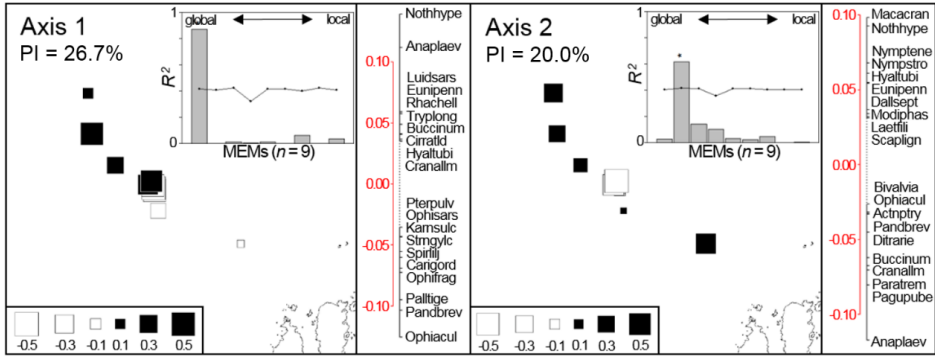
b) Infauna (meso-scale)
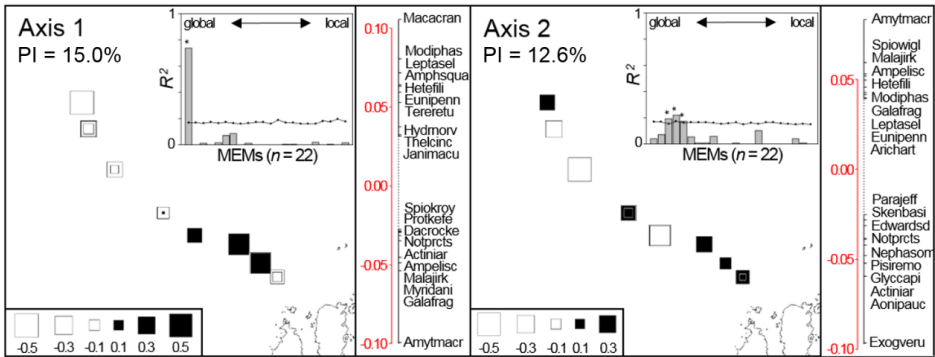
c) Infauna (fine-scale)
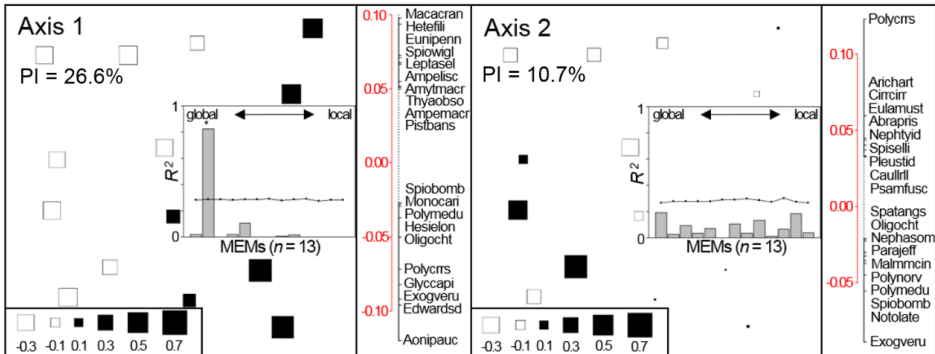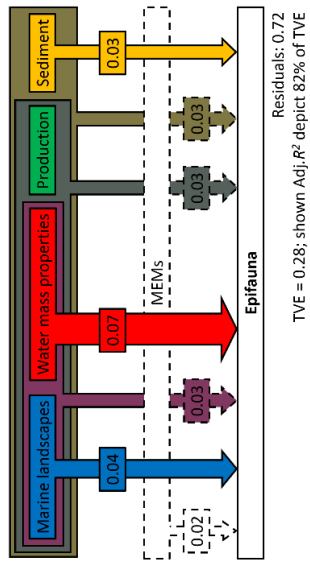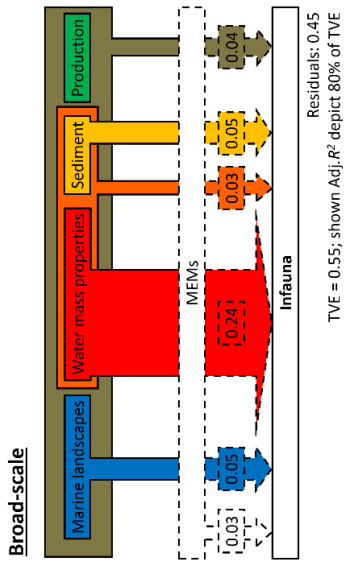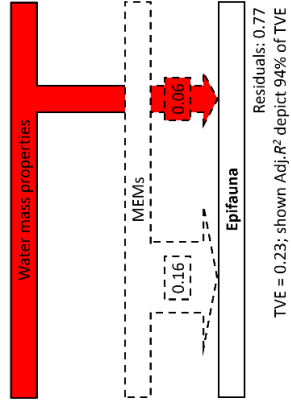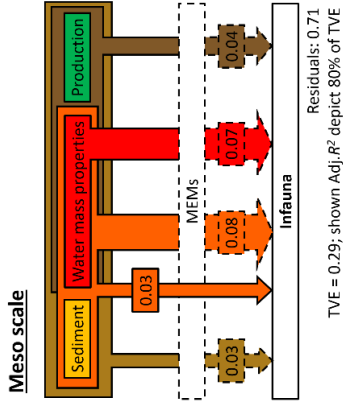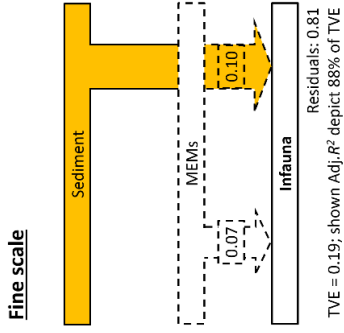
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934    **Fig. 6**



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**Fig. 7**

a) Broad-scale epifauna – marine landscapes
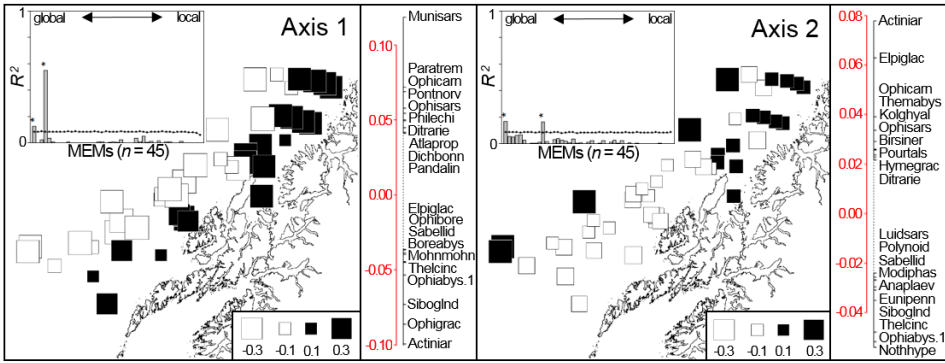
b) Broad-scale infauna – TVE not explained by water mass properties

**Fig. 8**
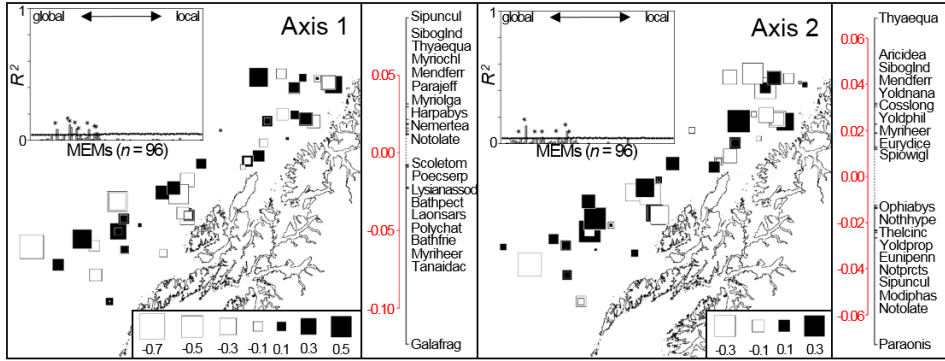
a) Meso-scale epifauna – exclusive spatial structure
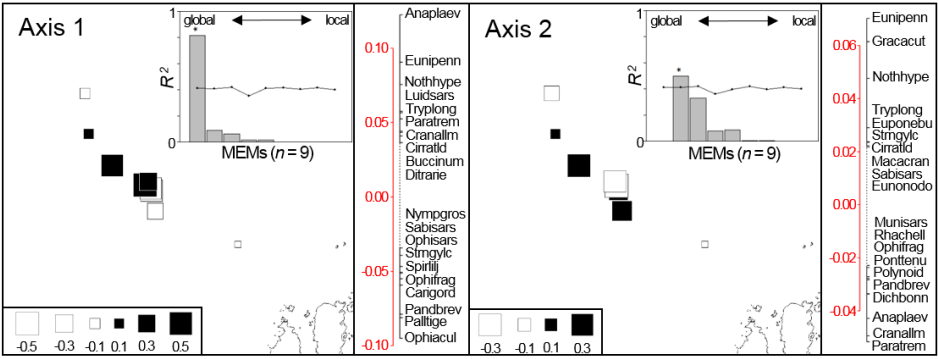


b) Meso-scale infauna – sediment
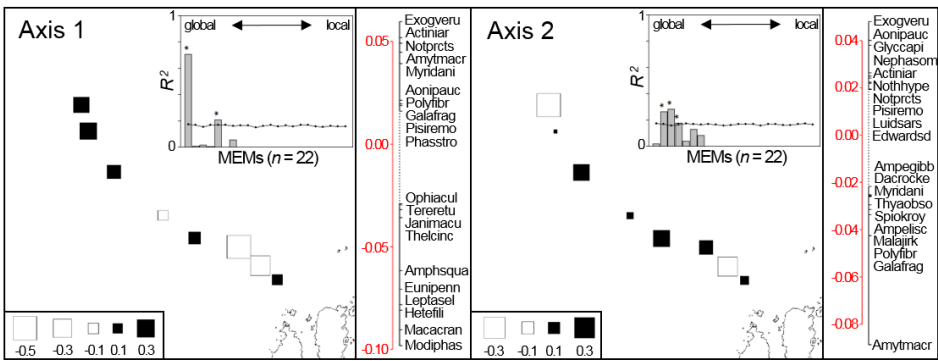


c) Fine-scale infauna – sediment
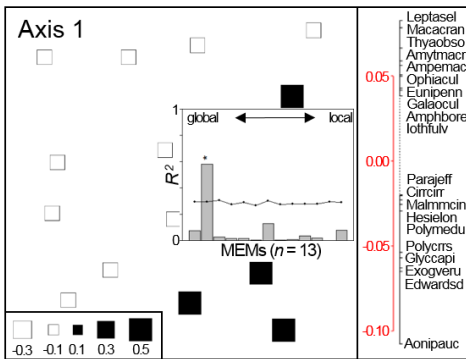


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Paper II

# Spatial and temporal structure of the meroplankton community in a sub-Arctic shelf system

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ABSTRACT: The early development of many benthic invertebrates involves planktonic larval stages enabling larvae to disperse over large distances and to utilize food from the productive upper water layers. Although many past studies have recognized the importance of this period in the benthic life cycle, knowledge of larval distribution in time and space remains limited, especially for high-latitude regions with pronounced seasonal variability in environmental conditions. Here, we present the first inventory of meroplankton over the continental shelf in the Lofoten–Vesterålen region, northern Norway, over a full annual cycle. Six stations were sampled during 8 sampling events between September 2013 and August 2014. We recorded a total of 65 taxa, a considerably higher diversity than reported in studies from more northern regions. We observed a distinct seasonal pattern with characteristic meroplankton communities defining the seasons: spring, summer, and winter. Abundance and diversity during winter was low, with higher values in spring, and maximum abundances for most taxa in summer. Meroplankton community patterns did not reflect weak environmental spatial structure. Particle tracking was used to identify source and settlement locations of spring and summer communities. Spring and summer communities originated from shore and shelf areas, respectively. Larvae were generally transported toward Andfjord and adjacent shelf regions, irrespective of season. This spatially restricted dispersal and larval settlement highlights the importance of the local benthic communities for the resilience of the ecosystem.

KEY WORDS: Planktonic larvae · Larval dispersal · Seasonality · Invertebrate larvae · Norwegian waters · Environmental factors · High latitude

## INTRODUCTION

The majority of benthic invertebrates are sedentary during their adult life, therefore limiting their dispersal largely to their early life stages. Consequently, many species have planktonic larvae to enable local and regional dispersal of their offspring (Becker et al. 2007). The planktonic phase also provides access to food in the productive upper water column, reduces intra- and interspecific competition, avoids predation by abundant benthic omnivores, and reduces inbreeding (Pechenik 1999, Palumbi 2003). At the same time, pelagic larvae risk being carried away from favorable settlement locations by the prevailing currents and expose themselves to

high predation pressure in the plankton (Pechenik 1999).

Larval duration in the water column varies among species (hours to several weeks), but substantial intraspecific variation also occurs depending on water temperature and food availability (Thorson 1950, Hadfield & Strathmann 1996, O'Connor et al. 2007). Furthermore, successful larval recruitment may hinge on the timing of spawning, and some species spawn in synchrony with phytoplankton blooms or increased spring temperatures (Crisp & Spencer 1958, Highfield et al. 2010). Seasonal variation in hydrodynamics also interacts with the timing of larval release because encounter with a suitable benthic habitat ultimately influences larval success

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(Metaxas 2001, Ayata et al. 2011). Although a substantial literature discusses reproductive strategies and larval nutrition in holoplankton (taxa spending their entire lives in the water column) (Varpe et al. 2009, Daase et al. 2013), the transferability of all of these conceptual models directly to studies of the pelagic developmental stage of benthic organisms (meroplankton) remains unclear.

Historically, aside from early studies indicating a decreasing importance of planktonic larvae for benthic reproduction with increasing latitude (Thorson 1950, Mileikovsky 1971), few studies have examined meroplankton in polar regions. Several recent studies have put this gap into perspective. Fetzer & Arntz (2008) provided detailed estimates on the relative importance of different developmental modes for the dominant benthic species in the Kara Sea, showing many species with benthic development (about 30%) driven almost exclusively by the large number of peracarid crustaceans in the study area that lack pelagic development. Their analysis showed a predominance of pelagic development outside this group. Furthermore, recent studies of Arctic meroplankton have shown that planktonic larval stages of benthic organisms comprise a considerable fraction of the total zooplankton community (Clough et al. 1997), and may dominate during productive seasons in terms of abundance and biomass (Stübner et al. 2016). Furthermore, meroplankton diversity observed in Arctic and sub-Arctic regions points to the importance of a bentho–pelagic life cycle in these regions (Andersen 1984, Schlüter & Rachor 2001) that can provide insight into adult distributions and potential range extensions for benthic species in the context of climate change (e.g. Renaud et al. 2015).

Distinct knowledge gaps about the spatio-temporal distribution of larvae remain. Kuklinski et al. (2013) and Stübner et al. (2016) investigated an Arctic meroplankton community over a 12 mo period, and detected a strong seasonal pattern with meroplankton present nearly year-round in a high Arctic fjord. Plankton community studies have provided limited additional information on the seasonality of Arctic and sub-Arctic meroplankton (Willis et al. 2006); however, these studies all investigated temporal patterns in enclosed fjord environments, with no studies specifically addressing open-shelf meroplankton seasonality. This lack of knowledge juxtaposes the importance of meroplankton dispersal and subsequent recruitment for the resilience of benthic ecosystems in response to natural and anthropogenic disturbances, including climate change (Kirby et al. 2008).

In this study, we present the first inventory of the meroplankton community at 6 stations in a sub-Arctic shelf system over a 12 mo period from September 2013 to August 2014. The main objectives were to (1) describe the spatial and temporal distribution of meroplankton in relation to large-scale benthic habitats and water mass properties; and (2) to further evaluate the importance of environmental variables and the spatial and temporal characteristics of the sampling regime in structuring the meroplankton community. Furthermore, we used a particle-tracking approach to identify possible source and settlement locations of the meroplankton sampled in this study.

## MATERIALS AND METHODS

### Study area

Although our study location on the continental shelf off the coast of the Vesterålen Islands in northern Norway (Fig. 1) occurs north of the Arctic Circle, and therefore experiences pronounced seasonality in day length with periods of complete darkness (polar night) and permanent light (midnight sun), the strong influence of the North Atlantic Current results
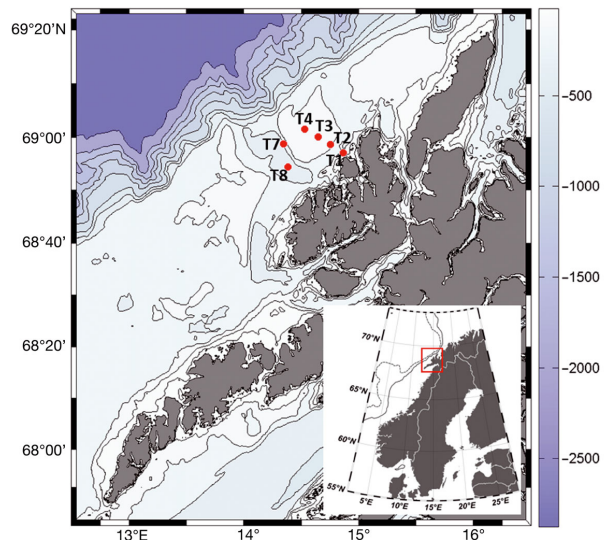


Fig. 1. Study area with bathymetry indicated by the color scale (unit: m). Sampling stations are indicated by red points. Inset: location of the study area in Norway, indicated by a red rectangle

in a permanently ice-free environment. Two major features comprise the narrow continental shelf in the area: shallow banks with hard substrate of bedrock and boulders contrast deep cross-shelf trenches with sandy or gravelly substrate (Buhl-Mortensen et al. 2012). Two northward-flowing currents characterize the regional hydrography. The low-salinity Norwegian Coastal Current flows over the shelf along the coast, whereas the warm and saline Norwegian Atlantic Current travels along the continental slope and frequently flushes onto the shelf (Bøe et al. 2009).

## Sampling and sample processing

Plankton samples were collected at 6 stations (Fig. 1, Table 1) during 8 sampling events between September 2013 and August 2014 (see Table 2 for sampling dates). The 6 stations were selected to represent the major marine landscapes in the study area (Mortensen et al. 2009) and to cover most of the shelf width, with distance from shore between 1 and 20 km (Table 1). A WP2 closing net (opening = 0.25 m², mesh size = 200 µm), equipped with a CTD profiler with fluorescence sensor (Saiv A/S, CTD/CSD – model SD 204), sampled the complete water column at shallow stations (T1–T4, depth <100 m) in a single vertical tow. At deeper stations (T7 and T8, depth >100 m), we collected plankton from 2 depth intervals: estimated maximum mixed-layer depth (50–0 m) and deeper water (bottom–50 m). At each of these stations, we also collected a separate CTD profile of the entire water column. We chose a mesh size commonly used for sampling larger and relative mobile meroplankton, such as decapod zoea (e.g. Highfield et al. 2010, Koettker & Lopes 2013). However, this sampling gear may under-represent small larvae and early stages of some groups (e.g. Bivalvia). Samples were fixed in 4% buffered formaldehyde until further processing. Unfavorable weather conditions precluded sampling at station

T8 on 10 September 2013 and a malfunctioning CTD resulted in no CTD data at station T7 on 1 May 2014.

CTD data (practical salinity, temperature, and pressure) were transformed following recommendations of the Intergovernmental Oceanographic Commission (IOC et al. 2010). All seawater properties were calculated using the Gibbs SeaWater package in R (Kelley et al. 2015). Absolute salinity ($S_A$), conservative temperature ($\Theta$), fluorescence ($F$), and the potential density anomaly referenced to 0 dbar ($\sigma_\theta$) were then averaged for 2 m depth bins, starting at 1 m depth, to smooth the data. The mixed-layer depth was defined as the depth where the difference between $\sigma_\theta$ and the surface value was 0.03 kg m$^{-3}$ (Talley et al. 2011).

Samples were split in the laboratory consecutively with a Motoda plankton splitter until a minimum count of 400 individuals or one-quarter of the total sample was processed. Meroplankton were identified to the lowest feasible taxonomic level. We standardized the original count data for the analyzed fraction to individuals per m² surface area (ind. m$^{-2}$) and integrated the 2 depth intervals for stations T7 and T8 to represent the whole water column.

## Statistical analysis

All statistical analyses were performed in R, version 3.2.0 (R Core Team 2015).

We calculated the number of taxa, total abundance, the Shannon index ($H'_{\log e}$) (Shannon 1948), and Pielou's evenness ($J'$) (Pielou 1977) for every sample to compare diversity between samples.

Although we report only results from log-transformed data unless otherwise stated, we ran multivariate analyses with 3 different transformations to explore all quantitative aspects of the data: (1) no transformation (raw), (2) natural logarithm (log), and (3) presence and absence data.

A triangular dissimilarity matrix was created using Bray-Curtis dissimilarities (Bray & Curtis 1957). Global nonmetric multidimensional scaling (GNMDS) ordinations were run with 100 restarts from random starting positions. The maximum number of iterations was set to 500 and the convergence criterion to 10$^{-7}$. Rescaling of the axes in half-change units was applied (Gauch 1973). Similarity profile analysis (SIMPROF) (average link-

Table 1. Geographic position, bottom depth, distance from shore, and marine landscape of the sampling stations

| Station | Longitude (°E) | Latitude (°N) | Depth (m) | Distance from shore (km) | Marine landscape |
|---------|---------------|---------------|-----------|--------------------------|------------------|
| T1 | 14°51.9846′ | 68°57.0048′ | 40 | 1.389 | Fjord and coast |
| T2 | 14°45.2226′ | 68°58.6056′ | 75 | 6.360 | Bank |
| T3 | 14°38.7630′ | 69°00.0378′ | 75 | 10.583 | Bank |
| T4 | 14°31.7700′ | 69°01.5690′ | 80 | 16.201 | Bank |
| T7 | 14°20.6526′ | 68°58.7430′ | 215 | 18.669 | Shelf trench |
| T8 | 14°23.1450′ | 68°54.4638′ | 260 | 11.927 | Shelf trench |

age; p < 0.01) verified patterns observed in the GNMDS ordinations. A species contribution analysis, as described by van Son & Halvorsen (2014), was performed to identify taxa contributing to observed differences in season patterns.

For variation partitioning, we created 4 matrices with explanatory variables. The first matrix contained 9 spatial variables: $x$, $y$, $x^2$, $xy$, $y^2$, $x^3$, $x^2y$, $xy^2$, and $y^3$. Universal Transverse Mercator (UTM) grid coordinates $x$ and $y$ of the sampling stations (5 digits for each coordinate) were used as the principal geographic information. Following Legendre (1990) and Anderson & Cribble (1998), we included all terms of a cubic trend surface regression in the matrix to allow more complex structures such as patches. The second matrix contained 11 environmental variables: depth, marine landscape, distance from shore (all constant over the study period), surface and bottom temperature, surface and bottom salinity, mean and maximum fluorescence, depth of maximum fluorescence, and mixed-layer depth. The marine landscape for each station was assigned following Mortensen et al. (2009). To determine the distance from shore of each sampling station, we used the gDistance function in the rgeos package (Bivand et al. 2015) together with the National Geospatial-Intelligence Agency's Prototype Global Shoreline Data (NGA 2009). All other parameters were based on individual CTD casts. Bottom CTD values were averages of the deepest 2 m bin, ending approximately 5 m above bottom. We included depth, marine landscape, and distance from shore in the matrix of environmental variables, even though they are not typical environmental variables in plankton research, because of their importance for local benthic communities. These measures also provide surrogates for other environmental variables not measured in our study (e.g. inputs of fresh water and terrigenous material decrease with distance from shore). The other 2 matrices contained a single temporal variable each: the sampling date expressed as day of year and sampling season, defined according to season-groups identified in the GNMDS ordinations. Two temporal matrices were used, since the season-groups were defined *a posteriori*. Including these 2 temporal sets of explanatory matrices allowed us to quantify additional variation in the meroplankton explained by knowledge of local seasons.

Each of the 4 matrices was subjected to forward selection using a series of constrained and partially constrained canonical correspondence analyses (CCA) followed by unrestricted permutation tests (999 permutations, p < 0.01). In each selection round, we

selected the variable with the highest significant explanatory power for use as a conditioning variable for all the following selection rounds. Variables were selected until none added significantly to the explanation of the variation in the meroplankton data. In this way, we avoided artificially inflating the explained variation by including co-variables in the analysis.

Given the lack of explanatory power in any spatial variables (see 'Results'), we performed a variation partitioning through constrained and partially constrained CCA with all possible combinations of the 2 temporal and the environmental datasets. Variation explained by environmental variables only (E), sampling date only (D), season only (S), environment and season combined (ES), environment and sampling date combined (ED), sampling date and season combined (DS), and a combination of all 3 (EDS) were determined following Anderson & Cribble (1998) for variation partitioning on 3 sets of explanatory variables. To visualize the results of the variation partitioning, we generated a Euler diagram with the eulerAPE software (Micallef & Rodgers 2014).

We tested for autocorrelation between the meroplankton community, the environmental dataset, and space using Mantel and partial Mantel tests (Legendre & Legendre 1998), removing the factor variable marine landscape from the environmental variables.

All multivariate analyses used the vegan package version 2.3-0 (Oksanen et al. 2015).

## Particle tracking

For tracking of larval dispersal pathways, we simulated velocity fields using the ocean modeling system NorKyst-800 (Albretsen et al. 2011). NorKyst-800 is based on the public domain Regional Ocean Modeling System, a 3D free-surface, hydrostatic, primitive equation ocean model using terrain-following s-coordinates in the vertical (Shchepetkin & McWilliams 2005, Haidvogel et al. 2008). In summary, we combined bathymetric data (50 m resolution) from the Norwegian Mapping Authority Hydrographic Service with lateral boundary conditions from the Norwegian Meteorological Institute (MET)'s Nordic4km, atmospheric forcing from MET's weather forecast model HIRLAM10km, tidal forces from a global inverse barotropic model of ocean tides (TPXO7.2), and Norwegian river discharge modeled by the Norwegian Water Resources and Energy Directorate. Recent studies have used the NorKyst-800 model

with success, showing relatively good agreement with field data (e.g. Myksvoll et al. 2014, Skarðhamar et al. 2015). The model domain covered the whole Norwegian Sea from 55.8° to 73.8° N and 0.5° W to 34.8° E, with 820 × 2420 grid cells in the horizontal, each 800 × 800 m in size.

Larval dispersal and origin were simulated using the individual-based model ICHTYOP (Lett et al. 2008), by tracking particles released inside an area around station T3. Hourly velocity fields from NorKyst-800 were used to simulate Lagrangian particle transport. A patch of 1000 particles was uniformly distributed in a 10 km diameter circular area between 20 m depth and the surface, and passively advected for 28 d, both forward and backward in time. Our simulation allowed transport of particles throughout the water column. We chose a duration of 28 d because the planktonic period for the majority of taxa in the study area (see Supplement 1 at www.int-res.com/articles/suppl/m555p079_supp.pdf) ranges from 3–6 wk (Mortensen 1927, Johannesson 1988, Shanks et al. 2003, Conway 2015). To account for the presence of different stages of larvae, we acquired weekly results in the simulations. Our simulation contrasted 2 periods during which typical spring (1 May 2014) or summer (22 July 2014) meroplankton communities were present.

## RESULTS

### Oceanography

Surface temperature and salinity in the study area varied seasonally, with high temperatures during summer and low salinity in late summer and autumn (Fig. 2). Surface temperature varied little spatially at any sampling date. Surface salinity, however, differed among sampling stations, but with no clear reoccurring pattern. Pronounced surface salinity outliers occurred, particularly at the deep stations T7 and T8, potentially indicating short-lived local high and low salinity patches over the shelf trench. Bottom temperature also showed distinct seasonality, with the highest temperatures in late summer and autumn. The strongest seasonality at the shallower stations (T1–T4; temperature range: 4.5–11.7°C) contrasted the weaker seasonality at the deeper stations (T7 and T8; temperature range: 6.1–8.0°C). In contrast to the other variables, bottom salinity varied spatially but not seasonally. Salinities above 35 characterized bottom waters at stations T7 and T8 throughout the year, with a single outlier at station
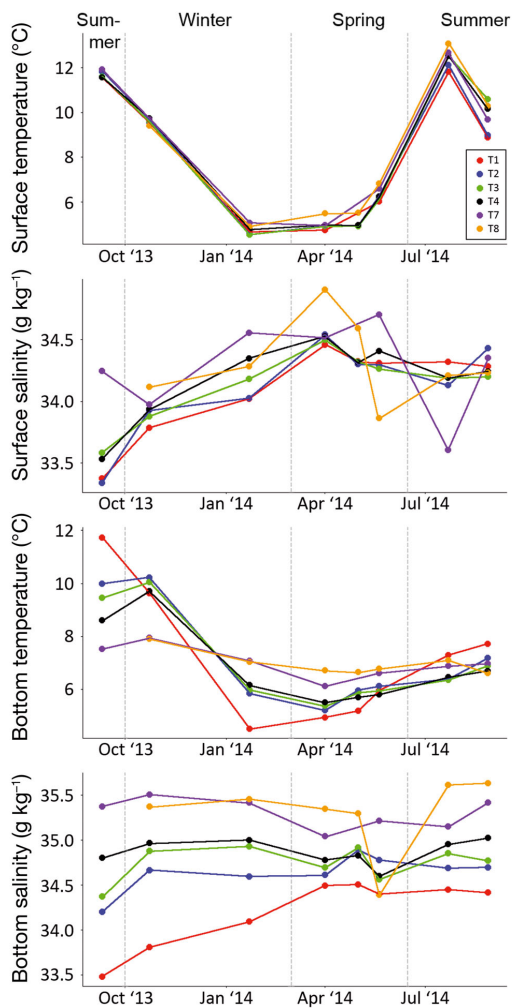


Fig. 2. Surface and bottom temperature and salinity at each sampling station over the whole study period. Sampling stations are indicated by different colors; identified seasons are separated by vertical lines

T8 in May. This high salinity over 35 assigns this bottom water to a Norwegian Atlantic Current origin. Salinities below 35 throughout the year, typical for the Norwegian Coastal Current, characterized bottom water at the shallower stations. The mixed-layer depth in the study area indicated deeper mixing from October to early May and a more stable surface layer in late spring and throughout the summer. The fluorescence values indicate mid-May and August phytoplankton blooms.

## Meroplankton community

All samples analyzed contained plank-tonic larvae of benthic invertebrates, which we assigned to 65 different taxa in 11 phyla (see Supplement 1 at www.int-res.com/articles/suppl/m555p079_supp.pdf). On average, samples contained 14 041 ind. m$^{-2}$ (range: 32–79 392 ind. m$^{-2}$) in 15 different taxa (range: 1–35). Mean number of taxa, abundance, $H'_{\log e}$ and $J'$ varied seasonally, with low abundances and diversity in October and January and a peak in the summer months (Table 2). Spatial variation was low relative to sea-sonal variation. Abundances were highest at stations closest to shore (T1 and T2). Lower average numbers of taxa occurred at the stations farthest offshore (T4 and T7). $H'_{\log e}$ and $J'$ did not vary spatially.

The 5 most abundant taxa in this study were the polychaete family Amphinomi-dae (mean abundance: 3724 ind. m$^{-2}$), the bryozoan *Membranipora membranacea* (2114 ind. m$^{-2}$), the barnacle *Verruca stroemia* (1642 ind. m$^{-2}$), echinoderms of the class Ophiuroidea (1048 ind. m$^{-2}$), and gastropods as-signed to the group Littorinimorpha type (979 ind. m$^{-2}$). These 5 taxa accounted for 67.7% of the total meroplankton abundance.



Fig. 3. Global nonmetric multidimensional scaling (GNMDS) results of logarithmic (log)-transformed meroplankton data. Sampling dates are in-dicated by different colors; labels are station numbers; symbols show season cluster according to similarity profile analysis: circles = winter; diamonds = spring; squares = summer

Multivariate community structure exhibited 3 dis-tinct seasons (winter: 23 October 2013; 22 January 2014; spring: 1 April 2014; 1 May 2014; 20 May 2014; summer: 22 July 2014; 27 August 2014, 10 September 2013) in the GNMDS ordinations of the log-trans-formed data (Fig. 3), presence and absence data, and untransformed data. The SIMPROF analysis (not presented) supported this pattern, preserving these 3 season groups irrespective of transformations. The GNMDS ordinations also separated spring samples, where the sampling dates arranged chronologically, indi-cating a gradual development of the community towards the summer.

The GNMDS ordination revealed a spatial pattern in late summer (Sep-tember) and a very weak pattern in early spring (April) only. In both months, samples from stations T7 and T8 were more similar to winter sam-ples than all other spring and summer samples. In September, station T1 had the highest abundance and highest diversity of all samples (79 392 ind. m$^{-2}$; 35 taxa). Abundance decreased substantially with distance from shore

Table 2. Number of taxa, total abundance, Shannon index ($H'_{\log e}$) and evenness ($J'$). Data shown are mean values ± SD for each station and each sampling date

|  | Taxa (n) | Abundance (ind. m$^{-2}$) | $H'_{\log e}$ | $J'$ |
|---|---|---|---|---|
| **Station** | | | | |
| T1 | 16.6 ± 10.4 | 20 780 ± 31 310 | 1.63 ± 0.48 | 0.66 ± 0.18 |
| T2 | 15.6 ± 9.6 | 19 388 ± 28 079 | 1.56 ± 0.79 | 0.62 ± 0.16 |
| T3 | 17.0 ± 8.6 | 12 408 ± 15 016 | 1.70 ± 0.56 | 0.69 ± 0.17 |
| T4 | 12.3 ± 7.5 | 12 772 ± 20 718 | 1.49 ± 0.79 | 0.73 ± 0.14[b] |
| T7 | 13.5 ± 7.7 | 9 690 ± 15 307 | 1.64 ± 0.37 | 0.72 ± 0.17 |
| T8[a] | 15.6 ± 7.2 | 8 491 ± 9 896 | 1.58 ± 0.42 | 0.63 ± 0.18 |
| | | | | |
| **Date** | | | | |
| 01.09.2013[a] | 23.0 ± 9.4 | 29 395 ± 34 898 | 2.19 ± 0.12 | 0.73 ± 0.13 |
| 23.10.2013 | 5.2 ± 3.1 | 403 ± 201 | 0.95 ± 0.68 | 0.63 ± 0.20[b] |
| 22.01.2014 | 2.7 ± 0.8 | 72 ± 30 | 0.88 ± 0.29 | 0.93 ± 0.11 |
| 01.04.2014 | 10.5 ± 2.5 | 3 029 ± 1 801 | 1.37 ± 0.41 | 0.59 ± 0.18 |
| 01.05.2014 | 19.5 ± 3.0 | 9 373 ± 2 740 | 2.02 ± 0.08 | 0.69 ± 0.05 |
| 20.05.2014 | 20.8 ± 3.4 | 11 677 ± 3 822 | 1.93 ± 0.22 | 0.64 ± 0.08 |
| 22.07.2014 | 19.8 ± 2.5 | 52 869 ± 16 993 | 1.69 ± 0.19 | 0.57 ± 0.08 |
| 27.08.2014 | 20.5 ± 2.6 | 8 037 ± 4 953 | 1.86 ± 0.38 | 0.62 ± 0.14 |

[a]Station T8 was not sampled on 1 September 2013. The presented results omit this sample; [b]Station T4 contained only 1 taxon on 23 October 2013 and therefore $J'$ could not be calculated. The presented $J'$ results omit this sample
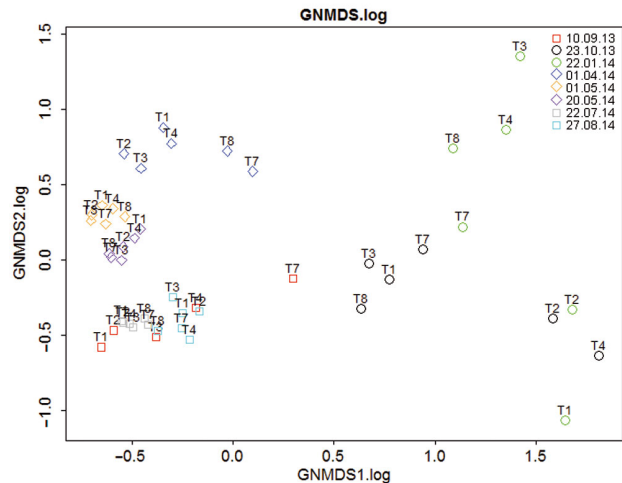
(T4: 4016 ind. m$^{-2}$; 18 taxa) and even more to the deep trough (T7: 400 ind. m$^{-2}$; 11 taxa). In April, we observed a difference in abundance between deep (T7 and T8: 1064 ind. m$^{-2}$) and shallow stations (T1–T4: 4012 ind. m$^{-2}$). In addition, we observed spatial patterns for some taxa. *Balanus balanus* and *Semibalanus balanoides* occurred almost exclusively at shallow stations, whereas most individuals of *Munida* spp. occurred at deep stations. In contrast, Amphinomidae were equally distributed throughout the study area during their peak abundance in July, but were only present in samples from the deep stations on 20 May.

Seventeen taxa contributed to at least 5% of the difference between at least one season pair for at least one transformation (Table 3). All 17 taxa were virtually absent from the winter samples (Fig. 4). Accordingly, the taxa with the highest spring and summer abundances contributed most to separating winter samples from those from other seasons. *S. balanoides* was the taxon that reached its annual maximum abundance earliest (in April), followed by *B. balanus*, Spionidae, and Ophiuroidea in early May. These 4 taxa were representative of the spring meroplankton community and disappeared almost completely before the summer. The remaining taxa were abundant during the summer, and of these, only bivalves with *Mya* type larvae were equally high in abundance in spring and summer.

Most taxa appeared suddenly in the plankton and disappeared again after a short abundance peak. In contrast, the 2 bryozoans (*M. membranacea* and *Electra pilosa*) occurred in high numbers from early May until September, increasing gradually over the season.

Although many taxa contributed to spring and summer differences, the dominant barnacle separated these seasons most clearly. Though present in all samples during the spring, *S. balanoides* and *B. balanus* effectively disappeared during the summer. In contrast, another barnacle, *V. stroemia*, occurred in very high abundances in all samples during summer, following low presence during spring. Furthermore, the ratio of *S. balanoides* to *B. balanus* changed from early spring to mid- and late spring, contributing to intraseasonal differences.

## Variables structuring the meroplankton community

Forward-selection CCA showed that variables from the environmental and both temporal datasets explained significant variation in the meroplankton data, whereas spatial variables did not (see Supplement 2 at www.int-res.com/articles/suppl/m555p079 _supp.pdf). Therefore, we applied the variation partitioning method only for the 3 datasets with significant explanatory variables. After forward selection, the datasets included the following variables: environmental data (surface temperature, bottom tem-

Table 3. Results of the species contribution analysis for spring, summer, and winter for presence and absence (Qual.), logarithmic (Log.), and untransformed (Raw) meroplankton data. The average contribution of a taxon is 1.54% (= 100% / 65 taxa). Taxa contributing over 5% to the difference between a cluster pair for one transformation are shown. Contributions over 5% given in bold and contributions over 10% are given in bold italic. Values are rounded to 2 decimals

| Taxa | Spring vs. summer | | | Spring vs. winter | | | Summer vs. winter | | |
|------|-------|------|------|-------|------|------|-------|------|------|
| | Qual. | Log. | Raw | Qual. | Log. | Raw | Qual. | Log. | Raw |
| *Galathea* spp. | 0.03 | 0.03 | 0.01 | 0.03 | 0.02 | 0.00 | **0.05** | 0.05 | 0.01 |
| *Verruca stroemia* | 0.01 | 0.04 | *0.14* | **0.05** | 0.05 | 0.02 | **0.05** | **0.08** | *0.15* |
| *Balanus balanus* | 0.05 | **0.06** | 0.03 | **0.07** | **0.08** | *0.12* | 0.01 | 0.01 | 0.00 |
| *Semibalanus balanoides* | **0.06** | **0.06** | 0.03 | **0.07** | **0.08** | **0.09** | 0.00 | 0.00 | 0.00 |
| *Membranipora membranacea* | 0.01 | 0.03 | *0.12* | 0.02 | 0.04 | *0.12* | 0.03 | **0.06** | *0.16* |
| *Electra pilosa* | 0.01 | 0.02 | 0.03 | **0.06** | **0.07** | **0.09** | **0.05** | **0.07** | **0.06** |
| Amphinomidae | 0.05 | **0.05** | *0.32* | 0.01 | 0.02 | 0.04 | **0.05** | **0.06** | *0.33* |
| Chaetopteridae | **0.06** | 0.05 | 0.02 | 0.00 | 0.00 | 0.00 | **0.05** | 0.05 | 0.02 |
| Spionidae | 0.02 | 0.02 | 0.00 | **0.06** | **0.06** | 0.02 | 0.04 | 0.03 | 0.00 |
| *Hiatella* type | **0.05** | **0.06** | 0.03 | 0.01 | 0.01 | 0.00 | 0.04 | **0.05** | 0.03 |
| *Mya* type | 0.04 | 0.04 | 0.01 | 0.02 | 0.03 | **0.07** | **0.05** | **0.06** | 0.03 |
| Mytilidae type | **0.06** | **0.06** | 0.02 | 0.01 | 0.00 | 0.00 | **0.06** | **0.06** | 0.02 |
| Anomiidae type | **0.05** | 0.04 | 0.01 | 0.00 | 0.00 | 0.00 | 0.05 | 0.04 | 0.01 |
| Littorinimorpha type | 0.01 | 0.03 | **0.07** | 0.01 | 0.03 | 0.03 | 0.02 | **0.05** | **0.08** |
| Nudibranchia | 0.02 | 0.04 | **0.07** | 0.01 | 0.02 | 0.01 | 0.01 | 0.02 | **0.07** |
| Ophiuroidea | 0.00 | 0.02 | **0.06** | **0.06** | **0.09** | *0.28* | 0.05 | **0.05** | 0.02 |
| Echinoidea | 0.02 | 0.02 | 0.00 | **0.07** | **0.07** | 0.04 | 0.04 | 0.04 | 0.01 |
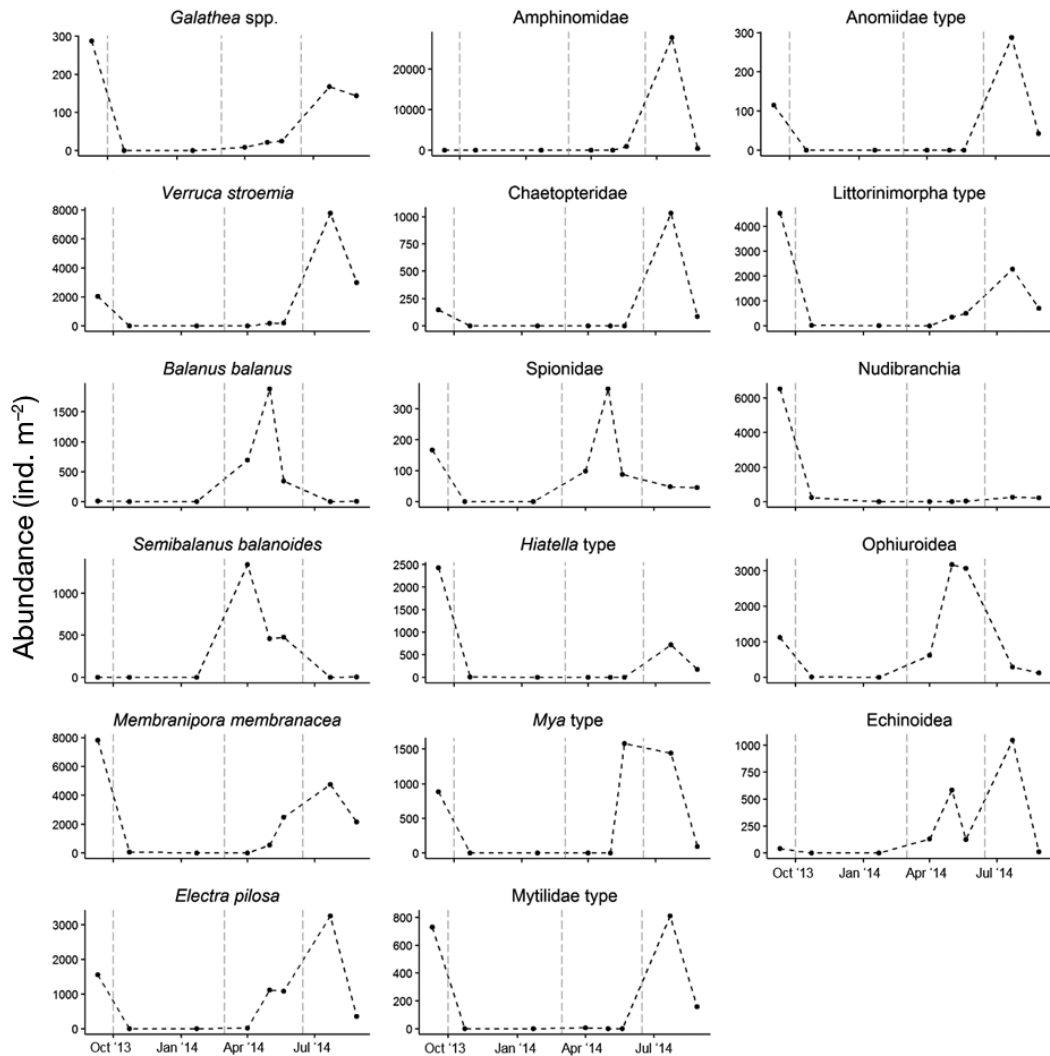
Fig. 4. Average abundances (ind. m$^{-2}$) of the taxa contributing over 5% to the separation of 2 season clusters according to species contribution analysis results. Identified seasons are separated by vertical lines

perature, fluorescence maximum, bottom salinity), temporal 1 (season), and temporal 2 (sampling date). In total, these variables explained 35.5% of the total variance (TVE), leaving 64.5% unexplained. Variation explained exclusively by the environmental data accounted for the largest portion of the TVE, followed by variation explained by season alone and variation explained by all 3 sets of explanatory variables (Fig. 5). The remaining 4 combinations of the datasets explained negligible variance.

Mantel and partial Mantel statistics (Table 4) support the results of the forward-selection CCA, indicating no significant correlations between the geographic distance matrix and the dissimilarity matrix of the log-transformed meroplankton data, but the environmental data correlated significantly with both.

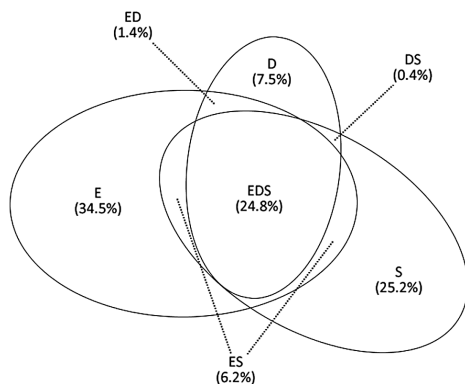Fig. 5. Euler diagram showing the results of the variation partitioning for the logarithmic-transformed meroplankton data. The percentages indicate the relative contribution of each explanatory data set (E = environment; D = sampling date; S = season) and all combinations of them to the total variation explained (TVE = 35.5%)

### Larval dispersal and origins

The May model advected a fraction of the particles northward relatively quickly along the continental slope, with some reaching 70.5° N latitude within just 2 wk and 9.7% of particles advected north of 71° N after 4 wk (Fig. 6A). The July simulation advected comparatively few particles along the slope, transporting particles northeastward onto the shelf and closer to the coast; 5.1% of the particles moved over 20° E by the end of the simulation. In both May and July, a significant percentage of the particles ended up in Andfjord (41.9% and 34.6%, respectively). Backward simulations showed different patterns for May and July (Fig. 6B). The May simulation advected a large fraction of the particles into the study area from the near coastal area all along the northwestern coast of the Lofoten Islands, in contrast to few particles from the off-shelf area farther south (5%). In July, most of the particles originated from the continental shelf adjacent to the release area, with 73.9% of the particles remaining north of 68° N 4 wk prior to sampling (compared with 11.9% in May).

Table 4. Mantel (upper triangle) and partial Mantel statistics (lower triangle) for logarithmic-transformed meroplankton data, environmental data, and space. p-values are given in parentheses

| | Meroplankton (log) | Environment | Space |
|---|---|---|---|
| Meroplankton (log) | – | 0.159 (0.029) | −0.014 (0.589) |
| Environment | 0.182 (0.020) | – | 0.426 (<0.001) |
| Space | −0.091 (0.969) | 0.434 (<0.001) | – |

## DISCUSSION

Our results showed that diverse planktonic larvae of benthic invertebrates contribute to the planktonic community on the Lofoten-Vesterålen shelf from at least April until September, with maximum abundances during summer. Although we identified 65 taxa in 11 phyla, indicating a considerably higher meroplankton diversity than reported for other northern polar regions (44 taxa in the Kara Sea [Fetzer & Arntz 2008] and 42 in a north Greenland fjord [Andersen 1984]), this number nonetheless falls short of the diversity reported for temperate waters (~160 taxa in the Danish Øresund [Thorson 1946]). We offer 3 possible explanations for this difference in diversity. (1) The meroplankton diversity may directly reflect local benthic diversity, because regional benthic communities ultimately determine meroplankton diversity (Mileikovsky 1968). (2) Following Thorson's rule (Mileikovsky 1971) that postulates fewer planktotrophic species with increasing latitude, meroplankton diversity may reflect the sub-Arctic environment of the Lofoten-Vesterålen region. (3) Differences in sampling protocols and taxonomic resolution may contribute to between-study differences. Presumably, all 3 explanations contribute in some way. The particularly heterogeneous benthic habitats that characterize the Lofoten-Vesterålen region (Buhl-Mortensen et al. 2012) provide niches for a diverse benthic community. Although recent studies refute Thorson's rule for the whole benthic community and instead suggest a shift from planktotrophy to lecitotrophy with increasing latitude, the rule apparently holds for Prosobranchia (Clarke 1992), which were represented by 9 taxa in our present study despite total absence in Kara Sea plankton samples (Fetzer & Arntz 2008). Furthermore, the higher diversity of bivalves (5 morphotypes in our study vs. 28–33 species in Thorson [1946]) reflects Thorson's taxonomic expertise for molluscs. Additionally, our 200 μm mesh size may have underestimated the diversity of bivalve larvae.

Nonetheless, studies of (sub-)Arctic meroplankton from Svalbard and the Barents Sea report the same major components of the meroplankton community as our study. Schlüter & Rachor (2001), for example, described a community from the central Barents Sea in May and June characterized by echinoderm, polychaete, and *Mya truncata* larvae. These taxa mirror the meroplankton community in our study on 20 May 2014, but lack abundant barnacles (*Semibalanus balanoides*, *Balanus balanus*)
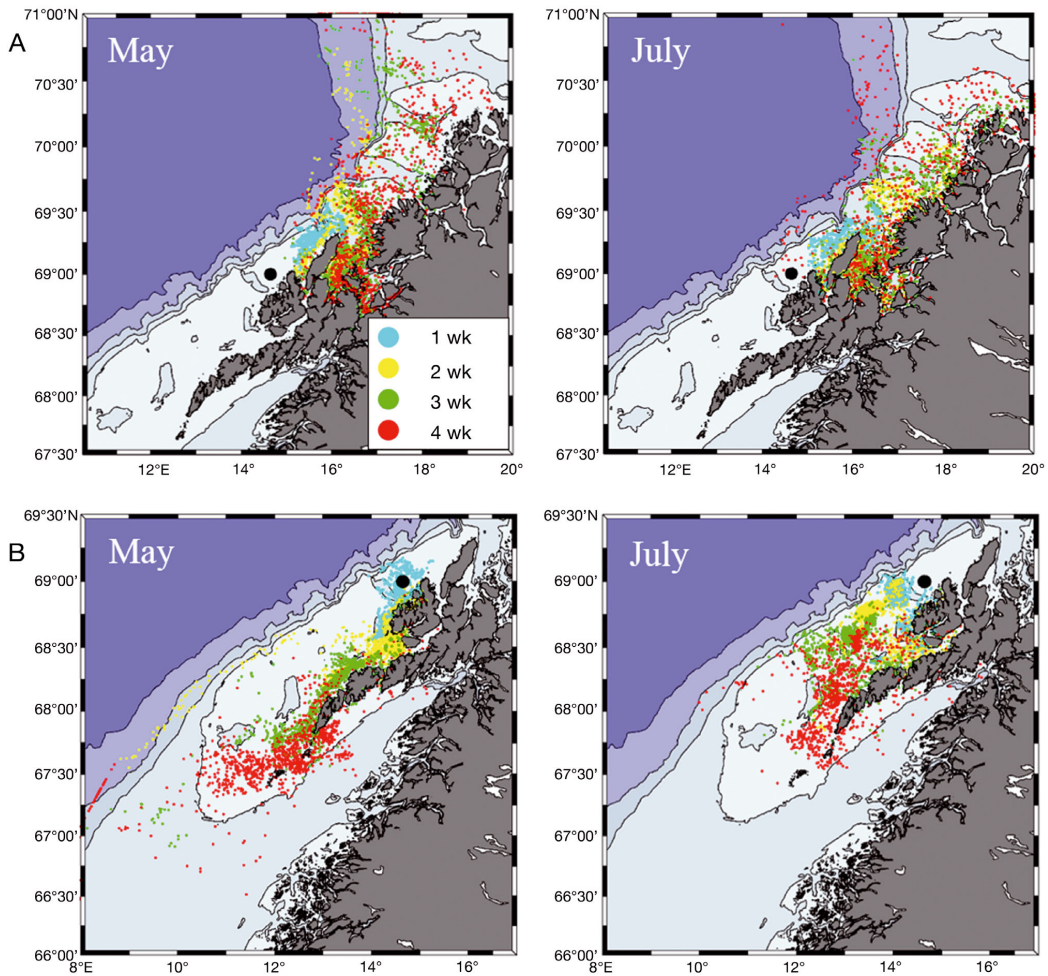
Fig. 6. Particle-tracking results. Forward (A) and backward (B) simulations of larval transport for the meroplankton community on 1 May 2014 (left) and 22 July 2014 (right). Particle distributions are presented in 1 wk steps (see color scale) following (A) or before (B) being observed at the black circle

and bryozoans (*Membranipora membranacea*, *Electra pilosa*), typically associated with hard substrates and shallow depth. In contrast, studies from Svalbard fjords reported peak abundances of barnacle larvae in May–June (Willis et al. 2006, Kuklinski et al. 2013, Stübner et al. 2016).

Only Kuklinski et al. (2013) and Stübner et al. (2016) have reported on a meroplankton community over a full annual cycle in an area similar to the Lofoten-Vesterålen region with respect to the physical environment. Like the Lofoten-Vesterålen region, their

Adventfjord study location on Svalbard experiences strong seasonality in day length and a short period of high primary production. In addition, the absence of winter sea-ice, the strong influence of Atlantic water, and increased freshwater input during the melting season in late summer characterize Adventfjord. Species with low-Arctic, boreal-Arctic, Arctic-boreal, and Atlantic biogeographic origin occur commonly in Adventfjord (Różycki 1993). Although the Adventfjord studies (Kuklinski et al. 2013, Stübner et al. 2016) used different sampling schemes to characterize the

meroplankton community over a 1 yr period, both studies nonetheless identified similar seasonal development, with meroplankton present in larger numbers from mid-April to the end of July. Within this period, they identified a spring community dominated by barnacles and a summer community dominated by molluscs. We report similar spring and summer communities in Lofoten-Vesterålen, characterized by the same groups. Two barnacle species dominated the spring community in contrast to abundant bivalve and gastropod taxa during the summer. The occurrence of other abundant taxa resulted in reduced dominance by the previously mentioned taxa in Lofoten-Vesterålen. Amphinomid polychaetes *Verruca stroemia* and the 2 bryozoan species occurred in lower numbers in Svalbard. This amphinomid, quite likely *Paramphinome jeffreysii*, occurs frequently and in high abundances in fjords of mainland Norway and on the continental shelf. No study has reported adults of *P. jeffreysii* in Svalbard. Regarding bryozoans, Stübner et al. (2016) reported a very different seasonal pattern than that in Kuklinski et al. (2013) or in our study. Stübner et al. (2016) observed very few bryozoans and exclusively during winter months, when virtually all other larvae were absent. In contrast, our samples contained high numbers of bryozoans almost throughout the complete spring and summer. Species with different larval types may explain this result (Temkin & Zimmer 2002). The planktivorous cyphonautes larvae of the species in our study spend a relatively long time in the plankton. Although Stübner et al. (2016) did not mention larval type, they likely observed small lecithotrophic larvae with a short planktonic period that do not require food while in the pelagic zone. Kuklinski et al. (2013) reported a high number of non-cyphonautes bryozoans, but also very low numbers of cyphonautes larvae. However, in their study the non-cyphonautes larvae appeared in April right after the spring phytoplankton bloom and disappeared from the water again in June.

### Spatial and seasonal structure

Our analysis identified seasonal as well as spatial structure in the environment. However, our results also showed strong seasonal structure in the meroplankton community with little spatial structure other than the spatial patterns described for *B. balanus*, *S. balanoides*, Amphinomidae, and *Munida* spp.

Studies that sample single time periods often report spatial structure in meroplankton communities, frequently relating patterns to observed water mass properties on a regional scale (Belgrano et al. 1995a,b, Ayata et al. 2011) or to differences in marine landscape (coast vs. shelf vs. oceanic) on a larger scale (Koettker & Lopes 2013). Year-round studies of meroplankton communities (Kuklinski et al. 2013, Weidberg et al. 2013) have not reported such spatial structure, perhaps relating to study design and the highly dynamic nature of pelagic ecosystems. Sampling campaigns for seasonal studies require extensive, repetitive sampling cruises. Therefore, the limited spatial coverage and number of samples make it impossible to detect weak spatial structure. However, the lack of spatial structure in the meroplankton community in our study could well be related to the particularly dynamic pelagic system in the study area (Røed & Kristensen 2013). A strong cross-shelf mixing in the study area is also in accordance with the particle-tracking results in this study. In each simulation, the particles were evenly distributed over the width of the shelf 1 wk before and after their release.

The strong seasonal changes in meroplankton in our study coincide with past studies of Arctic (Willis et al. 2006, Kuklinski et al. 2013, Stübner et al. 2016) and Antarctic (Stanwell-Smith et al. 1999) waters, as well as studies of temperate waters in Britain (Highfield et al. 2010) and northern Spain (Weidberg et al. 2013). We identified a winter period with very low abundances of meroplankton, as commonly reported in previous Northern Hemisphere temperate (~2 mo) and Arctic (~8 mo) studies.

The absence of early and late spawning species, or delayed and advanced spawning of early and late spawning species, respectively, may explain the shortened period of larval presence at high latitudes. The recurring dominance of barnacle larvae in spring characterizes meroplankton communities all along the European coast (Pyefinch 1948, Crisp 1962, Kuklinski et al. 2013, Weidberg et al. 2013). In British waters, early naupli of *S. balanoides*, *B. balanus*, and *V. stroemia* more or less co-occur in February–March (Pyefinch 1948, Crisp 1962), when the spring phytoplankton bloom triggers larval release (Crisp & Spencer 1958, Barnes & Stone 1973). Crisp (1962) showed a similar delay in larval release with increasing latitude for *S. balanoides* and *B. balanus*. In our study, however, *V. stroemia* appeared later in the season than the other barnacles. Stone (1989) showed experimentally that *S. balanoides* naupli feed on large diatoms, whereas *V. stroemia* develops better when fed small flagellates. Therefore, although the temporal succession of barnacle species in Lofoten-Vesterålen suggests adaptation to the regional tem-

poral succession of the phytoplankton community in northern Norway (Tande 1991), the causes for the longer delay in *V. stroemia* remain unclear.

Mytilidae larvae vary seasonally with environmental conditions on spatial scales of 100s–1000s of km (Philippart et al. 2012). Accordingly, Mytilidae abundance in our summer community strongly resembles the pattern in the White Sea (Günther & Fedyakov 2000), but differs from temperate regions in Europe (Philippart et al. 2012). Such large-scale similarities apparently hold for other bivalve species as seen by similarity in *Mya* spp. occurrence in Lofoten-Vesterålen and the Barents Sea (Schlüter & Rachor 2001).

### Parental populations and settlement locations

Our particle-tracking simulation indicated very different origins of spring (coast) and summer (shelf) meroplankton communities, but advection of a large proportion of the larvae into Andfjord in both seasons. Unfortunately, a lack of information on the distributions of adult benthic populations in the Lofoten-Vesterålen region precludes any validation of possible spawning or settlement locations. We assumed particles in our simulations behaved passively without behavior, though previous studies have shown that vertical migration can reduce transport distances and risk of offshore transport (Robins et al. 2013). Therefore, our simulation may overestimate dispersal distances for some taxa, and we assume that the fraction of larvae that settled in Andfjord and adjacent shelf areas may represent underestimates in both seasons. This high local settlement points to the importance of the meroplankton community for the resilience of local benthic assemblages. Furthermore, perhaps even fewer larvae were transported offshore than our simulations suggested. Therefore, we propose a minimal risk of offshore transport for meroplankton in the Lofoten-Vesterålen region, as proposed by Mileikovsky (1968) based on his observation of low larval abundances in Norwegian Sea offshore waters.

Species composition on 1 May 2014 supports a coastal origin for larvae. Given its intertidal distribution, we can easily presume a coastal origin for *S. balanoides* larvae (Hayward & Ryland 1995). *B. balanus* occurs on, though is not restricted to, hard substrates in shallow coastal waters. Various brittle stars with ophiopluteus larvae commonly occur in northern Norway (Mortensen 1927), including *Ophiopholis aculeata*, and several *Ophiura* species, which are very common on the Lofoten-Vesterålen and Nordland County coasts (M. J. Silberberger pers. obs.). Similar transport pathways were described for a 2011 early spring simulation (Espinasse et al. 2016). A simulated particle release in Vestfjorden on 15 March 2011 resulted in advection along the Lofoten coast and some particles reaching our study location within 3 wk.

Amphinomidae (*P. jeffreysii*), *V. stroemia*, and Mytilidae, all abundant taxa in samples from 22 July 2014, support the hypothesis of a dominant shelf origin of the summer community. However, these taxa occur beyond the shelf. *P. jeffreysii* also commonly occurs in north Norwegian fjords. *V. stroemia* occurs from the low littoral zone to several hundred meters depth (Stone & Barnes 1973). Likewise, the common Mytilidae species *Modiolus modiolus* occurs in northern Norway from a few meters to over 200 m depth. In contrast, the bryozoans *M. membranacea* and *E. pilosa* commonly associated with kelp and shallow waters originate from shore (Hayward & Ryland 1995). Although this observation contradicts our hypothesis of the summer community originating on the shelf, our particle-tracking simulation nonetheless showed a fraction of the particles originated from the coast in July as well.

Variability in circulation at small timescales can strongly influence generalizations drawn from the simulations regarding seasonal patterns in larval transport. Especially in the surface layer, changes in wind conditions can significantly alter transport. However, the 2 simulations identify some clear differences in seasonal patterns. Early in the year, prevailing southwest winds push water masses transported by the Norwegian Coastal Current towards the coast, thus strengthening the current. During summer, the prevailing northerly winds decrease Norwegian Coastal Current flow, producing lower advection and shorter transport pathways in summer compared with spring.

We conclude that a distinctly seasonal sub-Arctic meroplankton community, which is considerably more diverse than documented in previous Arctic studies, characterizes the Lofoten-Vesterålen region. Nonetheless, the diversity of meroplankton clearly reflects only a subset of the entire local benthic diversity. Low taxonomic resolution for some meroplankton may partly explain this discrepancy, but it may also indicate a high proportion of benthic organisms with direct development, short planktonic duration, or near-bottom larval distributions, which our sampling campaign did not capture. Our study revealed surprisingly little spatial variation across the continental shelf, despite large-scale differences in benthic habitats at the sampling locations. Particle tracking revealed some interesting transport patterns,

particularly given that water column properties at our sampling locations did not satisfactorily explain the observed variation in the meroplankton community. The simulated transport pathways indicate that meso- and large-scale oceanographic processes in the study area must be considered when estimating the potential of benthic communities for recovery from disturbances. At the same time, our study demonstrated the need for detailed knowledge of adult distributions and a better understanding of the mechanisms triggering larval release. Furthermore, assessment of the potential impacts of natural and anthropogenic disturbances on the resilience of Arctic and sub-Arctic benthic communities will likely require the use of new molecular methods that offer better taxonomic resolution than morphological approaches.

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Paper III

2

# Food-web structure in four locations along the European shelf indicates spatial differences in ecosystem functioning

6

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## Abstract

Studies of trophic interactions give valuable insights into the functioning of ecosystems and can be used to identify qualitative differences among ecosystems. Here, we use natural stable isotope concentrations ($\delta^{13}$C and $\delta^{15}$N) to study the food-web structure in four contrasting locations on the northern European continental shelf: two sub-Arctic locations in the Lofoten-Vesterålen region (fjord vs. open shelf) and two temperate locations (northern vs. southern North Sea). Phytoplankton was identified as the major primary producer in all studied ecosystems, even in the sub-Arctic fjord, where macroalgae only played a minor role in the food web. We used mixing models to determine the relative reliance on prey of benthic affinity and found that reliance on benthic prey was higher in the North Sea than in the Lofoten-Vesterålen region. Atlantic cod (*Gadus morhua*) was identified as the single top-predator in the North Sea, utilizing food from both, benthic and pelagic trophic channels. More separate benthic and pelagic trophic channels characterize the Lofoten-Vesterålen region, where *G. morhua* acts as part of the pelagic food chain. Furthermore, our data indicate that the recent mesopredator outburst in the southern North Sea might have been enhanced by reduced predation pressure due to the collapse of the local cod stocks. We conclude that the resilience towards a high fishing pressure is higher in the Lofoten-Vesterålen region than in the North Sea.

**Keywords:** Stable isotope analysis, pelagic-benthic coupling, benthic invertebrates, fish, North Sea, sub-Arctic, Lofoten-Vesterålen region, mesopredator release, fjord, cod

## Introduction

Food-web structure is a fundamental feature of marine ecosystems as it gives insight into how energy and contaminants are transferred from low trophic positions to upper trophic-level consumers (Hobson et al., 2002, Jardine et al., 2006, Schückel et al., 2015). It further provides insight in the relationships between biodiversity and ecosystem functioning (Cochrane et al., 2016, Duffy et al., 2005, Worm et al., 2002), and how trophic cascades may alter ecosystems (Frank et al., 2005). Knowledge of food web characteristics, such as key species, food chain length, or primary food sources, can be used to understand differences in ecosystem resilience in response to natural and anthropogenic disturbances (Kortsch et al., 2015), and is therefore essential to sustainably manage ecosystems and their harvestable resources in a changing environment.

Continental shelves sustain some of the most productive marine ecosystems in the world (Pauly and Christensen, 1995). They are estimated to contribute with over 20% to the total oceanic primary production, while contributing with less than 8% to the total surface of the oceans (Longhurst et al., 1995). They act as net carbon sink for atmospheric $CO_2$ (Thomas et al., 2004) and support the majority of all fisheries (Watson and Pauly, 2001). The northern European continental shelf, one such productive region, contains contrasting ecosystems, ranging from the temperate regions of the southern North Sea to the Arctic regions of northern Norway. Despite these differences, the marine ecosystems of the northern European continental shelf are characterized by some key overarching features: (1) Pronounced seasonality in the ecosystems with a strong influence of the North Atlantic Current (Neumann and Kröncke, 2011, Silberberger et al., 2016), (2) *Calanus* is the key zooplankton taxon and an important link between primary production and higher trophic levels (Espinasse et al., 2016, Williams et al., 1994), and (3) large stocks of commercially important fish species are sustained by these ecosystems (Ehrich et al., 2007, Føyn et al., 2002). In recent years, however, ongoing climate change has impacted all compartments of the marine ecosystem, leading to regime shifts of phytoplankton and zooplankton communities (Beaugrand and Ibanez, 2004, McQuatters-Gollop et al., 2007, Richardson and Schoeman, 2004), distributional shifts of benthos (Birchenough et al., 2015, Kröncke et al., 2011), and deepening of fish assemblages (Dulvy et al., 2008). Cod has disappeared almost completely from the southern North Sea due to overfishing and climate change (Beaugrand and Kirby, 2010, Daan et al., 2005), and the region has changed into flatfish dominated communities, including abundant commercial species (*e.g. Pleuronectes platessa*) and particularly high abundances of small non-commercial mesopredatory species (*e.g. Buglossidium luteum*) (Ehrich et al., 2007, Schückel et al., 2012, van Hal et

al., 2010). Furthermore, mackerel is extending its range northwards into the sub-Arctic (Stenevik and Sundby, 2007, Utne et al., 2012). In connection to the ongoing climate change, further changes are predicted, like the continuing shifts in benthic species distributions (Renaud et al., 2015b, Weinert et al., 2016). It remains unclear, however, whether the observed fisheries and climate induced changes in the ecosystem has resulted in altered food-web structures and, furthermore, whether the food webs of contrasting ecosystems across climate regions are expected to respond in a similar way to future environmental changes. Thus, comparing food web structures and their key trophic groups across climate zones might reveal potential consequences of natural and anthropogenic pressures on these ecosystems.

Ratios of naturally occurring carbon ($^{13}$C/$^{12}$C) and nitrogen ($^{15}$N/$^{14}$N) isotopes, expressed as $\delta^{13}$C and $\delta^{15}$N, have become one of the most common tools to study the trophic structure of marine ecosystems (Kürten et al., 2013, Post, 2002b, Renaud et al., 2011, Vander Zanden and Fetzer, 2007). The method makes use of the principle that the stable isotope composition of an animal depends on the isotopic composition of its food, with some characteristic enrichment of the heavier isotope during each trophic transfer (typically 3 – 4‰ for $\delta^{15}$N and 1‰ for $\delta^{13}$C) (DeNiro and Epstein, 1978, Minagawa and Wada, 1984, Post, 2002b). In stable isotope analysis, the large trophic enrichment of $^{15}$N makes it a reliable indicator of the trophic position of an organism. The rather small trophic enrichment of $^{13}$C, makes it a suitable tracer to identify carbon sources (Fry and Sherr, 1984, Hobson et al., 1995). Benthic invertebrates are generally enriched in $^{13}$C compared to pelagic species and may therefore be used to identify if carbon has been cycled through the benthos prior to consumption (Hobson et al., 2002, Nadon and Himmelman, 2006).

In this study, we utilize stable-isotope analysis to investigate the food-web structure of four contrasting ecosystems on the northern European continental shelf. The main objectives were (i) to compare sub-Arctic and temperate food webs of shelf seas and identify structural differences among the study systems and (ii) evaluate whether the food-web structure in the different systems could favor community shifts similar to shifts already observed in another location.

## Methods

### Study locations

Our study compares the food-web structure of four contrasting ecosystems on the northern European continental shelf (Fig.1). Two locations in the sub-Arctic Lofoten-Vesterålen region represent one open shelf location (Hola; 68°57.0'N, 14°10.8'E; depth: 195-220 m) and one fjord (Malnesfjord; 68°48.2'N, 14°36.5'E; maximum depth: 160 m). The other two locations are part of the German Small-scale Bottom Trawl Survey (GSBTS) as 'Box L' and 'Box A' (Ehrich et al., 2007), and are situated in the temperate northern North Sea (58°45.0'N, 02°33.3'E; depth: 105-119 m) and in the warm-temperate German Bight (54°22.2'N, 07°06.0'E; depth: 36-45 m). Besides representing different climatic regimes, the study locations also represent different exploitation regimes with fisheries targeting different components of the food web. Fisheries in these ecosystems range from beam trawling targeting flatfish (German Bight), over line- and trawl fisheries on gadoid fish (northern North Sea and Hola), to aquaculture and small-scale recreational fisheries (Malnesfjord) (Ehrich et al., 2007, ICES, 2013).

### Sampling

Samples from the Lofoten-Vesterålen region were collected with M/S *Skårungen* (Skå) in Malnesfjord on April 28-29, 2014, and in Hola with R/V *Helmer Hanssen* (HH) on April 19-26, 2015. Samples from the locations in the North Sea were collected with R/V *Walther Herwig III* (WHIII) as part of the GSBTS between July 28 and August 23, 2014.

Pelagic particulate organic matter (POM) was collected from the chlorophyll maximum using a rosette water sampler (WHIII, HH) or a single Niskin bottle (Skå) and filtered on pre-combusted GF/F filters (pore size: 0.7 µm, 2000-3000 mL filtered per sample). Filters were visually inspected under a dissecting microscope and mesozooplankton was removed. Particulate organic matter from the sediment (sediment) was collected from the upper 2 cm of van Veen grab samples. Sediment was visually inspected under a dissecting microscope and macro-invertebrates were removed. Macroalgae were collected using a beam trawl (opening 2 m, mesh size 4 mm) in Malnesfjord. Macroalgal detritus was collected from bottom trawls in the North Sea. Macroalgae and macroalgal detritus were cleaned of epiphytes and other attached material. A WP2 net (ø 0.57 m, mesh size 180 µm; Skå, HH) or a hand-towed plankton net (mesh size 100 µm; WHIII) were used to collect mesozooplankton samples. *Calanus* spp. was handpicked from these samples under a dissecting microscope. Beam trawls (opening 2 m, mesh size 4 mm) and van Veen grabs (sample area 0.1 m$^2$) were used to

153    collect epi- and infauna, respectively. Fish were collected by bottom trawling. No bottom
154    trawling was possible in Malnesfjord and fish were collected from beam trawls. Small
155    invertebrates were collected and kept alive for 18-24 hours to allow for gut evacuation
156    prior to freezing. All other samples were frozen immediately at -20°C until further
157    processing.
158
159    **Stable isotope analysis**
160
161    Sample preparation for stable isotope analysis followed the recommendations of
162    Jardine et al. (2003). For fish and larger crustaceans, muscle tissue was used for sample
163    preparation. For asteroids and ophiuroids we used one or several arms, for echinoids
164    we used gonads and internal viscera, and for molluscs we used only soft tissue. Small
165    fragments were used for bryozoans, cnidarians and macroalgae. For small invertebrates,
166    the entire animal was processed. One or several individuals were used for each isotope
167    sample and replicate samples were prepared for all taxa where enough individuals were
168    collected (compare Table 1). All samples were dried at 60°C for 24-72 hours. Sediment,
169    macroalgae, and animal samples were ground to a fine powder with mortar and pestle.
170    *Calanus* spp. was not ground due to their small size. Carbonates were removed from
171    samples through treatment with hydrochloric acid, since non-dietary carbonates may
172    affect $\delta^{13}C$ concentrations (DeNiro and Epstein, 1978). However, acidification adversely
173    affects $\delta^{15}N$ concentration (Bunn et al., 1995). Therefore, samples expected to contain
174    carbonates were split in half (see Table 1) and analyzed separately for $\delta^{13}C$ (acidified)
175    and $\delta^{15}N$ (non-acidified) concentrations. Samples were weighed in tin capsules and
176    analyzed for $\delta^{13}C$ and $\delta^{15}N$ by a Carlo Erba NC2500 elemental analyzer interfaced to a
177    Thermo Finnigan Delta Plus/Conflo II mass spectrometer or a Costech 4010 elemental
178    analyzer interfaced to a Thermo Finnigan Delta XP/Conflo III mass spectrometer in the
179    Stable Isotopes in Nature Laboratory, Department of Biology, University of New
180    Brunswick, Canada. Stable isotope measurements are reported in delta ($\delta$) notation in
181    parts per thousand (‰) relative to the international standard: Vienna Pee Dee
182    Belemnite for carbon, and atmospheric air for nitrogen. Isotope values were normalized
183    using secondary standards: Nicotinamide, bovine liver standard, and muskellunge
184    muscle standard for animal tissues; and corn meal standard, aquatic moss standard,
185    spirulina standard and ephedra plant standard for sediments and plant material.
186
187    **Data analysis**
188
189    High lipid content can affect $\delta^{13}C$ values and, therefore, lipid normalization was
190    performed for samples with C:N > 4 (Jardine et al., 2003, McConnaughey and McRoy,
191    1979):

192

193    $\delta'^{13}C = \delta^{13}C + 6 \times (-0.207 + 3.9 / (1 + 287 \times (1 + 1 / (0.246 \times C:N - 0.775)) / 93))$

194

195    We used $\delta^{15}N$-values to estimate the individual trophic position of each species. A
196    robust $\delta^{15}N$ baseline is indispensable for a reliable estimation of individual trophic
197    position (TP). Due to various practical reasons, the establishment of a primary producer
198    based $\delta^{15}N$ baseline may be very difficult and primary consumers have become the
199    common choice (Post, 2002b). We used a two-source mixing model to calculate TP based
200    on a benthic and pelagic primary consumer baseline at each study location (Post,
201    2002b):

202

203    $TP_{consumer} = \lambda + (\delta^{15}N_{consumer} - (\delta^{15}N_{benthic\ baseline} \times \alpha + \delta^{15}N_{pelagic\ baseline} \times (1 - \alpha))) / \Delta^{15}N$

204

205    Where $\lambda$ is the estimated TP of the established baseline (here $\lambda = 2$). As the benthic
206    baseline, we defined the benthic invertebrate with the lowest mean $\delta^{15}N$-value
207    (compare Fig. 2) at each sampling location (Hola: *Modiolula phaseolina*; Malnesfjord:
208    *Strongylocentrotus droebachiensis*; northern North Sea: *Acanthocardia echinata*;
209    German Bight: *Echinocardium cordatum*). *Calanus* spp. was used as pelagic baseline for
210    all stations. For the calculation of individual trophic position we assumed equal reliance
211    on the benthic and pelagic baseline ($\alpha = 0.5$). This provides a realistic estimate for the
212    majority of taxa which we expect to rely on a mixture of benthic and pelagic prey
213    (McMeans et al., 2015, McMeans et al., 2013, Renaud et al., 2015a). However, this might
214    misplace taxa relying completely on one of the sources for locations with large
215    differences between benthic and pelagic baseline. We used the widely applied trophic
216    fractionation ($\Delta^{15}N$) of 3.4‰ (Post, 2002b).

217

218    We estimated the reliance on benthic affinity prey (RBAP) for all faunal taxa. We
219    corrected for trophic fractionation of $\delta'^{13}C$, by applying a trophic fractionation ($\Delta^{13}C$) of
220    1‰ per trophic step (= 3.4‰ $\delta^{15}N$) (DeNiro and Epstein, 1978, Post, 2002b). The
221    correction is necessary for each taxon individually to standardize all taxa on the same
222    trophic level, and thereby account for differences in trophic positions between the
223    consumers and the used $\delta^{13}C$-baselines. The corrected values ($\delta''^{13}C$) were then used to
224    estimate RBAP in a two-source mixing model (Vander Zanden and Vadeboncoeur, 2002):

225

226    $RBAP = (\delta''^{13}C_{consumer} - \delta''^{13}C_{pelagic\ baseline}) / (\delta''^{13}C_{benthic\ baseline} - \delta''^{13}C_{pelagic\ baseline}) \times 100\%$

227

228    *Calanus* spp. was used as pelagic baseline for all study locations. The most $\delta''^{13}C$-
229    enriched taxon was defined as benthic baseline, assuming 100% RBAP for this taxon
230    (Hola: *Stichastrella rosea*; Malnesfjord: *Galathea dispersa*; northern North Sea:
231    *Neptunea antiqua*; German Bight: *Turritella communis*). We did not calculate RBAP for

232 *S. droebachiensis* in Malsnesfjord, since they showed strong reliance on macroalgae. Our
233 analysis showed that primary consumers (incl. *Calanus* spp.) in Lofoten-Vesterålen had
234 already picked up the isotopic signature of the ongoing spring bloom, while this signal
235 was not yet reflected in higher trophic positions (see results). Therefore, we used
236 available pre-bloom *Calanus* spp. isotopic data from 16 January 2015 from Hola to
237 calculate RBAP a second time, based on a winter planktonic baseline.
238
239    All faunal taxa were assigned to one of five functional groups: Fish (F), zooplankton
240 (Z), suspension feeding benthos (SF), deposit feeding benthos and grazer (DF) and
241 predator and scavenging benthos (PS) (Table 1). This assignment was done with the
242 World Register of Marine Species (WoRMS Editorial Board, 2016), supplemented with
243 information from Hayward and Ryland (1995) and MarLIN (Marine Life Information
244 Network) (2016).
245
246    We assumed a trophic fractionation of 4‰ for $\delta^{13}$C for the trophic transfer from
247 primary producers to primary consumers and of 1‰ per trophic step thereafter (Hobson
248 et al., 1995, Renaud et al., 2015a). Analysis of variance (ANOVA) was used to identify
249 differences in $\delta^{13}$C and $\delta^{15}$N signature between carbon sources (POM, sediment,
250 Phaeophyceae, Rhodophyta, Phaeophyceae detritus) at all locations. Welch's ANOVA
251 was performed for $\delta^{13}$C in Malnesfjord, since the ANOVA assumption of homogeneity of
252 variances was violated. *Post-hoc* tests (Tukey's HSD, Games-Howell for $\delta^{13}$C in
253 Malnesfjord) were performed for locations with more than two carbon sources
254 (Malnesfjord, German Bight). The single sample of Phaophyceae detritus from the
255 northern North Sea had to be excluded from statistical tests. ANOVA was used to test
256 for significant differences in isotopic signature between previously identified groups of
257 fish. Significance level were set to α = 0.05 for all tests. *P*-values are only reported for
258 significant results.
259
260    Three samples from Malnesfjorden were identified as outliers (2 × *Thyasira* spp., 1 ×
261 *Nephtys* sp.) and therefore excluded from all analyses but qualitative comparisons.
262

# Results

## Hola

Stable carbon and nitrogen isotope ratios of 33 faunal species (7 fish, 25 benthic species, 1 zooplankton species) and 2 potential carbon sources (POM, Sediment) were analyzed from Hola (Fig. 2a). Sediment was significantly enriched in $\delta^{15}N$ compared to POM ($p < 0.001$ [ANOVA]), while no difference in $\delta^{13}C$ was observed between the two carbon sources. The $\delta^{15}N$ baseline (TP = 2) was established at 5.3‰ (Benthic baseline: $\delta^{15}N_{M.\ phaseolina}$ = 5.0‰; pelagic baseline: $\delta^{15}N_{Calanus\ spp.}$ = 5.7‰). *Calanus* spp. and three suspension-feeding bivalves (*M. phaseolina*, *Karnekampia sulcata*, *Parvicardium* sp.) formed a cluster around TP 2 (Fig. 2a). The isotopic values of these taxa were almost identical, suggesting they all fed directly on POM from the ongoing spring bloom, although the observed trophic fractionation ($\Delta^{15}N \approx 5$; $\Delta^{13}C \approx 2.5$) did not exactly match the assumed trophic fractionation for the trophic transfer from primary producers to primary consumers. The remaining benthic invertebrate taxa occupied TP between 2.6 and 4.1, with no clear separation of the different feeding types. Atlantic cod (*Gadus morhua*) was the most $\delta^{15}N$-enriched species, with a calculated TP of 4.2. However, this did not differ strongly from the TP of the other fish species (range: 3.9 – 4.1).

Calculated RBAP was generally low, with a trend of decreasing RBAP with increasing TP. Some taxa with TP > 3.5 had an extremely negative RBAP, making it obvious that the $\delta^{13}C$ signal from the spring bloom was not yet transferred to these high trophic levels at the time of sampling (Fig. 3a). Therefore, we used available pre-bloom isotopic values of *Calanus* spp. ($\delta^{13}C$: -22.0‰; $\delta^{15}N$: 8.8‰), sampled a few km away but within Hola, to calculate more realistic RBAP values for higher trophic positions. The fish were separated in two groups according to $\delta^{13}C$ ($p < 0.001$ [ANOVA]): one group (*G. morhua*, *Pollachius virens*, *Myxine glutinosa*, *Argentina silus*) almost exclusively relying on pelagic prey, and the other group (*Microstomus kitt*, *Artediellus atlanticus*, *Hippoglossoides platessoides*) with 40-50% reliance on benthic prey.

## Malnesfjord

Isotopes of 19 faunal species (4 fish, 14 benthic species, 1 zooplankton species) and 7 potential carbon sources (3 Phaeophyceae, 2 Rhodophyta, POM, sediment) were analyzed from Malnesfjord (Fig. 2b). *Thyasira* sp. and one of the *Nephtys* sp. samples in Malnesfjord were extremely depleted in $\delta^{13}C$ and $\delta^{15}N$ and therefore identified as outliers. POM in Malnesfjord was significantly depleted in $\delta^{15}N$ in comparison to Rhodophyta, Phaeophyceae, and sediment ($p < 0.001$ [Tukey's HSD] for all), which did

not differ significantly from each other. In terms of $\delta^{13}C$, however, Rhodophyta were substantially and significantly depleted compared to Phaeophyceae ($p = 0.001$ [Games-Howell]), POM ($p = 0.003$ [Games-Howell]), and sediment ($p = 0.002$ [Games-Howell]). Phaeophyceae were also depleted in $\delta^{13}C$ compared to POM ($p = 0.038$ [Games-Howell]) and sediment ($p = 0.002$ [Games-Howell]), which did not differ significantly from each other. The $\delta^{15}N$-baseline (TP = 2) was established at 6.8‰ (Benthic baseline: $\delta^{15}N_{S. droebachiensis}$ = 7.0‰; pelagic baseline: $\delta^{15}N_{Calanus\ spp.}$ = 6.6‰). Because of their extreme depletion in $\delta^{13}C$, the collected Rhodophyta were clearly not important as carbon source for any of the collected fauna. Phaeophyceae, however, were identified as a possible carbon source for *S. droebachiensis*; although the assumed $\Delta^{13}C$ and $\Delta^{15}N$ were not met. Of all other benthic taxa, only *Brisaster fragilis* was identified as a candidate to rely on Phaeophyceae as carbon source. Surprisingly, all other taxa showed strong similarities in isotopic signature with the pattern described for Hola, although the variability in $\delta^{13}C$ was larger (overall and individual taxa). Furthermore, the collected taxa did not include any suspension feeders with similar isotopic signature to *Calanus* spp.

The fish collected in Malnesfjord did not include any typical pelagic species and all individuals were small compared to the same species collected in Hola. This was probably related to the collection method and not the absence of these fish from Malnesfjord. All the fish occupied a TP < 4, similar to a group of the most $\delta^{15}N$-enriched benthic taxa (*Hormathia digitata*, *Neptunea despecta*, *Nicomache* spp., *Ctenodiscus crispatus*) with TP 3.5-3.8. However, the two individual cod samples in Malnesfjord differed strongly from each other (TP 4.2 vs. TP 3.5).

Similar to Hola, calculated RBAP was low for TP > 3.5, but values were not as negative as in Hola. Only four benthic taxa (*G. dispersa*, *Hyas coarctatus*, *Astropecten irregularis*, *Ophiura sarsii*) showed a high reliance on benthic affinity prey (RBAP > 40%). These results indicate a similar situation as in Hola. However, no pre-bloom isotopic data for *Calanus* spp. were available, and therefore no second RBAP calculation was conducted.

**Northern North Sea**

Isotopes of 28 faunal species (9 fish, 18 benthic species, 1 zooplankton species) and 3 potential carbon sources (1 Phaeophyceae (detritus), POM, sediment) were analyzed from the northern North Sea (Fig. 2c). The single sample of Phaeophyceae detritus (*Ascophylum nodosum*) was particularly enriched in $\delta^{13}C$ compared to all other samples collected at this location, indicating that it has little or no importance as food item for any collected fauna. POM was significantly depleted in $\delta^{13}C$ ($p < 0.001$ [ANOVA]) compared to sediment, but not in $\delta^{15}N$ concentration. The $\delta^{15}N$ baseline (TP = 2) was

established at 5.7‰ (Benthic baseline: $\delta^{15}N_{A.\,echinata}$ = 5.0‰; pelagic baseline: $\delta^{15}N_{Calanus\,spp.}$ = 6.4‰). The $\delta^{15}N$-enrichment of *Calanus* spp. in comparison to POM was in accordance with the expected $\Delta^{15}N$, while differences in $\delta^{13}C$ were virtually absent. Besides the suspension feeding bivalve *A. echinata* (TP 1.8), all other potential benthic primary consumers (DF and SF) were assigned a TP 2.4-2.8 and thereby at a generally lower TP than the bulk of benthic secondary consumers (PS: TP 2.7-3.9). All benthic taxa were considerably $\delta^{13}C$-enriched compared to *Calanus* spp.

Fishes generally occupied higher TP than benthos (TP 3.4-4.6) with *G. morhua* occupying the position as top predator in this system. Only *Myxine glutinosa* reached a similar TP (4.4), while all other species were assigned to a TP < 4. According to $\delta^{13}C$, these fish were divided into two significant groups ($p < 0.001$ [ANOVA]): (1) predominantly pelagic feeding (RBAP 26-45%; *Scomber scombrus*, *Clupea harengus*, *Pollachius virens*) and (2) predominantly benthic feeding (RBAP 61-72%; *Limanda limanda*, *Hippoglossoides platessoides*, *P. platessa*, *Amblyraja radiata*). *G. morhua* and *M. glutinosa* had an intermediate RBAP of 57% and 50% respectively. Furthermore, RBAP indicated an overall high reliance of benthos on benthic prey (49-100%).

**German Bight**

Isotopes of 23 faunal species (8 fish, 14 benthic species, 1 zooplankton species) and 7 potential carbon sources (2 Phaeophyceae (detritus), POM, sediment) were analyzed from the German Bight (Fig. 2d). Isotopic signature of POM and sediment in the German Bight were virtually identical, representing potential food sources for all potential benthic primary consumers (*E. chordatum*, *Nucula nitida*, *Turitella communis*, *Chamelea gallina*). In comparison to POM and sediment, macroalgal detritus was enriched in $\delta^{13}C$ ($p \leq 0.001$ [Tukey's HSD] for both) and $\delta^{15}N$ ($p < 0.001$ [Tukey's HSD] for both). Especially *A. nodosum* detritus had a $\delta^{13}C$ value that clearly indicated no considerable role as food for any of the collected fauna. The other collected detritus in the German Bight (*Cystoseira* sp.) cannot be ruled out as potential food source based on its $\delta^{13}C$. However, its $\delta^{15}N$ value was considerable higher than all the collected potential primary consumers. The $\delta^{15}N$ baseline (TP = 2) was established at 11.2‰ (Benthic baseline: $\delta^{15}N_{E.\,cordatum}$ = 9.5‰; pelagic baseline: $\delta^{15}N_{Calanus\,spp.}$ = 12.9‰). *Calanus* spp. was particularly $\delta^{15}N$ enriched, placing it one TP above the benthic deposit feeder and even slightly higher than mackerel (*S. scombrus*), which was particularly depleted in $\delta^{15}N$. The isotopic signature of *Calanus* spp. indicated no reliance on the collected POM. All assumed benthic secondary consumers (PS) occupied a much higher TP (2.4-3.4) than the potential primary consumers (TP 1.5-1.9). Among the fishes, *G. morhua* occupied the highest TP (4.1), which is considerably higher than for all the other fish species (TP 2.2-3.6).

380

381      The RBAP in the German Bight was quite high overall. All benthic species with the
382 exception of *C. gallina* (RBAP: 35%) had a calculated RBAP of over 60%. For fish, the
383 planktonic feeding *C. harengus* and *S. scombrus* had a low RBAP (< 35%). Conversely, the
384 medium sized flat fish *L. limanda* and *P. platessa* were almost exclusively feeding on
385 benthic prey (RBAP 78-83%). The two collected mesopredatory species (*B. luteum* (RBAP
386 63%), *Agonus cataphractus* (RBAP 67%)) showed a similar reliance on benthic prey as *G.*
387 *morhua* (RBAP 68%).

388

## Discussion

**Carbon sources and the δ¹⁵N-baselines**

The isotopic signature of *Calanus* spp. suggests that the pelagic food web in Hola, Malnesfjord, and the northern North Sea were directly linked to POM. In the German Bight, however, *Calanus* spp. was $^{15}$N-enriched and relied on a carbon source not represented in our data. We propose two possible explanations for this: (i) *Calanus* spp. might not have acted as primary consumer in the German Bight, and feeding in late summer was primarily on microzooplankton (Corner et al., 1976), or (ii) *Calanus* spp. could have selectively fed on $^{15}$N-enriched components in the collected POM samples. Isotopic signatures of POM and sediment in the German Bight were virtually identical, indicating that resuspended organic material may have dominated these POM samples. Large parts of such resuspended material are probably unsuitable as food for *Calanus* (DeMott, 1988), and could explain the differences in isotopic signatures of *Calanus* spp. and POM.

In contrast to the pelagic δ¹⁵N-baselines, the benthic δ¹⁵N-baselines showed strong differences between the Lofoten-Vesterålen region and the North Sea. Isotopic signatures suggest a high importance of fresh primary production in Lofoten-Vesterålen, while the sediment had a high importance in the North Sea, although POM and sediment were indistinguishable in the German Bight. This difference could well be an artifact of the different sampling seasons and not a functional difference between the ecosystems. The majority of benthic primary consumers are considered temporal couplers (McMeans et al., 2015), utilizing primary production, but changing to a detritus based diet when no fresh primary production is available.

We included various macroalgae as potential carbon sources in Malnesfjord. Only the echinoids *S. droebachiensis* and *B. fragilis* were identified to utilize carbon from Phaeophyceae, while red algae do not seem to play a role as food for any collected taxa. *S. droebachiensis* is known to graze on macroalgae. The lack of other taxa relying on macroalgae was surprising, since it seems in contrast to other studies from Norwegian fjords and coast (Fredriksen, 2003, Nilsen et al., 2008, Renaud et al., 2015a). The total absence of macroalgal grazers in our study, however, was at least partly related to the sampling methods (grabs and trawls). We did not use scuba diving or focus on collecting fauna that live and feed directly on macroalgae (Fredriksen, 2003). In addition, studies that have identified macroalgae as an important carbon source were able to do so since macroalgae had a distinct (enriched) δ¹³C signal compared to POM. Among the macroalgae in Malnesfjord, none was more δ¹³C-enriched than POM. Benthic organisms

428  from all locations in our study, however, were enriched in δ$^{13}$C compared to
429  zooplankton. Nadon and Himmelman (2006) pointed out that other carbon sources
430  (terrestrial carbon or microphythobenthos) or $^{13}$C enrichment of POM during sinking can
431  result in the heavy carbon signal seen in the benthos throughout our study. We cannot
432  rule out that other more $^{13}$C-enriched macroalgae were used as a carbon source by
433  benthos in Malnesfjord, but the general similarity of isotopic signatures in Hola and
434  Malnesfjord indicates that the processes described by Nadon and Himmelman (2006)
435  are more likely explanations for the observed pattern.
436
437  The established δ$^{15}$N-baseline in the German Bight (11.2‰) was very high in
438  comparison to all other locations (5.3 – 6.8‰). Accordingly, the δ$^{15}$N values in the
439  complete German Bight were high, which is known from other human impacted coastal
440  regions (Sherwood and Rose, 2005) and reflects the known high δ$^{15}$N values in surface
441  sediments in the German Bight. This has been attributed to the large riverine input of
442  reactive nitrogen in the German Bight (Pätsch et al., 2010).
443
444  Food-chain length and TP estimates are strongly dependent on the choice of δ$^{15}$N-
445  baseline in stable isotope studies (Post, 2002b). We used a two-source δ$^{15}$N-baseline
446  estimate, since this approach leads to more realistic TP for most taxa, which we
447  expected to rely on a mixture of benthic and pelagic prey (McMeans et al., 2015,
448  McMeans et al., 2013, Renaud et al., 2015a). The difference between the benthic and
449  pelagic δ$^{15}$N-baseline was small for Hola, Malnesfjord, and the northern North Sea.
450  Therefore, we are confident that the calculated TPs are realistic estimates of the TP
451  regardless of exact proportions supplied by each potential carbon source. The δ$^{15}$N-
452  baseline in the German Bight, however, was based on very different benthic and pelagic
453  baselines. Therefore, the individual TPs need to be interpreted with care, taking into
454  account the calculated RBAP of the different taxa. A large number of taxa in the German
455  Bight relied predominantly on benthic affinity prey (RBAP > 70%). For these taxa, the
456  presented TP should be considered underestimates of approximately 0.2-0.3 TP.
457
458  In addition to the choice of δ$^{15}$N-baseline, assumptions have to be made about the
459  trophic fractionation to estimate trophic position in a food web. The trophic
460  fractionation factor of 3.4‰, used in this study, is widely used, due to its general good
461  performance (Post, 2002b, Vander Zanden and Fetzer, 2007). This being said, it needs
462  to be noted that a scaled fractionation factor approach describes the actual trophic
463  position more accurately, since the trophic fractionation declines with increasing trophic
464  position (Hussey et al., 2014). However, applying such an approach would require the
465  assumption of 100% reliance on a single carbon source, which we did not assume, hence
466  the two source δ$^{15}$N-baseline. The benefit of a scaled approach would be a more
467  accurate individual TP estimate, which was not the primary focus of this study, but it

468  would not affect the relative trophic position within the food web and the observed
469  food-web structures. Furthermore, due to the common application of 3.4‰, a scaled
470  approach would hinder a direct comparison with the majority of the existing literature
471  (Vander Zanden and Fetzer, 2007).
472

**Benthic invertebrates**

474

475  Our study has shown that the *a priori* assigned feeding groups for the benthos were
476  well supported by the isotopic data from both North Sea locations. Potential primary
477  consumers were assigned to the lowest TPs, while secondary consumers occupied
478  clearly higher TPs (Fig. 2). Kürten et al. (2013) came to a similar conclusion for their
479  studies in the North Sea. In the Lofoten-Vesterålen region, however, the potential
480  primary consumers occupied a wide range of TPs. This was observed for suspension
481  feeders (Hola: 1.89 – 3.74; Malnesfjord: 2.68 – 3.03) and deposit feeders and grazers
482  (Hola: 3.00 – 3.81; Malnesfjord: 2.06 – 3.70) (Fig. 2). This observation is probably related
483  to a combination of various factors including: (i) Feeding relationships are better studied
484  for temperate species, and (ii) Feeding relationships are more variable at high latitudes
485  and at greater depth, since food pulses are more variable. For example, the assumed
486  suspension feeding ophiuroid *Asteronyx loveni* is known to switch from microphagous
487  to macrophagous filter feeding and has also been suggested to feed on the sea pen
488  *Funiculina quadrangularis* (von Salvini-Plawen, 1972), to which it is normally attached.
489  Such a feeding relation would be in accordance with the particularly high TP of *A. loveni*
490  and the relative isotopic signatures of both species in our study. A third factor leading
491  to these feeding differences may be due to our sampling in Lofoten-Vesterålen during
492  the spring bloom. This fresh organic matter may not be reflected in all taxa equally, since
493  turnover times of tissue vary among taxa (Jardine et al., 2006). The isotopic signal from
494  the spring bloom was reflected in taxa at low TPs in Lofoten-Vestrålen, but not at
495  intermediate and high TPs. This can be expected, since the typical seasonal variation at
496  the base of the food web (Kürten et al., 2013) is dampened by the longer turnover times
497  and the integration of various food sources at higher TP (Jardine et al., 2006, McMeans
498  et al., 2015). Nonetheless, structural differences at high TP in the benthic compartment
499  of the food webs were observed between Lofoten-Vesterålen and the North Sea: (i)
500  RBAP was lower in Lofoten-Vesterålen than in the North Sea. (ii) Many benthic taxa
501  occupied high TPs, similar to fish, in Lofoten-Vesterålen, while TPs of benthos were
502  clearly lower than fish in the North Sea. This indicates that top-down control by fish
503  might play an important role for benthic communities in the North Sea, while bottom-
504  up processes are dominating the ecosystem in Lofoten-Vesterålen.
505

506    Within our samples from Malnesfjord, we identified three samples (2 × *Thyasira* sp.,
507    1 × *Nephtys* sp.) as outliers since they were extremely depleted in both, $\delta^{13}$C and $\delta^{15}$N.
508    *Thyasira* sp. have previously been identified as particularly $\delta^{13}$C- and $\delta^{15}$N-depleted
509    (Rigolet et al., 2014), due to symbiotic chemo-autotrophic bacteria in their gill tissue
510    (Dando and Spiro, 1993). The strong depletion of one *Nephtys* sp. sample is more
511    difficult to explain. It is however possible that the collected individual partly fed on
512    *Thyasira* sp.
513
514    **Fish**
515
516    Estimated food-chain lengths (*i.e.* the TP of the top predator) in Hola (4.2),
517    Malnesfjord (3.9), and the German Bight (4.1) correspond well with the reported global
518    average (3.97±0.47) for marine ecosystems (Vander Zanden and Fetzer, 2007). Food
519    chain length in the northern North Sea (4.6), however, was longer than this average.
520    Such a longer food chain might be linked to a number of ecosystem characteristics,
521    including the history of community organization, resource availability, predator–prey
522    interactions, disturbance, and ecosystem size (Post, 2002a). However, Post (2002a)
523    showed that no single characteristic can satisfactory explain a longer food chain and it
524    is likely that the longer food chain in the northern North Sea is attributed to a
525    combination of several of these ecosystem characteristics. The slightly longer food chain
526    in Hola compared to Malnesfjord was probably caused by the size differences of the
527    collected top predators in Malnesfjord (*M. kitt* ≈ 30 cm; *G. morhua* < 25 cm) and Hola
528    (*M. kitt* ≈ 50cm; *G. morhua* > 70 cm). Prey size generally increases with fish predator size
529    (Scharf et al., 2000), possibly indicating feeding on higher TP (Barnes et al., 2010). For
530    cod, a major diet change from predominantly benthic invertebrates to predominantly
531    fish occurs commonly at a size of 25-30 cm (Hislop et al., 1997). We do not believe that
532    bigger fish were absent from Malnesfjord, but we were not able to collect them, and
533    therefore, the difference in food chain length between the two locations in Lofoten-
534    Vesterålen should be considered an artifact.
535
536    Furthermore, it has to be considered that sampling during the spring bloom in
537    Lofoten-Vesterålen could have affected our estimation of the food-chain length in
538    comparison to the North Sea. A depletion in $\delta^{15}$N during the spring bloom only at the
539    base of the food web (Kürten et al., 2013), could result in an overestimation of food-
540    chain length. This would mean that food chain length in Lofoten-Vesterålen is generally
541    shorter than in the North Sea. Renaud et al. (2011), however, found only little change in
542    food-web structure across seasons and it remains questionable whether the estimated
543    food chain lengths were affected by the sampling season in our study.
544

545    Atlantic cod (*G. morhua*) occupied the highest TP at all locations. In both North Sea
546    locations, *G. morhua* was identified as the single top predator, while its TP was similar
547    to other fish species in the Lofoten-Vesterålen region. Not only did the TP of *G. morhua*
548    in relation to the other fish species differ between Lofoten-Vesterålen and the North
549    Sea, but also its reliance on benthic affinity prey was much lower in the Lofoten-
550    Vesterålen region than in the North Sea. This is in accordance with previous studies of
551    gut contents (Michalsen et al., 2008) that showed that planktivorous fish, particularly
552    herring (*C. harengus*) and Norway pout (*Trisopterus esmarkii*), constitute the main prey
553    for adult cod in the Lofoten-Vesterålen region (same size range as cod from Hola in this
554    study). This high reliance on pelagic feeding prey indicates that cod stocks in the Lofoten-
555    Vesterålen region might be affected by the northward extension of typical pelagic
556    species (Stenevik and Sundby, 2007). With the ongoing climate change, feeding
557    migrations of mackerel to the North are expected earlier in the season (Utne et al.,
558    2012). This will lead to a large temporal overlap of mackerel and larvae of Norwegian
559    spring spawning herring, and the resulting predation could have regulatory effects on
560    the herring stock (Skaret et al., 2015), and consequently on the available food for cod.
561    In contrast, North Sea cod relied approximately equally on pelagic and benthic affinity
562    prey, which is in accordance with previous studies of stable isotopes from
563    Newfoundland and Labrador (Sherwood and Rose, 2005), and stomach contents from
564    the North Sea (Hislop et al., 1997).
565
566    Today, cod is only present in very low numbers in the southern North Sea and the
567    ecosystem has shifted towards a flatfish dominated community, along with particularly
568    high abundances of small, demersal, mesopredatory fish (*B. luteum*, *Arnoglossus*
569    *laterna*, *A. cataphractus*, *Pomatoschistus* spp.) (Daan et al., 2005, Ehrich et al., 2007, van
570    Hal et al., 2010). Surprisingly, our results suggest a higher TP of *B. luteum* (3.47) and *A.*
571    *cataphractus* (3.59) than for medium sized flatfishes (*L. limanda*: 3.19; *P. platessa*: 3.15)
572    in the German Bight, although this was not identified as significant at the chosen
573    significance level. Furthermore, the medium sized flatfish species showed a higher RBAP
574    than the small mesopredators. Therefore, our data support the results of Schückel et al.
575    (2012), who found little dietary overlap between small and medium sized flatfishes. Cod
576    is known to be the most frequent predator of *B. luteum* and *A. cataphractus* in the
577    southern North Sea (Pinnegar, 2014). Our data showed that cod was the only species at
578    a higher TP than these species in the German Bight. Furthermore, cod showed a similar
579    RBAP to *B. luteum* and *A. cataphractus*, indicating cod as the only predator of these
580    species in the German Bight. Therefore, we suggest that the recent cod decline and the
581    associated reduced top-down control might have resulted in the release of
582    mesopredators in the southern North Sea.
583

584    In contrast to benthos, fish can move among habitats, and isotopic signatures might
585    not always be related to the sampling site (Hansson et al., 1997). We found the isotopic
586    signature of *S. scombrus* in the German Bight to be unrelated to other samples from this
587    location, but instead was virtually identical to mackerel from the northern North Sea,
588    and could reflect the migratory nature of mackerel (Iversen, 2002). It is possible that the
589    collected mackerel from the German Bight had just migrated into this region prior to
590    sampling, and therefore they would still reflect the isotopic signature of their previous
591    feeding grounds.
592

## Conclusion

Our study has shown that the coupling of the benthic and pelagic compartments of food webs differs between the Lofoten-Vesterålen region and the North Sea, and therefore food webs might be affected differently by environmental changes (Krause et al., 2003). Top predators feed either from pelagic or benthic trophic channels in Lofoten-Vesterålen, while the only top predator (*G. morhua*) in the North Sea feeds from both channels. Our data suggest that the collapse of the cod stock in the southern North Sea might have enhanced the mesopredator outburst in the region. High structural similarity in both North Sea food webs indicate that the northern North Sea might undergo a similar mesopredator release (fish or invertebrate) if the cod stock decreases due to overfishing or climate change. In the Lofoten-Vesterålen region, however, overfishing of a single species would not be expected to have such an extreme effect on the system. Both, the pelagic and benthic channel sustain a larger number of species that could fill an opening niche, indicating a higher resilience of the Lofoten-Vesterålen region towards high fishing pressure. Furthermore, differences between fjord and shelf were limited to individual species in the Lofoten-Vesterålen region and no overall structural difference was identified.

## Acknowledgements

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802
803

804 **Tables**

805

806 **Table 1** Sampled taxa with according code used in figures 2 and 3. Number of analyzed
807 samples and numbers of individuals per samples (Ind.) are given. Taxa assumed to
808 contain carbonate are marked with ×

| Sampled taxa | Code | Hola | | Malnes-fjord | | Northern North Sea | | German Bight | |
|---|---|---|---|---|---|---|---|---|---|
| | | n | Ind. | n | Ind. | n | Ind. | n | Ind. |
| *INVERTEBRATES* | | | | | | | | | |
| **Zooplankton** | ZP | | | | | | | | |
| *Calanus* spp. | Calspp | 3 | 50-100 | 3 | 50-100 | 3 | 50-100 | 3 | 50-100 |
| **Suspension feeders** | SF | | | | | | | | |
| × *Ophiopholis aculeata* | Ophacu | 2 | 1 | 2 | 1 | | | | |
| × *Asteronyx loveni* | Astlov | 2 | 1 | | | | | | |
| × *Funiculina quadrangularis* | Funqua | 2 | 1 | | | | | | |
| *Modiolula phaseolina* | Modpha | 2 | 4 | | | | | | |
| *Parvicardium* sp. | Par_sp | 2 | 1 | | | | | | |
| *Karnekampia sulcata* | Karsul | 2 | 1 | | | | | | |
| *Astarte sulcata* | Astsul | | | 2 | 1 | | | | |
| *Chamelea gallina* | Chagal | | | | | 1 | 1 | 1 | 1 |
| *Turritella communis* | Turcom | | | | | | | 1 | 1 |
| × *Securiflustra securifrons* | Secsec | | | | | 1 | 1 | | |
| *Acanthocardia echinata* | Acaech | | | | | 1 | 1 | | |
| **Deposit feeder / Grazer** | DF | | | | | | | | |
| × *Spatangus purpureus* | Spapur | 2 | 1 | | | | | | |
| × *Gracilechinus acutus* | Graacu | 2 | 1-2 | | | 2 | 3-4 | | |
| × *Parastichopus tremulus* | Partre | 2 | 1 | | | | | | |
| × *Acanthochitona crinita* | Acacri | 1 | 1 | | | | | | |
| × *Leptochiton* sp. | Lep_sp | 1 | 3 | | | | | | |
| × *Brisaster fragilis* | Brifra | | | 2 | 2 | | | | |
| × *Strongylocentrotus droebachiensis* | Strdro | | | 1 | 6 | | | | |
| × *Ctenodiscus crispatus* | Ctecri | | | 2 | 2 | | | | |
| *Nicomache* sp. | Nic_sp | | | 2 | 1 | | | | |
| *Thyasira* sp | Thy_sp | | | 2 | 3-4 | | | | |
| × *Echinocardium cordatum* | Echcor | | | | | | | 2 | 1 |
| *Nucula nitidosa* | Nucnit | | | | | | | 2 | 6 |
| *Thelepus cincinnatus* | Thecin | | | | | 2 | 1-3 | | |
| **Predator / Scavenger** | PS | | | | | | | | |
| × *Ophiura sarsii* | Ophsar | 1 | 1 | 2 | 1 | | | | |
| × *Leptychaster arcticus* | Leparc | 1 | 1 | | | | | | |
| × *Stichastrella rosea* | Stiros | 1 | 1 | | | | | | |
| × *Luidia sarsii* | Luisar | 1 | 1 | | | | | | |
| *Munida sarsi* | Munsar | 2 | 1 | | | | | | |
| *Spirontocaris liljeborgii* | Spilil | 2 | 1 | | | | | | |
| *Sabinea sarsii* | Sabsar | 2 | 1 | | | | | | |
| *Anapagurus laevis* | Analae | 2 | 1 | | | | | | |
| *Dichelopandalus bonnieri* | Dicbon | 2 | 1 | | | | | | |
| *Nephtys* sp. | Nep_sp | 1 | 1 | 2 | 1 | | | 2 | 1-2 |
| *Eunice dubitata* | Eundub | 2 | 1-4 | | | | | | |
| *Eunoe nodosa* | Eunnod | 1 | 1 | | | | | | |

26

| | Code | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Neptunea antiqua* | Nepant | 1 | 1 | | | 2 | 1 | | |
| *Hormathia digitata* | Hordig | 1 | 1 | 2 | 1 | 2 | 1-2 | | |
| × *Astropecten irregularis* | Astirr | | | 2 | 1 | 2 | 2 | 2 | 1-2 |
| *Galathea dispersa* | Galdis | | | 1 | 1 | | | | |
| *Hyas coarctatus* | Hyacoa | | | 2 | 1-3 | 1 | 1 | | |
| *Neptunea despecta* | Nepdes | | | 1 | 1 | | | | |
| × *Ophiura ophiura* | Ophoph | | | | | | | 2 | 2 |
| × *Asterias rubens* | Astrub | | | | | 2 | 2 | 2 | 2 |
| *Liocarcinus holsatus* | Liohol | | | | | | | 2 | 1-2 |
| *Cancer pagurus* | Canpag | | | | | | | 1 | 1 |
| *Pagurus bernhardus* | Pagber | | | | | 2 | 1 | 1 | 1 |
| *Corystes cassivelaunus* | Corcas | | | | | | | 2 | 2 |
| *Nephrops norvegicus* | Nepnor | | | | | | | 1 | 1 |
| *Aphrodita aculeata* | Aphacu | | | | | | | 2 | 1-2 |
| × *Hippasteria phrygiana* | Hipphr | | | | | 2 | 1 | | |
| *Crangon allmanni* | Craall | | | | | 2 | 3 | | |
| *Pandalus montagui* | Panmon | | | | | 2 | 2 | | |
| *Hyalinoecia tubicola* | Hyatub | | | | | 2 | 2 | | |
| *Scaphander lignarius* | Scalig | | | | | 2 | 2 | | |
| *Colus gracilis* | Colgra | | | | | 2 | 1 | | |
| *Euspira nitida* | Eusnit | | | | | 1 | 1 | | |
| ***FISH*** | | | | | | | | | |
| *Pollachius virens* | Polvir | 2 | 2 | | | 2 | 2 | | |
| *Argentina silus* | Argsil | 2 | 2 | | | | | | |
| *Clupea harengus* | Cluhar | | | | | 2 | 1 | 2 | 4 |
| *Hyperoplus lanceolatus* | Hyplan | | | | | | | 2 | 1 |
| *Scomber scombrus* | Scosco | | | | | 2 | 1 | 2 | 1 |
| *Gadus morhua* | Gadmor | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 1 |
| *Hippoglossoides platessoides* | Hippla | 2 | 2 | 1 | 1 | 2 | 1 | | |
| *Microstomus kitt* | Mickit | 1 | 1 | 1 | 1 | | | | |
| *Myxine glutinosa* | Myxglu | 1 | 1 | | | 1 | 1 | | |
| *Artediellus atlanticus* | Artatl | 2 | 1 | | | | | | |
| *Lumpenus lampretaeformis* | Lumlam | | | 1 | 1 | | | | |
| *Buglossidium luteum* | Buglut | | | | | | | 1 | 1 |
| *Agonus cataphractus* | Agocat | | | | | | | 1 | 1 |
| *Pleuronectes platessa* | Plepla | | | | | 2 | 1 | 1 | 1 |
| *Limanda limanda* | Limlim | | | | | 2 | 1 | 2 | 1 |
| *Amblyraja radiata* | Ambrad | | | | | 1 | 1 | | |
| ***CARBON SOURCE*** | | | | | | | | | |
| POM | POM | 9 | 1 filter | 3 | 1 filter | 9 | 1 filter | 9 | 1 filter |
| × Sediment | Sed | 3 | n/a | 2 | n/a | 3 | n/a | 2 | n/a |
| **Phaeophyceae** | | | | | | | | | |
| *Laminaria hyperborea* | Lamhyp | | | 3 | 1 | | | | |
| *Saccharina latissima* | Saclat | | | 2 | 1 | | | | |
| *Desmarestia aculeata* | Desacu | | | 3 | 1 | | | | |
| **Rhodophyta** | | | | | | | | | |
| *Ptilota gunneri* | Ptigun | | | 2 | 1 | | | | |
| *Odonthalia dentata* | Ododen | | | 2 | 1 | | | | |
| **Phaeophyceae detritus** | | | | | | | | | |
| *Ascophyllum nodosum* | Ascnod | | | | | 1 | 1 | 2 | 1 |
| *Cystoseira* sp. | Cys_sp | | | | | | | 1 | 1 |

809

**Figure legends**

811

812   **Figure 1**. Map of north-west Europe with sampling locations indicated. Top left: Detail
813   of the Lofoten-Vesterålen region.

814

815   **Figure 2**. Mean $\delta^{13}$C ± 1SD and mean $\delta^{15}$N ± 1SD at all study locations. Labelling according
816   to taxon code shown in Table 1. Red algae (*Ptilota gunneri* [$\delta^{13}$C: -35.7±0.0, $\delta^{15}$N:
817   6.3±0.0]; *Odonthalia dentata* [$\delta^{13}$C: -32.7±0.5, $\delta^{15}$N: 5.4±0.5]) and identified outliers
818   (*Thyasira* sp. [$\delta^{13}$C: -35.2±0.6, $\delta^{15}$N: -5.3±0.5]; *Nephtys* sp. [$\delta^{13}$C: -29.4, $\delta^{15}$N: 2.1]) are
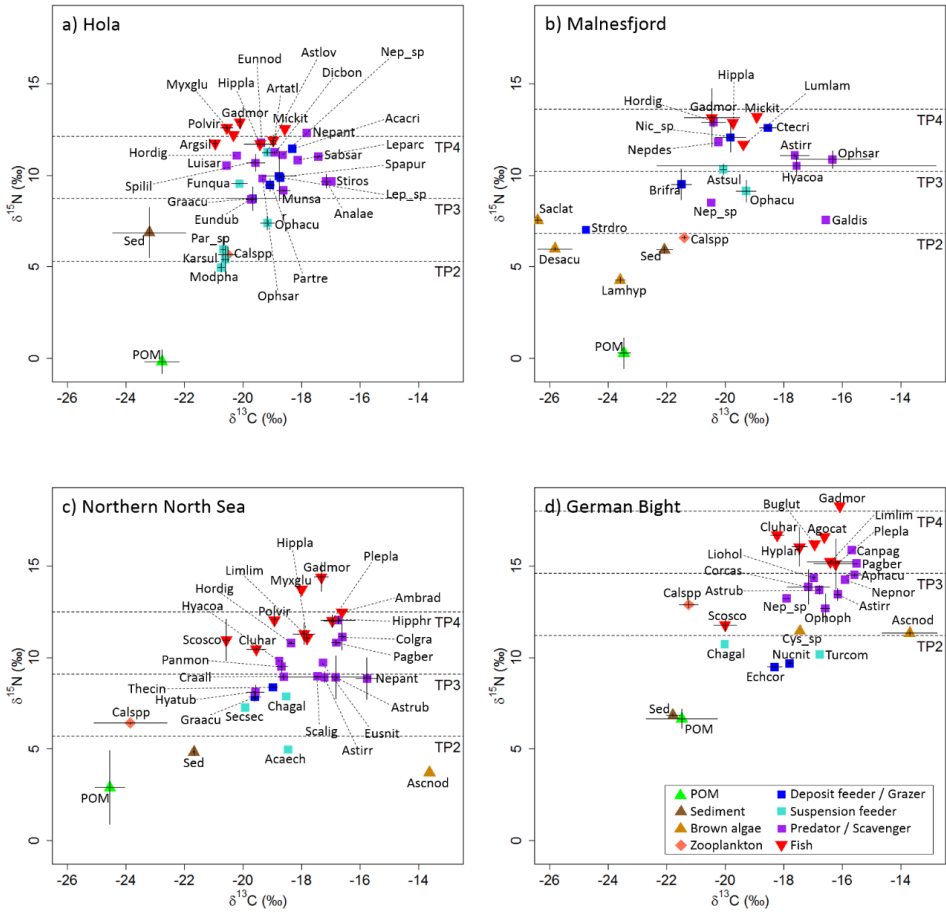819   not shown for Malnesfjord.

820

821   **Figure 3**. Reliance on benthic affinity prey and trophic position for all faunal taxa.
822   Labelling according to taxon code shown in Table 1. A second x-axis (top) for Hola shows
823   the calculated reliance on benthic affinity prey using a winter pelagic baseline.
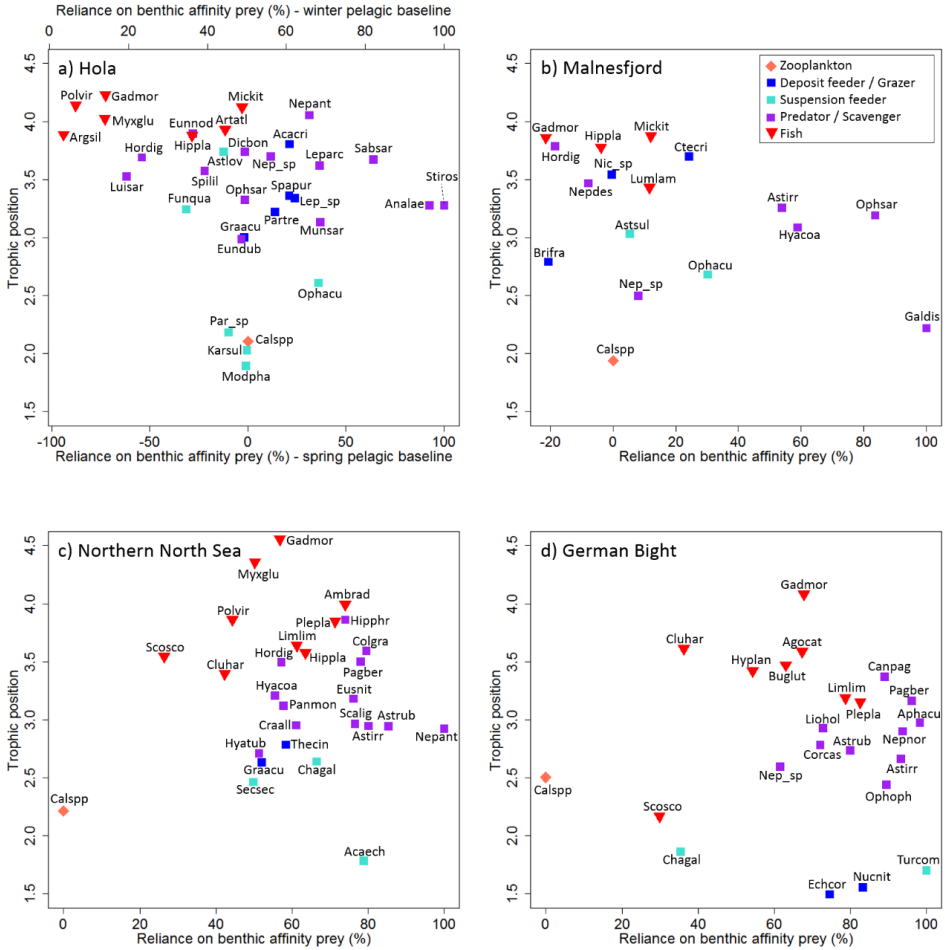
824    **Fig. 1**
825



826

**Fig. 2**
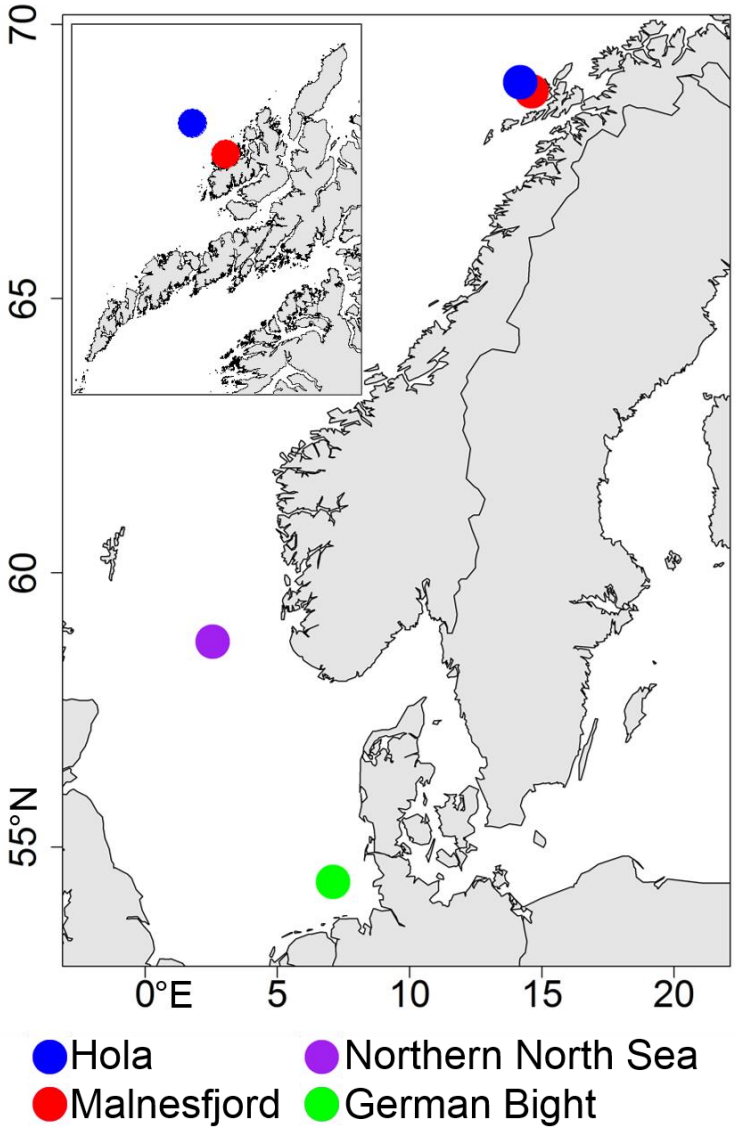
**Fig. 3**



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833

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The marine ecosystem of the sub-Arctic Lofoten-Vesterålen region
is commercially and ecologically extremely valuable, due to its strong
implications for the Norwegian and Barents Sea. As part of the marine
ecosystem, seafloor (benthic) habitats play an important role for a variety
of ecosystem services, including food production, carbon sequestration,
or nutrient cycling. By studying spatial scales of benthic community
structure, larval dispersal, and food-web structure, this dissertation
contributes knowledge that is important to secure a sustainable marine
spatial management of the Lofoten-Vesterålen region. Collectively,
epifauna and infauna reflect different environmental drivers of spatial
variability. Nevertheless, benthic ecosystem functioning in the Lofoten-
Vesterålen region is largely tied to distinct warm- and cold-water
benthic communities associated with Atlantic and Arctic water masses,
respectively. In addition, retention of larval stages on the continental
shelf maintains the separation of these communities. A considerable
habitat connectivity and a preserved food-web structure that supports
different top predator fish species, characterize the local ecosystem on
the continental shelf. The presented work illustrates the multiscale nature
of benthic ecosystems and identifies environmental variables that can be
used to assess benthic habitats and their resilience in areas with similar
environmental settings.