PhD in Aquatic Biosciences // No. 39 - 2021

Macrobenthic communities of sub-Arctic deep fjords: composition, spatial patterns and community assembly

Valentin Kokarev

FACULTY OF BIOSCIENCES AND AQUACULTURE

NORD
University

www.nord.no

Macrobenthic communities of sub-Arctic deep fjords: composition, spatial patterns and community assembly

Valentin Kokarev

A thesis for the degree of
Philosophiae Doctor (PhD)

PhD in Aquatic Biosciences no. 39 (2021)
Faculty of Biosciences and Aquaculture

PhD in Aquatic Biosciences no. 39 (2021)

Valentin Kokarev
Macrobenthic communities of sub-Arctic deep fjords: composition, spatial patterns and community assembly

ISBN: 978-82-93165-38-5

Print: Trykkeriet NORD

Nord University
N-8049 Bodø
Tel: +47 75 51 72 00
www.nord.no

Preface

The thesis is submitted in fulfilment of the requirements for the degree of Philosophiae Doctor (PhD) at the faculty of Biosciences and Aquaculture (FBA), Nord University. The presented original research was performed at Nord University, Bodø.

The project team consisted of the following members:

Valentin Kokarev, MSc, FBA, Nord University: PhD student

Henning Reiss, Associate Professor, FBA, Nord University: primary supervisor

Sylvie Bolla, Associate Professor, FBA, Nord University: co-supervisor

Eivind Oug, Research scientist, Norwegian Institute for Water Research: co-supervisor

Valentin Kokarev

Bodø, August, 2021

Acknowledgments

First of all, I would like to thank my main supervisor Henning Reiss for giving me the opportunity to work in such a beautiful place. I really enjoyed exploring the spectacular surroundings of Bodø and studying these very fjords at the same time.

This project would not have been possible without help of Morten Krogstad, especially the field part. One of the brightest of my whole PhD time was the moment Tanteyen would not start, and we were towed to Bodø through Saltstraumen maelstroms.

I would like to thank my co-supervisor Sylvie Bolla for teaching me the fatty acid analysis and who made the fourth chapter of this PhD possible.

I would like to thank all the co-authors for their valuable contributions to the manuscripts and Èric Jordà Molina, Marthe Austad, and Egor Gaidukov who collected and sorted the majority of material that served as a basis for my studies. I would like also to thank Anjana Palihawadana and Martina Kopp for their help in the labs.

The population genetics part of this PhD was not included in the final version of the thesis due to the lack of time. However, I learned a lot working with these samples and I would like to thank Joost Raeymaekers for inspiring me to do this study. I am grateful to Amalia Mailli and Marvin Choquet for their help with the labwork, and especially, to my best officemate ever, Leona Milec, for refiltering the SNPs and sharing her scripts.

During this project I relied a lot on the knowledge I got during my work at Shirshov Institute of Oceanology, and I would like to thank all my colleagues there. Especially I am grateful to Andrey Azovsky, who introduced me to the world of marine benthic ecology, Mikhail Flint, who always invited me to the Arctic cruises, Elena Krylova for sharing her experience in bivalve taxonomy and Andrey Vedenin for sharing his knowledge on the Arctic fauna.

Last but not the least, I would like to thank my family and friends for their constant support. Going through the last stage of my PhD would have not been possible if I were alone. Special thanks go to Isabel Abihssira Garcia, who would take me outside to chill when I needed it most.

Table of contents

Preface i

Acknowledgments ii

Table of contents iv

Abstract vi

List of figures viii

List of papers ix

1. Introduction 1

1.1. Diversity of soft-bottom macrobenthos 2

1.2. Biological traits of macrobenthos 3

1.3. From species to communities: community assembly 6

1.4. Fjord deep basins as a habitat for benthos 10

1.5. Fjords of Vestfjord region 11

2. Objectives 16

3. Main results 17

3.1. Environmental drivers of benthic community structure in a deep sub-arctic fjord system (Paper I) 17

3.2. Strong macrobenthic community differentiation among sub-Arctic deep fjords on small spatial scales (Paper II) 18

3.3. Combining species and biological trait composition to assess macrobenthic community assembly in deep sub-Arctic fjords (Paper III) 19

3.4. Combining stable isotope and fatty acid analyses to assess trophic niches of macrofauna in an anthropogenically influenced deep fjord basin (Paper IV) 20

4. General discussion 21

4.1. Composition of macrobenthic communities in fjord basins 21

4.2. Spatial patterns and community assembly 23

4.3. Trophic niches and resource partitioning.. 26

5. Conclusions and further perspectives... 29

References 33

Abstract

There is a well-established link between biodiversity and ecosystem properties, including functioning and stability. Biodiversity estimates such as species richness are not standalone entities but rather properties of biological communities. Therefore, understanding of assembly and dynamics of these communities is essential to comprehend patterns of biodiversity and how they can be affected by human impacts. Macrobenthic communities are an important component of marine habitats, which contribute to various ecological processes on the seafloor such as organic matter remineralisation. Despite their important ecological role, there is a major gap in knowledge on macrobenthic diversity and community assembly in deep sub-Arctic fjords that limits the understanding of these depositional habitats.

The aim of the present thesis is to investigate the structure of macrobenthic communities in eight deep sub-Arctic fjord basins (>290 m) located in the Vestfjord region (Norwegian coast). In general, the composition of macrobenthos was similar to other deep depositional environments influenced by Atlantic water masses, such as deep boreal fjords in Western Norway and deep Skagerrak. However, considerable differences were observed in macrobenthic community structure between shallow-silled and deep-silled fjords, which were characterised by distinct bottom water masses. Shallow sill hampers the inflow of more saline and warmer Atlantic water masses, and, therefore, acts as a hydrological barrier that limits dispersal of macrobenthic taxa. Some species recorded only in shallow-silled basins might be isolated populations which distributions are restricted to colder bottom water masses. Biological trait composition revealed that, generally, basins with a shallow sill have a higher proportion of deep-dwelling subsurface deposit feeding fauna, indicating differences in benthic functioning.

Further strong community differentiation was observed even among fjords with similar levels of water exchange with surrounding waters on approximately a basin scale. These communities were characterised by different levels of diversity and redundancy, suggesting that ecosystem functioning in some basins is more vulnerable to species loss. Within one studied fjord, local organic input from a fish farm seemed to have a minor impact on the sediment organic matter in the deep basin. However, most macrofaunal taxa showed clear trophic niche separation, possibly indicating the importance of biological interactions and resource partitioning for the community structure. I suggest that low connectivity among basins/fjord systems, and particularly the presence of dispersal barriers such as a shallow sill, results in independent community assembly and, consequently, among-basin macrobenthos variation. This finding indicates that ecological processes in closely situated fjords are only weakly interconnected.

List of figures

Figure 1. Conceptual scheme of community assembly processes. Red arrows indicate deterministic processes, blue ones indicate stochastic processes. 9

Figure 2. Map of the study area, showing locations of the sampled basins............. 13

Figure 3. A scheme representing the difference between deep-silled (top) and shallow-silled fjords (bottom) in water exchange: shallow sill hampers inflow of Atlantic water into the basin and resulting bottom water masses are colder and less saline.. 14

List of papers

Paper I. Jordà Molina È, Silberberger MJ, Kokarev V, Reiss H (2019) Environmental drivers of benthic community structure in a deep sub-arctic fjord system. Estuar Coast Shelf Sci 225:106239.

Paper II. Kokarev V, Tachon M, Austad M, McGovern M, Reiss H (2021) Strong macrobenthic community differentiation among sub-Arctic deep fjords on small spatial scales. Estuar Coast Shelf Sci 252:107271.

Paper III. Kokarev V, Oug E, Reiss H Combining species and biological trait composition to assess macrobenthic community assembly in deep sub-Arctic fjords. Manuscript.

Paper IV. Kokarev V, Bolla S, Reiss H Combining stable isotope and fatty acid analyses to assess trophic niches of macrofauna in an anthropogenically influenced deep fjord basin. Manuscript.

1. Introduction

Most ecosystem functions and services that benefit society rely upon biodiversity (Palumbi et al., 2009; Strong et al., 2015), which is a major determinant of the main ecosystem properties, including productivity, stability, and nutrient dynamics (Tilman et al., 2014). Biodiversity patterns can be altered by global stressors, such as ocean warming and acidification, together with local stressors, such as eutrophication (Doney, 2010; Hoegh-Guldberg and Bruno, 2010; Nagelkerken and Connell, 2015). Changes in biodiversity affect ecosystem functioning often with unknown consequences (Gamfeldt et al., 2015; Bulling et al., 2010). While the majority of the studies focus on the local biodiversity, little is known how broader spatial context influences community assembly and the resulting biodiversity-ecosystem functioning relationships (Leibold et al., 2017).

Community structure in marine ecosystems can be significantly altered due to expected shifts in the distribution of species associated with increasing temperature as well as climate-driven extinctions and invasions (Cheung et al., 2009; Doney et al., 2012; Molinos et al., 2016; Weinert et al., 2021). Thus, it is important to understand the processes underlying the formation of local biodiversity and communities to better understand the current patterns and, consequently, to predict future changes due to altered climate or other anthropogenic impacts. Macrobenthos is an ecosystem component that plays a key role in marine ecosystems, although its importance for ecosystem functioning is often underestimated (Norling et al., 2007; Woodin et al., 2016; Snelgrove et al., 2018). Moreover, changes in macrobenthic communities reflect ecosystem processes on various spatial scales integrated over time, and macrobenthos is widely used for environmental monitoring (Borja et al., 2009; Węsławski et al., 2011; Grebmeier et al., 2012; Rice et al., 2012). Therefore, studying the drivers that determine spatial distribution and community assembly of macrobenthos can provide essential knowledge for both understanding marine ecosystem functioning as well as providing a baseline for detecting changes in the marine environment and decoupling such changes from natural variability.

1.1. Diversity of soft-bottom macrobenthos

Benthos comprises all organisms that live in direct association with the seafloor. Macrobenthos can be distinguished based on the size class (500 µm- 5 cm) or a taxonomic basis (Gray and Elliot, 2009). Taxonomically macrobenthos is a very diverse ecosystem component with polychaetes, crustaceans, molluscs, and echinoderms being the most species-rich groups (Snelgrove et al., 1997). The species diversity of soft-bottom macrobenthos is hard to estimate as new species are constantly described even from well-studied areas. Many species have restricted distributional ranges and/or lower abundances (“rare species”), therefore, limited sampling effort might result in underestimation of species richness (Ellingsen, 2001; Ellingsen et al., 2007). Moreover, previously reported species appear to comprise high levels of cryptic diversity discovered with molecular markers, especially for polychaetes (e.g. Braiser et al., 2016; Nygren et al., 2018). Cryptic species might have high morphological similarity yet have some other adaptations to the environment, e.g. physiological, that would result in different responses to various stressor impacts, and, consequently, might not be entirely ecologically equal (Feckler et al., 2014). While molecular markers show an increased potential in biodiversity studies, particularly for the inventory of cryptic biodiversity, the lack of molecular data is hampering its wider use to date (Hestetun et al., 2020). Thus, currently, morphological identifications remain the main tool for biodiversity assessment of macrofauna, although the species richness might be underestimated due to the complicated taxonomy of some groups and the presence of species, that are not morphologically delimited.

Nevertheless, the functional role of macrofauna, e.g. their feeding behaviour, can be inferred from morphology (Snelgrove et al., 1997). This comes from the assumption that phylogenetically related species show to some extent conservatism of an ecological niche (Webb et al., 2002), and, therefore, representatives of the same genus/family would have similar traits. For instance, the well-developed feeding guild classification of polychaetes shows that the lifestyles of representatives of the same family are often similar (Jumars et al., 2015). The diversity of feeding habits within other major macrobenthic groups is also well-documented (Arruda et al., 2003; Scipione, 2013; Jangoux and Lawrence, 1982). Apart from feeding, various morphological, behavioural and life history traits of macrobenthic species have been used to describe functional role of macrofauna (Bremner et al., 2006; Beauchard et al., 2018; Degen et al., 2018). Therefore, macrofaunal diversity and community composition can be perceived through two different approaches: species diversity as a number of species/operational taxonomic units found in a specific locality and functional diversity as the range of functional niches occupied by these species.

1.2. Biological traits of macrobenthos

A trait is a well-defined property of an organism that is comparable among species (McGill et al., 2006). Recently, the use of traits to understand species-environment relationships considerably increased in marine community ecology (Beauchard et al., 2017). Communities may converge in trait composition but diverge in species composition, as the latter is more influenced by historical contingencies, while trait composition of a community better reflects adaptations to the environment (Fukami et al., 2005). Thus, trait approaches might allow for better generalisations and comparison, especially among different biogeographic regions with different species pools (Bremner et al., 2006). As mentioned above, various morphological, behavioural, and life history traits are used to describe the functional role of macrofauna. Traits, expressed by macrofauna, are associated with different ecosystem functions and properties such as energy and nutrient cycling, secondary production, stability, and heterogeneity (Bremner et al., 2006, Bremner, 2008; Degen et al., 2018). The combination of morphological traits (e.g. body size, body design) and behavioural traits (e.g. feeding habit, living habit) can be used to classify species into functional (resource use) guilds (Wilson, 1999). Together these characteristics qualitatively describe the ability of a given animal to process or redistribute sedimentary particles (Aller, 1977). Therefore, species that share traits, or belong to the same functional guild, are ecologically similar in the way they utilise resources and modify their habitat, and, therefore, contribute similarly to the ecosystem functioning.

The number of species within a functional guild, known as functional redundancy, is an important ecosystem property, as it provides robustness of ecosystem processes in case of species loss (Naeem, 1998; Hooper et al., 2005; Micheli and Halpern, 2005). In case of species loss, ecologically similar species might occupy the newly available vacant niches as the realized niche of a species is generally narrower compared to its fundamental niche as the result of competition and resource partitioning (McGill et al., 2006). Therefore, it is vital to understand the variety of responses to an environmental disturbance among species within the same functional guild, termed as “response diversity” (Elmqvist et al., 2003). For instance, species within the same functional guild can respond differently to hypoxia (Diaz and Rosenberg, 1995). Thus, higher functional redundancy possibly ensures ecosystem functioning in a changing environment, but only if species from the same functional guild differ in their response diversity. Currently little is known about the functional redundancy of macrobenthic communities, but previous studies suggested low functional redundancy of marine macrobenthic communities (Micheli and Halpern, 2005; Kokarev et al., 2017; Liu et al., 2019).

Historically, many functional classifications of macrobenthos were related to trophic/feeding groups, and the trait “feeding mode/habit” is the most frequent trait used in functional studies of macrobenthos (Lam-Gordillo et al., 2020). Macrobenthic feeding habits are diverse, including microphages (suspension, surface deposit, and subsurface deposit feeders) and macrophages (carnivores, herbivores, and omnivores) (Jumars et al., 2015). Soft bottom macrobenthic communities are typically dominated either by suspension or deposit feeders that rely on various food sources such as plankton-derived detritus or bacteria associated with sediment organic matter (Levinton, 1972). Both groups utilise a high ratio of mineral to organic particles (Aller, 1977). Therefore, indirect methods such as stable isotope and fatty acid analyses are often used to assess food sources that are assimilated by benthic consumers (Dang et al., 2009; North et al., 2014; Blanchet-Aurigny et al., 2015; Rossi et al., 2015). Stable isotopes of carbon and nitrogen are often used to characterize the trophic niche of a species, particularly carbon sources and trophic levels (Newsome et al., 2007). Fatty acids are used as dietary markers for different food sources such as phytoplankton, bacteria macroalgae, and vascular plants (Kelly and Scheibling, 2012). These methods can provide useful information on resource partitioning of species with similar feeding habits (Karlson et al., 2015; Richoux et al., 2014), and, thus, contribute to a better understanding of macrobenthic community organization through accounting for information that cannot be assessed through traits classifications only.

Many processes during community assembly might be influenced by dispersal (Leibold et al., 2004; Heino et al., 2015). Therefore, traits related to the dispersal capabilities of a species might but not directly associated with resource use might be also important to understand community patterns. For instance, the importance of competition in structuring communities might be overridden by high dispersal (Gravel et al., 2006). Therefore, life history traits, particularly larval type, might be important for understanding spatial patterns in community ecology as long-living pelagic larvae allow for higher dispersal capabilities (Mileikovsky, 1971; Fetzer and Arntz, 2008).

1.3. From species to communities: community assembly

The definition of a community has a long history in marine ecology related to the debates whether communities are discrete systems or represent a continua along environmental gradients (Mills, 1969). It seems impossible to define what a community is without understanding the mechanisms of its formation and organization. A community forms from species that can potentially colonise a habitat, referred to as species pool, which on a large scale is influenced by evolutionary and historical processes (Carstensen et al., 2013; Mittelbach and Schemske 2015). For instance, the species composition and speciation of amphi-boreal fauna were influenced by trans-Arctic dispersal events of the past (Laakkonen et al., 2020). Modern distribution of biogeographical boundaries largely corresponds to the distribution of water masses with different properties, particularly, temperature, and might reflect physiological adaptations of species as well as dispersal with major currents (Gaylord and Gaines, 2000; Clarke, 2003; Clarke et al., 2009; Jirkov, 2013; Petryashov et al., 2013; Renaud et al., 2015; Ravelo et al., 2020).

Two main processes contribute to community assembly from the available pool of species: environmental filtering and competitive exclusion (Götzenberger et al., 2012; Kraft et al., 2015). Early studies of benthic communities suggested that similar environmental conditions, e.g. depth and sediment type, would be inhabited by similar or “parallel” communities with dominant species being biogeographic variants of the same genus (Thorson, 1966). Sediment properties are related to near-bed flow conditions, which determine grain size as well as food and larvae supply, all being important factors for the distribution of macrobenthos (Snelgrove and Butman, 1994). For some localities, sediment grain size alone correlates well with the distribution of macrobenthic communities (e.g. Degraer et al., 2008). However, many benthic species are able to colonize different types of sediment (Wu and Shin, 1997), suggesting that the grain size has an indirect influence on benthic community structure, which could potentially include the influence on competition outcome among species. Competition among benthic invertebrates is documented (Wilson, 1990), which implies that some degree of niche differentiation and resource partitioning among coexisting species is present in natural communities in accordance with the limiting similarity principle (Abrams, 1983; Götzenberger et al., 2012). The possible niche differentiation/resource partitioning mechanisms include trophic niche separation by utilizing qualitatively different resources (Blanchet-Aurigny et al., 2015) or selecting for different particle sizes of sediment (Whitlatch, 1980), sediment dwelling depth (Hughes, 1979; Lopez and Elmgren, 1989), spatial avoidance of overlapping in feeding area on sediment surface (Dauer et al., 1981) and association with different habitat patches caused by activities of ecosystem engineers (Donadi et al., 2015). Although environmental filtering clearly affects the distribution of macrofauna, especially when major disturbance events select for species with specific traits, e.g. hypoxia (Diaz and Rosenberg, 1995; Levin et al., 2009), salinity fluctuations (van der Linden et al., 2012), glacier and terrestrial sedimentation (Wlodarska-Kowalczuk et al., 2005; Kokarev et al., 2017; McGovern et al., 2020), it is not always possible to distinguish its effects from biological interactions. Kraft et al. (2015) suggested to use the term “environmental filtering” only when abiotic environment hampers an establishment of a species population in a particular habitat in absence of other competitors. The term “species sorting” is often used to describe the combined effects of biotic and abiotic factors along environmental/resource gradient (Leibold et al., 2004).

Both competitive exclusion and environmental filtering can be considered deterministic factors, in a sense that in environmentally similar habitats that share a pool of species, the resulting communities should be similar. This is opposed to recognized stochasticity during community assembly that results in community divergence and higher species turnover (beta diversity) across similar habitats than can be expected from deterministic outcome only (Chase, 2007; Chase and Myers, 2011). The stochasticity in community assembly includes fluctuations in populations due to demographic stochasticity, termed “ecological drift”, as well as the order of species colonising the habitat, termed “priority effects” (Orrock and Watling, 2010; Fukami, 2015). Ecological drift might override results of competition, particularly in smaller communities (Orrock and Watling, 2010). Priority effects reflect the influence of immigration history on community assembly on species composition as early arriving species might occupy and modify available niches preventing late-arriving species from establishing a population (Fukami, 2015). It has been hypothesised that the relative importance of deterministic and stochastic processes depends on the level of disturbance of the habitat since disturbance events would result in a deterministic community assembly due to environmental filtering of species that can tolerate such conditions (Chase, 2007; Lepori and Malmqvist, 2009).

Spatial structure of macrobenthos is linked not only to environmental drivers but also to dispersal processes, suggesting that community assembly should be considered on different spatial scales in accordance with metacommunity theory (Josefson, 2016; Corte et al., 2018; Rao et al., 2020). Metacommunity theory suggests that local communities, where species are directly interacting with each other, are influenced on a larger scale by neighbouring communities through dispersal (Leibold et al., 2004). It has been suggested that in marine coastal ecosystems with high dispersal rates communities may be homogeneous, irrespective of their environmental heterogeneity (“mass effects”; Heino et al., 2015). Thus, community assembly along with deterministic or stochastic processes might be influenced by dispersal abilities of species as well as connectivity among local communities and presence of dispersal barriers. Dispersal patterns are reflected in population connectivity, which might range from fully open to fully closed (Cowen and Sponaugle, 2009); therefore, understanding processes on a population level might be essential to understand community assembly.

Mills (1969) defined communities as follows: “a group of organisms occurring in a particular environment, presumably, interacting with each other and with the environment, and separable by means of ecological survey from other groups”. From a metacommunity point of view, this would be a definition for a local community, but on larger spatial scales these local communities can interact with each other via dispersal. Moreover, local diversity is not formed strictly locally and is influenced by regional diversity, which is shaped by historical evolutionary and ecological processes (Ricklefs, 2007). The relationship between local and regional diversity is well established for macrobenthic communities (Gray, 2002; Gage, 2004). The scheme that represents all possible processes related to community assembly is present in figure 1. However, the relative importance of these processes can be different depending on the studied system.

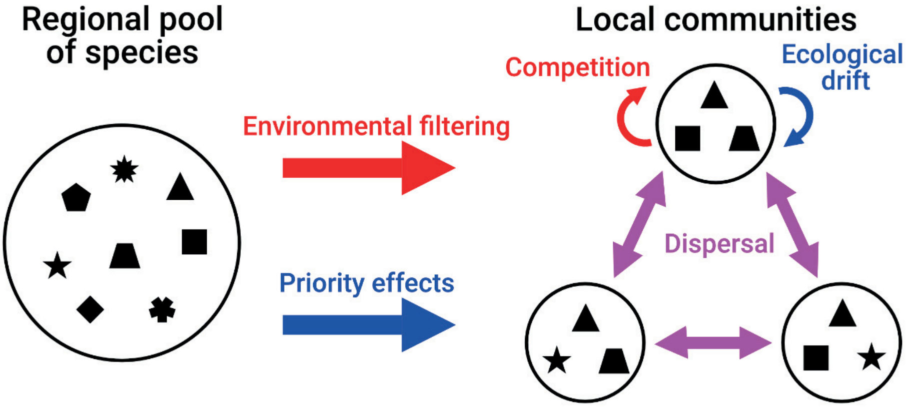


Figure 1. Conceptual scheme of community assembly processes. Red arrows indicate deterministic processes, blue ones indicate stochastic processes.

1.4. Fjord deep basins as a habitat for benthos

Fjords are deep estuaries located at high latitudes in both hemispheres (Syvitsky et al., 1987). Basins of fjords are considered important coastal areas for carbon cycling due to their relatively high sedimentation rates and organic matter burial in the basins (Faust and Knies, 2019). Generally, such deeper depositional environments differ from other coastal habitats in their benthic community structure and are dominated by deposit feeding fauna (Dauwe et al., 1998). However, several characteristics of fjords distinguish them from depositional environments offshore, particularly, enclosure by land and isolation by a sill at the entrance as well as freshwater runoff. Generally, fjords have three distinct water layers: a surface brackish water layer, the intermediate layer below the brackish layer and above the sill, and deep water trapped below the sill depth (Syvitsky et al., 1987; Inall and Gillibrand, 2010; Aksnes et al., 2019). For some fjords, deep water renewal happens on a yearly scale, which might cause hypoxia in the bottom water layer and reduction of diversity in benthic communities (Diaz and Rosenberg, 1995; Levin et al., 2009). In fjords with high sedimentation rates from glacier/riverine runoff, reduction in diversity may result in environmental filtering of fauna adapted to unstable sediment conditions (Holte and Gulliksen, 1998; Wlodarska-Kowalczuk et al., 2005; McGovern et al., 2020). Habitat deterioration was suggested as the main driver for the observed differences in macrobenthic communities and decreased diversity between Svalbard fjords and the Barents Sea shelf (Włodarska-Kowalczuk et al., 2012). Decreased diversity was also observed in deep fjords of Western Norway which was related to higher fluxes of organic matter compared to habitats offshore that might favour dominance of opportunistic species, although it was acknowledged that shallow sills may act as dispersal barriers for some taxa (Buhl-Mortensen and Høisæter, 1993). In a deep fjord system of New Zealand, basin-scale processes were suggested as main drivers for structuring macrobenthic communities, including local connectivity, disturbance, and productivity, as well as fjord connectivity through the regional species pool (Brewin et al., 2011). Therefore, environmental filtering and connectivity can be proposed as factors structuring basin communities in fjords. But fjords are distributed in a wide range of environmental settings and biogeographic regions, and, consequently, observed patterns might be specific to a study region. The deep basins of fjords, with the depths considerably exceeding the euphotic zone, might share many similarities in ecological processes with deep sea environments (Brattegard, 1980; Witte et al., 2003; Sweetman and Witte, 2008). Well-ventilated sub-euphotic deep basins in boreal and sub-Arctic fjords can be perceived as partially isolated and physically stable habitats for benthos, for which export of labile carbon from overlaying waters might be a major limiting factor (Burrell, 1988). Such systems can be used to study community assembly in deep sea macrobenthos: located in the direct vicinity of each other they share biogeographic species composition and geographical setting, yet each basin can be perceived as a local community due to its partially isolated nature.

1.5. Fjords of Vestfjord region

Vestfjord is a large fjord, located north of the Arctic circle, between mainland Norway and the Lofoten islands (Figure 2). Vestfjord has hydrological characteristics of a bay with two distinct water masses: more saline Atlantic waters are overlayed by water masses brought with the Norwegian Coastal Current that originates from the Baltic Sea (Mitchelson-Jacob and Sundby, 2001). Several fjord systems with deep basins (>300 m) are connected to Vestfjord on the mainland side, including Saltfjord/Skjerstadfjord, Folda, Sagfjord, Tysfjord, and Ofotfjord. The general circulation pattern in Vestfjord follows the Norwegian mainland along the east side and flows out along the Lofoten to the west (Mitchelson-Jacob and Sundby, 2001). This circulation pattern in Vestfjord can be altered by strong winds, and such wind-induced circulation influences the water exchange with the mainland fjords: southwesterly winds cause coastal water flow into the mainland fjords and presses the underlying Atlantic water out, while north-easterly winds have the opposite effects (Furnes and Sunby, 1981). Unlike the basins with deep (>200 m) sills, which are characterized by Atlantic basin water masses, shallower sills allow only for inflow of less dense coastal water masses transported with Norwegian Coastal Current (Figure 3; Skreslet et al., 2020). Deep waters show almost no seasonal variation in salinity and temperature but surface water temperature and salinity experience seasonal variation associated with river runoff (Skreslet et al., 2000; Myksvoll et al., 2011). Due to the influence of relatively warm currents, the fjords remain seasonally ice-free. However, seasonality affects the light regime, which changes from dark winters with little light radiation during the Polar night to 24 hours of daylight during the Midnight Sun. This results in a shorter phytoplankton growth season compared to fjords at lower latitudes, but also might affect photoperiod-regulated processes (Eilertsen and Degerlund, 2010). Despite shorter phytoplankton vegetation season, the inflow of nutrient-rich Atlantic water supports high marine productivity in the area that results in comparatively high rates of marine organic carbon burial in the basin of the Vestfjord and adjacent fjord systems (Faust and Knies, 2019).

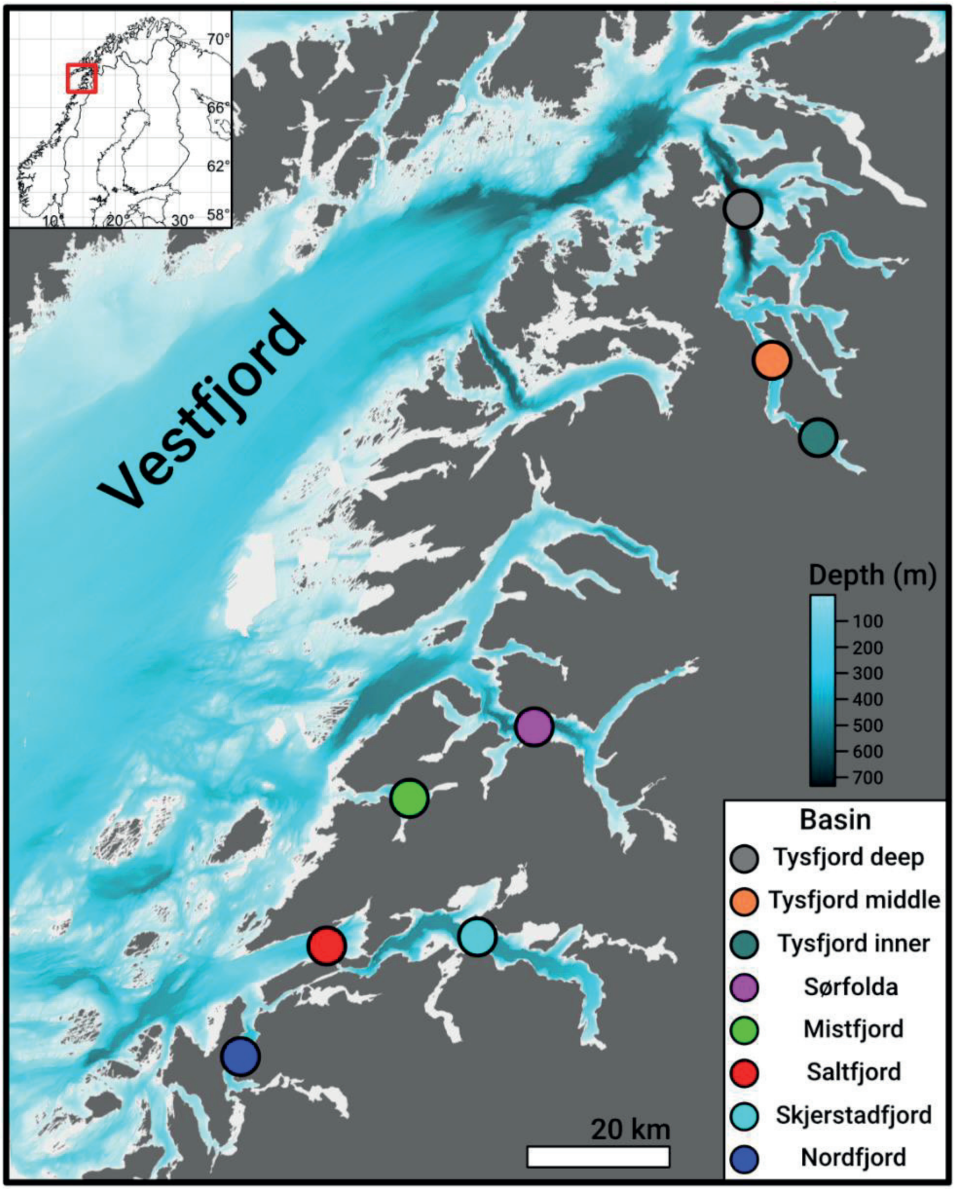


Figure 2. Map of the study area, showing locations of the sampled basins

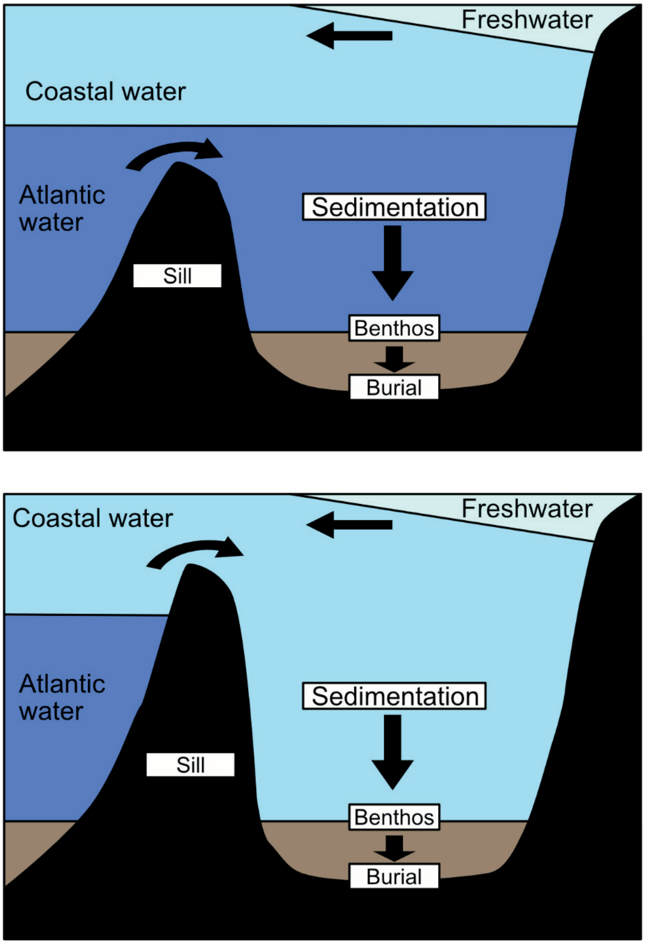


Figure 3. A scheme representing the difference between deep-silled (top) and shallowed-silled fjords (bottom) in water exchange: shallow sill hampers inflow of Atlantic water into the basin and resulting bottom water masses are colder and less saline.

Vestfjord and adjacent fjords are considered ecologically important overwintering areas for populations of planktonic copepods *Calanus finmarchicus* (Espinasse et al., 2016) and herring *Clupea harengus* (Huse et al., 2010), and spawning grounds for Atlantic cod *Gadus morhua* (Ottersen et al., 2014). The studies on the zooplankton populations of these fjords show a very dynamic basin-scale pattern, influenced by sill depth, particularly the size of overwintering populations in deep basins (Espinasse et al., 2018; Skreslet et al., 2015; 2020). There is some evidence that basin-scale patterns affect population dynamics of other pelagic and benthic components of these fjords, such as Atlantic cod and European lobster. Retention of Atlantic cod eggs in fjords suggests that the fjord populations of this species have low connectivity with the coastal cod population, and fjord populations can be considered a metapopulation (Myksvoll et al., 2011; 2014). Similarly, fjord-scale populations can be suggested for European lobster based on the genetic differences documented between Folda and Tysfjord populations (Jørstad et al., 2004). Considering stated above, it might be suggested that there is low connectivity among fjord systems, and consequently limited dispersal, which might affect community assembly and structure of macrobenthos. The present study is the first step towards describing these systems as a habitat for macrobenthos and understanding the pattern of its communities.

2. Objectives

The main aim of the present study is to describe macrobenthic communities of the mainland fjords in the Vestfjord region. Located in close vicinity of each other, these fjords are characterized by the same environmental setting, yet as mentioned earlier, there might be low connectivity, and, consequently, low dispersal among fjord systems. Therefore, macrobenthic communities would reflect assembly processes on a fjord/basin scale. This is one of the few studies on fjord macrofauna that assesses the spatial pattern on both within- and among-basin scales in detail. Specifically, I aimed to:

Paper I: Describe macrobenthic communities in a deep multibasin fjord system (Tysfjord) and the main drivers affecting its distribution along the fjord axis.

Paper II: Compare macrofaunal communities and environmental conditions of three sub-Arctic fjord basins with different morphologies and assess the degree of differentiation of inhabitant macrobenthic communities with respect to within-basin variation.

Paper III: Assess the main differences between species and functional trait composition of fjord basin communities on among-basin spatial scales to evaluate their degree of functional redundancy and possible factors affecting community assembly.

Paper IV: Describe the trophic niche differentiation among dominant species of macrofauna in a deep basin and assess whether their trophic niche is influenced by aquaculture using a combination of stable isotopes and fatty acids analyses.

3. Main results

The fjords of the Vestfjord region have been rarely studied and little information is available about their macrobenthic composition in the literature. A comprehensive dataset of 80 grab stations (116 samples) was used to describe species composition, diversity, and spatial patterns of macrobenthic communities in the study area.

3.1. Environmental drivers of benthic community structure in a deep sub-arctic fjord system (Paper I)

The distribution of macrobenthic communities in Tysfjord largely corresponded to the multibasin topography of this fjord system. The community in the deepest basin was similar to the community in the adjacent Vestfjord basin and was dominated by the bivalve *Kelliella miliaris.* In the inner branch of the fjord system, Hellmofjord, the two basins separated by a shallow (60 m) sill were inhabited by two distinct communities. In the middle basin, the relative abundance of *K. miliaris* decreased, where it was dominant along with the bivalves *Thyasira obsoleta*, *Mendicula ferruginosa*, *Abra nitida,* and the polychaete *Heteromastus filiformis*. In the innermost basin, the bivalve *Parathyasira equalis* was the most dominant species along with the polychaetes *H. filiformis* and *Terebellides stroemii.* Several environmental drivers correlated with the distribution of the communities: depth, organic matter content in sediment, and bottom water properties. Organic matter content was highest in the deepest basin and decreased towards the middle basin. Restricted water exchange by a shallow sill resulted in decreased temperature, salinity, and lower oxygen content. Our results demonstrate that a multibasin topography and associated environmental factors are important drivers of ecological processes that result in distinct communities.

3.2. Strong macrobenthic community differentiation among sub-Arctic deep fjords on small spatial scales (Paper II)

The three fjords studied here were inhabited by distinct macrobenthic communities. The deep-silled fjords, Saltfjord and Sørfolda, were characterised by similar bottom water mass properties, and the community in the inner basins of these fjords were similar to the ones in the respective adjacent basins. Saltfjord was largely dominated by the sipunculid *Onchnesoma steenstrupii*, followed by the polychaete *Spiochaetopterus typicus.* The latter was the most abundant species in Sørfolda, followed by the polychaete *Heteromastus filiformis.* Skjerstadfjord was the only fjord where a change in the community structure along the fjord axis was evident. The shallow (26 m) sill between Saltfjord and Skjerstadfjord restricts water exchange to the uppermost layers. Denser surface water masses from Saltfjord are advected into Skjerstadfjord by strong tidal forcing and sink to the deeper layers of Skjerstadfjord, resulting in turbulent mixing of bottom water masses in Skjerstadfjord and probably enhancing bentho-pelagic coupling at the fjord entrance. The resulting communities close to the fjord entrance were more abundant and diverse compared to the rest of the fjord and differ in their dominance structure with higher abundances of polychaetes *Galathowenia oculata, Paramphinome jeffreysii,* and *Chaetozone setosa*. Further down-fjord, communities were dominated by *H. filiformis* and the bivalve *Parathyasira equalis*. The strong differentiation of macrobenthos among different nearby fjords could be only partially attributed to differences in depth and measured sediment parameters. Moreover, in all three fjords relatively high number of unique taxa (present only in a particular fjord) was found with the highest number observed in Sørfolda. Therefore, it is suggested that the observed communities developed independently with stochastic processes during community assembly as an additional driver of the observed pattern.

3.3. Combining species and biological trait composition to assess macrobenthic community assembly in deep sub-Arctic fjords (Paper III)

The joint community analysis of the data from papers 1 and 2 with the inclusion of additional data on two shallow-silled fjords (Nordfjord and Mistfjord) confirmed the previously described pattern of distinct fjord/basin scale communities. There was also a clear and significant difference in community structure based on species composition between shallow- and deep-silled fjords. Biological trait composition revealed that, generally, basins with a shallow sill had a higher proportion of deep-dwelling subsurface deposit feeding fauna, indicating differences in benthic functioning. However, Nordfjord with a relatively deep sill (120 m) has a trait composition similar to the deep-silled basins, while the species composition was similar to the other shallow silled fjords, resulting in a discrepancy between taxonomic and functional community structure. It is suggested that trait composition reflects community adaptation to the fluxes of fresh pelagic organic matter, which is mediated by the water exchange over the sill. In contrast, community assembly with regard to species composition might be more influenced by local connectivity among basins and inflow of Atlantic water in deep basins, which facilitates connectivity between fjords and the offshore species pool. The relationship between taxonomic and functional diversity appeared to be similar between two groups of fjords: first functional diversity increased rapidly at low levels of species diversity before slowing down as functional space reaches saturation. However, shallow-silled fjords had higher functional diversity at low species diversity, while deep-silled fjords showed higher functional diversity at higher levels of species diversity. This pattern indicates that both groups of fjords have a high functional redundancy at high levels of taxonomic diversity.

3.4. Combining stable isotope and fatty acid analyses to assess trophic niches of macrofauna in an anthropogenically influenced deep fjord basin (Paper IV)

The importance of food resource partitioning on macrobenthic community structure was studied in Nordfjord, where salmon farming close to the main basin was an additional potential source of organic matter. Fatty acid markers indicated that this community, dominated by deposit feeders, relied on bacterially reworked detritus of phytoplankton origin. The biomass dominant species (bivalves *Abra nitida* and *Nucula tumidula*, polychaetes *Melinna cristata*, *Aphelochaeta* sp. and *Phylo norvegicus*, pectinarid and maldanid polychaetes, and the seastar *Ctenodiscus crispatus*) were characterised by distinct trophic niches. Although the sampling was performed in the direct vicinity of a fish farm (≥500 m) at the end of the production cycle, the role of the fish farm waste as an additional carbon source for macrobenthos could not be traced in this study. It is concluded that in sub-euphotic basins resource partitioning might be important for species coexistence due to its isolated nature and low amounts of phytoplankton-derived organic matter reaching the seafloor due to weak bentho-pelagic coupling.

4. General discussion

4.1. Composition of macrobenthic communities in fjord basins

Vestfjord is an area influenced by two major currents: the Norwegian Atlantic Current and the Norwegian Coastal Current. Water masses transported with the Norwegian Atlantic Current (salinity over 34.5 and temperature over 6.5 °C) form the bottom water layer in Vestfjord and deep-silled basins (Mitchelson-Jacob and Sundby, 2001; **Paper I**; **Paper II**). The major currents might have important implications for benthos distributions defining their distributional range (Gaylord and Gaines, 2000; Gaston, 2009). This is reflected in the composition of the macrobenthos in the studied fjords with dominant species reported in **Paper I** and **Paper II** being widely distributed further south in the Atlantic Ocean, e.g. thyasirid bivalves *Thyasira obsoleta, Genaxinus eumyarius, Parthyasira equalis, Mendicula ferruginosa* (Payne and Allen, 1991), the bivalve *Kelliella miliaris* (Allen, 2001), the sipunculid *Onchnesoma steenstrupii* (Murina and Sørensen, 2004), the polychaete *Paramphinome jeffreysii* (Gunton et al., 2015). The composition of the fauna in the fjords found in our studies resemble other deep-water depositional habitats influenced by Atlantic water masses at lower latitudes, particularly deep parts of Skagerrak and deep fjords of Western Norway, where similar bottom water masses were observed (Brattegard, 1967; Josefson, 1985; Buhl-Mortensen and Høisæter, 1993; Rosenberg et al., 1996). Therefore, it may be assumed that the inflow of Atlantic water masses also affects the species composition in the sub-Arctic fjords of our study region, possibly through larval recruitment from offshore habitats. Indeed, Thomsen and Vorren (1986) showed that boreal Atlantic fauna replaced representatives of the Arctic fauna in the deep basins, which were the first to colonize fjords after deglaciation, and such changes corresponded to the inflow of Atlantic water. In this sense, it may be noted that the connectivity of macrobenthic fjords along the Norwegian coast might be related to the distribution of meroplanktonic larvae with Norwegian coastal current, as shown for herring larvae, which are generally transported from spawning grounds on the west coast of Norway into the Barents Sea, but might be advected into the fjords depending on wind conditions (Skagseth et al., 2015). However, most of the species recorded in the basins do not have a planktotrophic larva (Josefson, 1985; **Paper III**), and not so many meroplanktonic larvae that would correspond to species in the basins were recorded over the nearby shelf area, e.g. polychaetes of the families Amphinomidae, Chaetopteridae, Spionidae (Silberberger et al., 2016). Therefore, distribution with coastal waters masses that overlay water masses of Atlantic origin might be important for a limited number of macrobenthic taxa in the basins.

Analyses on a large spatial scale in the study area showed differences in macrobenthic composition especially between deep-silled basins, which are characterized by bottom water masses of Atlantic origin with recorded temperatures >7 °C and salinity >35, and shallow-silled basins with colder (<7 °C) and less saline (<35) water masses, indicating only inflow of less dense coastal water advected into Vestfjord with Norwegian Coastal Current (**Paper III**). Although the temperature limits for distribution can be considered a species-specific trait, an upper limit of 2-6 °C was observed in several Arctic taxa (Renaud et al., 2015). Some of the species, recorded only in shallow-silled basins in this study, might be the populations of the Arctic fauna that inhabited basins before the inflow of Atlantic waters and living at the limit of their distribution range, e.g. the seastar *Ctenodiscus crispatus,* the polychaete *Praxillella gracilis*, the scaphopod *Siphonodentalium lobatum* (**Paper III**). These species have an upper limit of distribution at 6-7 °C, e.g., 4-6 °C for *C. crispatus* (Renaud et al., 2015), 5.8 °C for *S. lobatum* (Ivanov and Zarubina, 2004), 7 °C for *P. gracilis* (Jirkov, 2001). This finding is in line with previous ideas that fjord basins might act as biogeographical enclaves for some species (Brattegard, 1980; Węsławski et al., 2011). For instance, a higher proportion of Arctic species has also been recorded in the inner fjords of Svalbard that are less influenced by Atlantic waters (Wlodarska-

Kowalczuk et al., 1998). The basins with shallower sills are less affected by hydrological fluctuations and retain colder bottom water masses, therefore their transition from Artic to boreal communities possibly happened on a longer timescale, allowing some populations to adapt to warmer temperatures (Węsławski et al., 2011). However, there were further differences in species composition and community structure of macrobenthos among basins with similar bottom water masses (**Paper I**, **Paper II**, **Paper III**), which are most probably related to the possible differences in community assembly described below.

4.2. Spatial patterns and community assembly

Understanding community dynamics and assembly relies on adequate delineating of local communities. Significant differences in community structure (relative abundances of dominant species) and composition (presence of unique species) show that local communities can be defined approximately on a basin scale (**Paper I**; **Paper II**). Our results demonstrate that sufficient sampling effort is required to distinguish within and among fjord variation. Although it was acknowledged before that nearby basins can differ considerably in their species composition (Brattegard, 1980), this study is the first study, to my knowledge, to describe such a pattern on an extensive dataset comprising several fjord systems.

Community structure based on biological traits composition revealed that basins in the study area can be divided into two groups: deep-silled basins and Nordfjord, which has a higher proportion of surface deposit and suspension feeders, and the rest of shallow-silled basins, where subsurface deposit feeding is more common (**Paper III**). Benthos relies on organic matter sedimentation from overlaying waters, and, accordingly, differences in organic matter fluxes might be a major structuring factor in deep boreal and sub-Arctic fjords, where deep basin environment can be considered physically stable (Burrell, 1988). Populations of subsurface deposit feeders might feed on more refractory microbially degraded sediment organic matter, and, in general, their populations are less dependent on episodic inputs of high-quality detritus (Rice and Rhoads, 1989; Josefson et al., 2002; Levinton and Kelaher, 2004). Therefore, differences in sedimentation regime among basins might be a major driver for the functional community structure. In line with this finding, in Skjerstadfjord, a down-fjord gradient was observed in community structure, with decreasing abundances of surface deposit feeders *Galathowenia oculata* and *Chaetozone setosa* which was related to stronger bentho-pelagic coupling at the fjord mouth (**Paper II**). In turn, such differences in community structure might suggest differences in ecosystem functioning among the basins, particularly the amount of sedimented phytodetritus that is remineralised on sediment surface versus the amount that is buried deeper in sediments (Josefson et al., 2002; Sweetman and Witte, 2008).

The differences between shallow- and deep-silled basins cannot be attributed solely to shifts in functional structure based on biological traits as discrepancy was observed between analyses of community structure based on species and trait compositions, mostly related to Nordfjord community converging in functional structure with deep-silled fjords (**Paper III**). This finding supports the hypothesis that species and traits compositions are different levels of community organisation, with the former being influenced by historical contingencies and priority effects (Fukami et al., 2005; Fukami, 2015). The species composition in fjords might be also influenced by colonisation history from an offshore pool of species (Smith, 2001). Shallow sills that restrict the inflow of Atlantic water masses may serve as dispersal barriers for the majority of taxa in the deep basins with lecithotrophic development as they are mainly distributed with near-bottom currents (Josefson, 1985; **Paper III**). This hypothesis was not favored for the fjords in Western Norway (Buhl-Mortensen and Høisæter, 1993). However, our data on population connectivity obtained using a genotyping-by-sequencing approach for the bivalve *Parathyasira equalis* with lecithotrophic development suggest low but significant Fst values between Saltfjord and Skjerstadfjord (Fst = 0.005), separated only by a shallow sill, but not between Saltfjord and Sørfolda (Fst = -0.001) separated by distance, but both characterized by Atlantic water masses (own unpublished data). Therefore, a continuous population in Atlantic waters is "interrupted" by a shallow sill.

Communities in the deep-silled fjord basins (Saltfjord, Sørfolda Tysfjord deep, and Tysfjord middle basins) have a similar species composition as the adjacent basins beyond the sill (**Paper I**; **Paper II**). Such a pattern indicates high dispersal, which results in the homogenization of communities ("mass effects"; Heino et al., 2015). While this connectivity between adjacent basins is most probably a result of the inflow of Atlantic water over a deep sill several times a year (Skreslet et al., 2020), the connectivity among different fjord systems for macrobenthos still might be low as an outflow of bottom water masses from below the sill depth is unlikely. The outflow is generally limited to the uppermost desalinated layer during periods with strong stratification (Myksvoll et al., 2011), while wind-induced advection in and out of fjord over a sill is more important for connectivity of plankton through coastal waters (Asplin et al., 1999; Espinasse et al., 2018). However, even this connectivity through coastal waters can be low, particularly between Tysfjord and Sørfolda. This is supported by simulation of dispersal of Atlantic cod eggs, which are retained in the fjords (Myksvoll et al., 2011; 2014), and genetically isolated populations of European lobster, a species with a planktonic larva (Jørstad et al., 2004). Dispersal limitation and priority effects, enhanced by larvae retention in deep basins, might hamper establishments of populations in fjords otherwise environmentally suitable for a species, affecting species sorting and increasing the role of stochasticity in community assembly (Heino et al., 2015; Fukami, 2015).

The resulting communities are distinct with different levels of diversity, with species-poor communities such as the ones in Mistfjord and Saltfjord having the lowest functional redundancy (**Paper III**). However, at some point increase in species diversity did not lead to an increase in functional diversity, indicating high functional redundancy (Micheli and Halpern, 2005). It may be assumed that functional redundancy depends on the number of co-existing species, which is influenced by many factors including demographic stochasticity, dispersal, available resources, and resource partitioning (Hart et al., 2017; **Paper IV**). Generally, the number of coexisting species increases with habitat area, however, smaller and isolated habitats might be an exception as they are more influenced by demographic stochasticity and disturbance events, which might result in different species richness irrespective of habitat size ("small island effects"; Lomolino, 2000). The communities appear to be very different in their dominance structure with the ones largely dominated by a single species, e.g. *Onchnesoma steenstrupii* in Saltfjord and *Kelliella miliaris* in Tysfjord deep basin, while in others several species are equally dominant, e.g. Tysfjord middle basin (**Paper I**; **Paper II**). Studying resource partitioning and population dynamics on a basin scale might give further insights into factors structuring these local communities.

4.3. Trophic niches and resource partitioning

Several potential carbon sources can be important for benthic consumers in fjord ecosystems. Fjords are estuarine environments, and accordingly input of terrestrial carbon to the sediments can be expected, which might be a carbon source for benthic invertebrates (McGovern et al., 2020). Fjords in the study are characterised by the low contribution of terrestrial organic matter, however, an increase in terrestrial input can be expected in the more inner parts (Faust and Knies, 2019; **Paper II**, **Paper IV**). The main source of marine carbon is phytoplankton production, but contributions of macroalgal carbon to deeper habitats devoid of vegetation have been recently investigated (Renaud et al., 2015; Silberberger et al., 2018; Zaborska et al., 2018). Deposit feeders, a group that is dominant in the basins (**Paper III**), might consume detritus of various origins and associated bacteria in the sediments, but might depend on less degraded organic matter of phytoplankton origin as a source of certain compounds, such as polyunsaturated fatty acids (Lopez and Levinton, 1987). Phytoplankton is a major source of polyunsaturated fatty acids, such as 20:5n-3 and 22:6n-3, which are incorporated by benthic consumers (Bell and Sargent, 1985; Kelly and Scheibling, 2012). Fatty acid analysis in Nordfjord suggested that both phytoplankton and bacteria are important for benthic consumers in fjord basins, although the combination of fatty acid and stable isotope analyses revealed differences in trophic niches among species studied (**Paper IV**). Although fish farm waste can be consumed by benthos as well (Witte et al., 2019), no clear shifts in trophic niches of the deposit feeders were observed relative to the distance from the fish farm suggesting insignificant contributions of this carbon source to the deep basin (**Paper IV**).

Distinct trophic niches of common taxa in Nordfjord suggested that food resource partitioning might be an important factor structuring communities on a basin scale (**Paper IV**). The differences were observed even between taxa with the same feeding habit, e.g. surface deposit feeders bivalves *Abra nitida*, *Nucula tumidula,* and the polychaete *Melinna cristata*. This is not always the case for marine macrobenthos as many studies did not observe such differences in trophic niches, e.g. deposit feeding bivalves on the Bering Sea shelf (Oxtoby et al., 2016), native species of deposit feeders in the Baltic Sea (Karlson et al., 2015), echinoderm species in a shallow Swedish fjord (Godbold et al., 2009). However, evidence of resource partitioning was documented for bathyal holothurians in the Northeast Atlantic (Hudson et al., 2003) and rocky shore suspension feeders (Richoux et al., 2014). It seems that the relative importance of competition for macrobenthos depends on the habitat. Rocky shores are highly competitive habitats for sessile organisms due to high competition for space (Worm and Karez, 2002). In the soft-bottom communities, the competition for space is less pronounced as animals can adjust their position in the sediment, including the sediment dwelling depth (Wilson, 1990). The persistent supply of organic material to the benthos may also decrease interspecific competition for the food resource (Wigham et al., 2008). Indeed, generally, deep sub-euphotic fjord basins are characterised by low amount of phytoplankton detritus reaching the seafloor (Burrell, 1988). Sub-euphotic basins, like the fjord basins I have studied, might be a more resource-limited environment for macrobenthos due to weak bentho-pelagic coupling and irregular input of labile organic matter, which would increase the role of competition for food resources.

5. Conclusions and further perspectives

Our results suggest the differentiation of macrobenthic fjord communities approximately on a basin scale. Such differentiation reflects the semi-isolated nature of fjords and low connectivity among basins. These communities can be described based on two levels of organisation: species composition and functional structure based on traits composition. Species composition might reflect more the history of community assembly, particularly colonization from the offshore pool of species and priority effects, while trait composition might be more driven by adaptation of the community to the environment, such as organic matter fluxes to the seafloor mediated by water exchange with adjacent waters. In addition, competition and resource partitioning might structure communities on the within-basin scale. A combination of the above-suggested processes results in a unique pattern of among-fjord variation.

Undisturbed habitats are generally characterised by high variation among local communities, such as observed in this study, while anthropogenic activities can result in human-induced homogenization due to loss of endemics or prevalence of cosmopolitan species (Mori et al., 2018). The ecosystems of Norwegian fjords are potentially vulnerable to anthropogenic impacts due to restricted water exchange and, consequently, accumulation of discharged pollutants and waste, however, baseline knowledge on different ecosystem components is currently lacking (Manzetti and Stenersen, 2010). In fjords of Western Norway, recent distribution of an opportunistic species *Polydora* sp. was observed accompanied by increasing temperatures of water masses and organic matter content in sediments and decreasing oxygen content (Johansen et al., 2018). Dominance of few opportunistic species, such as *Polydora* sp., is often linked to hypoxia rather than organic enrichment per se (Gray et al., 2002), and might result in homogenization of benthic communities in the basins, consequently affecting ecosystem functioning (Mori et al., 2018). Warming of Atlantic water can alter water exchange of fjords in Western Norway leading to a decrease in oxygen in the bottom water layer (Aksnes et al., 2019). The organic loading from fish farm production can also contribute to oxygen depletion in the basin waters, although current monitoring results suggest low impact for the majority of farming locations (Taranger et al., 2015). Fjords in the study area are characterised by deep sills or good water exchange (e.g. Skjerstadfjord, **Paper II**) compared to the fjords of Western Norway, and, therefore might be less affected by decreasing oxygen in the deep water, although Mistfjord (Skreslet et al., 2020) and Tysjord inner basin (**Paper I**) might be exceptions. Comparison of fjords along the Norwegian coast as well long-term monitoring, both in terms of benthic fauna and water exchange, might give further insights into factors structuring benthic communities, as well as how they can be affected by increasing organic load or increasing temperatures.

As indicated by our data, monitoring results from one fjord might not reflect that ecosystem processes in adjacent fjords, particularly if they are separated by a shallow sill. Accordingly, long-term data sets are also necessary to distinguish between spatial and temporal variation. Understanding of population dynamics of species with different reproduction strategies and connectivity of these populations might give useful insights into the temporal dynamics of basin communities. In **Paper II** interannual changes are briefly discussed, particularly an increase in abundances in the fjords in 2015 compared to 2013. Many potential factors might result in interannual changes of carbon export to the seafloor and consequently in the abundances of macrobenthic consumers, which are currently poorly understood for the fjords in the study area, e.g. differences in primary productivity, wind-induced advection of nutrients/phytoplankton/organic matter in and out of fjords, abundance of plankton grazers in the mesopelagic zone (Burrell, 1988; Wassmann et al., 1996; Lalande et al., 2020). Therefore, studies of vertical export of carbon to the seafloor might give useful insights into the dynamics of macrobenthic communities in the basins. Further, palaeoecological data would allow studying actual colonization history and responses of these communities on a longer timescale and, particularly, on how stable are populations in the basins, whether they are subject to stochastic extinctions and recolonizations (Levinton, 1970; Thomsen and Vorren, 1986; Einarsson et al., 2016).

We observed a difference in functional structure between deep-silled and shallowed-silled basins (**Paper III**). Whether this difference corresponds to differences in ecosystem functioning, such as carbon burial, remains unknown. The fjords in the Vestfjord region are characterised by high burial rates of marine organic matter burial (Faust and Knies, 2019). Further investigation on sedimentation and the role of macrobenthos in organic matter remineralization are needed to understand carbon cycling in these depositional habitats (Burrell, 1988).

The observed trophic niche differentiation in Nordfjord (**Paper IV**) suggested the possible importance of competition in structuring communities. Comparison of trophic niches of the same species, but from different communities, would give further insights on the role of competition and how it affects realized niches of species. Moreover, as invasive species often occupy vacant niches (Karlson et al., 2015), such an approach would indicate the susceptibility of the communities in the study area to possible invasions by comparing data with fjords in Western Norway, which are already invaded by *Polydora* sp. (Johansen et al., 2018).

It is not clear whether such basin-specific communities, described for macrobenthos, are characteristic for different size classes of benthos. Different size classes can have different scales of their spatial organization as body size is one of the main scaling factors for ecological patterns (Azovsky, 2000). However, little is known about megabenthic and meiobenthic communities in the Vestfjord region. Meiobenthic communities might be structured differently from macrobenthos as these two groups differ not only taxonomically, but also functionally in generation time, life-history traits, dispersal mode, and resource use (Warwick, 2014). . Megabenthic epifaunal communities might be structured on different spatial scales compared to macrofauna as well due to more exposed mode of life (Silberberger et al., 2019; Meyer et al., 2020). However, how such functional differences between different benthic components affect among-fjord variation remains a topic for future investigations.

These are only a few examples of possible future research that could foster our understanding of fjord ecosystems. As mentioned by Brattegard (1980) deep basins can be treated as unique natural laboratories for studying deep-sea communities and might be used to study all aspects of biology and ecology of deep-sea fauna.

References

Abrams P (1983) The Theory of Limiting Similarity. Annu Rev Ecol Syst 14:359–376.

Aksnes DL, Aure J, Johansen PO, Johnsen GH, Vea Salvanes AG (2019) Multi-decadal warming of Atlantic water and associated decline of dissolved oxygen in a deep fjord. Estuar Coast Shelf Sci 228:106392.

Allen JA (2001) The family Kelliellidae (Bivalvia: Heterodonta) from the deep Atlantic and its relationship with the family Vesicomyidae. Zool J Linn Soc 131:199–226.

Aller RC (1977) The Influence Of Macrobenthos On Chemical Diagenesis Of Marine Sediments. Yale University. Diss. Ph. D. Thesis, 599p.

Arruda EP, Domaneschi O, Amaral ACZ (2003) Mollusc feeding guilds on sandy beaches in São Paulo State, Brazil. Mar Biol 143:691–701.

Asplin L, Salvanes AGV, Kristoffersen JB (1999) Nonlocal wind-driven fjord-coast advection and its potential effect on plankton and fish recruitment. Fish Oceanogr 8:255–263.

Azovsky AI (2000) Concept of scale in marine ecology: Linking the words or the worlds? Web Ecol 1:28–34.

Beauchard O, Veríssimo H, Queirós AM, Herman PMJ (2017) The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. Ecol Indic 76:81–96.

Bell M V., Sargent JR (1985) Fatty acid analyses of phosphoglycerides from tissues of the clam Chlamys islandica (Muller) and the starfish Ctenodiscus crispatus (Retzius) from Balsfjorden, Northern Norway. J Exp Mar Bio Ecol 87:31–40.

Blanchet-Aurigny A, Dubois SF, Quéré C, Guillou M, Pernet F (2015) Trophic niche of two co-occurring ophiuroid species in impacted coastal systems, derived from fatty acid and stable isotope analyses. Mar Ecol Prog Ser 525:127–141.

Borja A, Miles A, Occhipinti-Ambrogi A, Berg T (2009) Current status of macroinvertebrate methods used for assessing the quality of European marine waters: Implementing the Water Framework Directive. Hydrobiologia 633:181–196.

Brasier MJ, Wiklund H, Neal L, Jeffreys R, Linse K, Ruhl H, et al. (2016) DNA barcoding uncovers cryptic diversity in 50% of deep-sea antarctic polychaetes. R Soc Open Sci 3:160432.

Brattegard T (1967) Pogonophora and associated fauna in the deep basin of Sognefjorden. Sarsia 29:299–306.

Brattegard T (1980) Why biologists are interested in fjords. In: Freeland HJ, Farmer DM, Levings C (eds) Fjord Oceanography. Plenum Press, New York and London, pp 53–66.

Bremner J (2008) Species' traits and ecological functioning in marine conservation and management. J Exp Mar Bio Ecol 366:37–47.

Bremner J, Rogers SI, Frid CLJ (2006) Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecol Indic 6:609–622.

Brewin PE, Probert PK, Barker MF (2011) Relative influence of processes structuring fjord deep-water macrofaunal communities across multiple spatial scales. Mar Ecol Prog Ser 425:175–191.

Buhl-Mortensen L, Hoisaeter T (1993) Mollusc fauna along an offshore-fjord gradient. Mar Ecol Prog Ser 97:209–224.

Bulling MT, Hicks N, Murray L, Paterson DM, Raffaelli D, White PCL, et al. (2010) Marine biodiversity-ecosystem functions under uncertain environmental futures. Philos Trans R Soc B Biol Sci 365:2107–2116.

Burrell DC (1988) Carbon Flow in Fjords. Ocean Mar Biol Annu Rev 26:143–226.

Carstensen DW, Lessard JP, Holt BG, Krabbe Borregaard M, Rahbek C (2013) Introducing the biogeographic species pool. Ecography (Cop) 36:1310–1318.

Chase JM (2007) Drought mediates the importance of stochastic community assembly. Proc Natl Acad Sci U S A 104:17430–17434.

Chase JM, Myers JA (2011) Disentangling the importance of ecological niches from stochastic processes across scales. Philos Trans R Soc B Biol Sci 366:2351–2363.

Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D (2009) Projecting global marine biodiversity impacts under climate change scenarios. Fish Fish 10:235–251.

Clarke A (2003) Costs and consequences of evolutionary temperature adaptation. Trends Ecol Evol 18:573–581.

Clarke A, Griffiths HJ, Barnes DKA, Meredith MP, Grant SM (2009) Spatial variation in seabed temperatures in the Southern Ocean: Implications for benthic ecology and biogeography. J Geophys Res Biogeosciences 114:1–11.

Corte GN, Gonçalves-Souza T, Checon HH, Siegle E, Coleman RA, Amaral ACZ (2018) When time affects space: Dispersal ability and extreme weather events determine metacommunity organization in marine sediments. Mar Environ Res 136:139–152.

Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. Ann Rev Mar Sci 1:443–466.

Dang C, Sauriau PG, Savoye N, Martinez P, Millaret C, Haure J, et al. (2009) Determination of diet in Manila clams by spatial analysis of stable isotopes. 387:167–177.

Dauer DM, Maybury CA, Ewing RM (1981) Feeding behavior and general ecology of several spionid polychaetes from the chesapeake bay. J Exp Mar Bio Ecol 54:21–38.

Dauwe B, Herman PMJ, Heip CHR (1998) Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. Mar Ecol Prog Ser 173:67–83.

Degen R, Aune M, Bluhm BA, Cassidy C, Kędra M, Kraan C, et al. (2018) Trait-based approaches in rapidly changing ecosystems: A roadmap to the future polar oceans. Ecol Indic 91:722–736.

Degraer S, Verfaillie E, Willems W, Adriaens E, Vincx M, Van Lancker V (2008) Habitat suitability modelling as a mapping tool for macrobenthic communities: An example from the Belgian part of the North Sea. Cont Shelf Res 28:369–379.

Diaz RJ, Rosenberg R (1995) Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanogr Mar Biol an Annu Rev Vol 33 245–303.

Donadi S, van der Heide T, Piersma T, van der Zee EM, Weerman EJ, van de Koppel J, et al. (2015) Multi-scale habitat modification by coexisting ecosystem engineers drives spatial separation of macrobenthic functional groups. Oikos 124:1502–1510.

Doney SC (2010) The growing human footprint on coastal and open-ocean biogeochemistry. Science 328:1512–1516.

Doney SC, Ruckelshaus M, Emmett Duffy J, Barry JP, Chan F, English CA, et al. (2012) Climate change impacts on marine ecosystems. Ann Rev Mar Sci 4:11–37.

Eilertsen HC, Degerlund M (2010) Phytoplankton and light during the northern high-latitude winter. J Plankton Res 32:899–912.

Einarsson Á, Hauptfleisch U, Leavitt PR, Ives AR (2016) Identifying consumer-resource population dynamics using paleoecological data. Ecology 97:361–371.

Ellingsen KE (2001) Biodiversity of a continental shelf soft-sediment macrobenthos community. Mar Ecol Prog Ser 218:1–15.

Ellingsen KE, Hewitt JE, Thrush SF (2007) Rare species, habitat diversity and functional redundancy in marine benthos. J Sea Res 58:291–301.

Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, et al. (2003) Response diversity, ecosystem change, and resilience. Front Ecol Environ 1:488–494.

Espinasse B, Basedow SL, Tverberg V, Hattermann T, Eiane K (2016) A major Calanus finmarchicus overwintering population inside a deep fjord in northern Norway: Implications for cod larvae recruitment success. J Plankton Res 38:604–609.

Espinasse B, Tverberg V, Kristensen JA, Skreslet S, Eiane K (2018) Winter mortality in Calanus populations in two northern Norwegian fjords from 1984 to 2016. Polar Biol 41:1405–1415.

Faust JC, Knies J (2019) Organic matter sources in North Atlantic fjord sediments. Geochemistry, Geophys Geosystems 20:2872–2885.

Feckler A, Zubrod JP, Thielsch A, Schwenk K, Schulz R, Bundschuh M (2014) Cryptic species diversity: An overlooked factor in environmental management? J Appl Ecol 51:958–967.

Fetzer I, Arntz WE (2008) Reproductive strategies of benthic invertebrates in the Kara Sea (Russian Arctic): Adaptation of reproduction modes to cold water. Mar Ecol Prog Ser 356:189–202.

Fukami T (2015) Historical contingency in community assembly: Integrating niches, species pools, and priority effects. Annu Rev Ecol Evol Syst 46:1–23.

Fukami T, Bezemer TM, Mortimer SR, Van Der Putten WH (2005) Species divergence and trait convergence in experimental plant community assembly. Ecol Lett 8:1283–1290.

Furnes GK, Sundby S (1981) Upwelling and wind induced circulation in Vestfjorden. Nor Coast Curr Proc Nor Coast Curr Symp Vol. 1, 152-177.

Gage JD (2004) Diversity in deep-sea benthic macrofauna: The importance of local ecology, the larger scale, history and the Antarctic. Deep Res Part II Top Stud Oceanogr 51:1689–1708.

Gamfeldt L, Lefcheck JS, Byrnes JEK, Cardinale BJ, Duffy JE, Griffin JN (2015) Marine biodiversity and ecosystem functioning: What's known and what's next? Oikos 124:252–265.

Garciá Molinos J, Halpern BS, Schoeman DS, Brown CJ, Kiessling W, Moore PJ, et al. (2016) Climate velocity and the future global redistribution of marine biodiversity. Nat Clim Chang 6:83–88.

Gaston KJ (2009) Geographic range limits: Achieving synthesis. Proc R Soc B Biol Sci 276:1395–1406.

Gaylord B, Gaines SD (2000) Temperature or transport? Range limits in marine species mediated solely by flow. Am Nat 155:769–789.

Godbold JA, Rosenberg R, Solan M (2009) Species-specific traits rather than resource partitioning mediate diversity effects on resource use. PLoS One 4: e7423.

Götzenberger L, de Bello F, Bråthen KA, Davison J, Dubuis A, Guisan A, et al. (2012) Ecological assembly rules in plant communities-approaches, patterns and prospects. Biol Rev 87:111–127.

Gravel D, Canham CD, Beaudet M, Messier C (2006) Reconciling niche and neutrality: The continuum hypothesis. Ecol Lett 9:399–409.

Gray JS (2002) Species richness of marine soft sediments. Mar Ecol Prog Ser 244:285–297.

Gray JS, Elliott M (2009) Ecology of marine sediments: from science to management. Oxford University Press.

Gray JS, Wu RSS, Ying YO (2002) Effects of hypoxia and organic enrichment on the coastal marine environment. Mar Ecol Prog Ser 238:249–279.

Grebmeier JM (2012) Shifting patterns of life in the pacific Arctic and sub-Arctic Seas. Ann Rev Mar Sci 4:63–78.

Gunton LM, Neal L, Gooday AJ, Bett BJ, Glover AG (2015) Benthic polychaete diversity patterns and community structure in the Whittard Canyon system and adjacent slope (NE Atlantic). Deep Res Part I Oceanogr Res Pap 106:42–54.

Hart SP, Usinowicz J, Levine JM (2017) The spatial scales of species coexistence. Nat Ecol Evol 1:1066–1073.

Heino J, Melo AS, Siqueira T, Soininen J, Valanko S, Bini LM (2015) Metacommunity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes and prospects. Freshw Biol 60:845–869.

Hestetun JT, Bye-Ingebrigtsen E, Nilsson RH, Glover AG, Johansen PO, Dahlgren TG (2020) Significant taxon sampling gaps in DNA databases limit the operational use of marine macrofauna metabarcoding. Mar Biodivers 50:70.

Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. Science 328:1523–1528.

Holte B, Gulliksen B (1998) Common macrofaunal dominant species in the sediments of some north Norwegian and Svalbard glacial fjords. Polar Biol 19:375–382.

Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK, Hungate BA, Matulich KL, et al. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105–108.

Hudson IR, Wigham BD, Billett DSM, Tyler PA (2003) Seasonality and selectivity in the feeding ecology and reproductive biology of deep-sea bathyal holothurians. Prog Oceanogr 59:381–407.

Hughes TG (1979) Mode of life and feeding in maldanid polychaetes from St . Margaret's Bay , Nova Scotia. J Fish Board Canada 36:1503–1507.

Huse G, Fernö A, Holst JC (2010) Establishment of new wintering areas in herring co-occurs with peaks in the "first time/repeat spawner" ratio. Mar Ecol Prog Ser 409:189–198.

Inall ME, Gillibrand PA (2010) The physics of mid-Latitude fjords: a review. Geol Soc London, Spec Publ 344:17–33.

Ivanov D, Zarubina E (2004) Distribution of Scaphopod molluscs in the N Atlantic and Arctic oceans based on materials of Russian and Soviet expeditions. Ruthenica 1:89–104.

Jangoux M, M. Lawrence J (1982) Echinoderm nutrition. A.A. Balkema, Rotterdam.

Jirkov IA (2001) Polychaeta of the Arctic ocean. Janus-K, Moscow.

Jirkov IA (2013) Biogeography of the Barents Sea benthos. Invertebr Zool 10:69–88.

Johansen PO, Isaksen TE, Bye-Ingebrigtsen E, Haave M, Dahlgren TG, Kvalø SE, et al. (2018) Temporal changes in benthic macrofauna on the west coast of Norway resulting from human activities. Mar Pollut Bull 128:483–495.

Jørstad KE, Paulo A. Prodöhl, Agnalta A-L, Hughes M, Apostolidis AP, Triantafyllidis A, et al. (2004) Sub-arctic populations of European lobster, Homarus gammarus, in northern Norway Knut. Environ Biol Fishes 69:223–231.

Josefson AB (1985) Distribution of diversity and functional groups of marine benthic infauna in the skagerrak (Eastern north sea) - can larval availability affect diversity? Sarsia 70:229–248.

Josefson AB (2016) Species sorting of benthic invertebrates in a salinity gradient - Importance of dispersal limitation. PLoS One 11:1–21.

Josefson AB, Forbes TL, Rosenberg R (2002) Fate of phytodetritus in marine sediments: Functional importance of macrofaunal community. Mar Ecol Prog Ser 230:71–85.

Jumars PA, Dorgan KM, Lindsay SM (2015) Diet of worms emended: An update of polychaete feeding guilds. Ann Rev Mar Sci 7:497–520

Karlson AML, Gorokhova E, Elmgren R (2015) Do deposit-feeders compete? Isotopic niche analysis of an invasion in a species-poor system. Sci Rep 5:1–8.

Kelly JR, Scheibling RE (2012) Fatty acids as dietary tracers in benthic food webs. Mar Ecol Prog Ser 446:1–22.

Kokarev VN, Vedenin AA, Basin AB, Azovsky AI (2017) Taxonomic and functional patterns of macrobenthic communities on a high-Arctic shelf: A case study from the Laptev Sea. J Sea Res 129:61–69.

Kraft NJB, Adler PB, Godoy O, James EC, Fuller S, Levine JM (2015) Community assembly, coexistence and the environmental filtering metaphor. Funct Ecol 29:592–599.

Laakkonen HM, Hardman M, Strelkov P, Väinölä R (2021) Cycles of trans-Arctic dispersal and vicariance, and diversification of the amphi-boreal marine fauna. J Evol Biol 34:73–96.

Lalande C, Dunlop K, Renaud PE, Nadaï G, Sweetman AK (2020) Seasonal variations in downward particle fluxes in Norwegian fjords. Estuar Coast Shelf Sci 241:106811.

Lam-Gordillo O, Baring R, Dittmann S (2020) Ecosystem functioning and functional approaches on marine macrobenthic fauna: A research synthesis towards a global consensus. Ecol Indic 115:106379.

Leibold MA, Chase JM, Ernest SKM (2017) Community assembly and the functioning of ecosystems: how metacommunity processes alter ecosystems attributes. Ecology 98:909–919.

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, et al. (2004) The metacommunity concept: A framework for multi-scale community ecology. Ecol Lett 7:601–613.

Lepori F, Malmqvist B (2009) Deterministic control on community assembly peaks at intermediate levels of disturbance. Oikos 118:471–479.

Levin LA, Ekau W, Gooday AJ, Jorissen F, Middelburg JJ, Naqvi SWA, et al. (2009) Effects of natural and human-induced hypoxia on coastal benthos. Biogeosciences 6:2063–2098.

Levinton J (1972) Stability and trophic structure in deposit-feeding and suspension-feeding communities. Am Nat 106:472–486.

Levinton J, Kelaher B (2004) Opposing organizing forces of deposit-feeding marine communities. J Exp Mar Bio Ecol 300:65–82.

Levinton JS (1970) The paleoecological significance of opportunistic species. Lethaia 3:69–78.

Liu K, Lin H, He X, Huang Y, Li Z, Lin J, et al. (2019) Functional trait composition and diversity patterns of marine macrobenthos across the Arctic Bering Sea. Ecol Indic 102:673–685.

Lomolino M V. (2000) Ecology' s most general, yet protean pattern : The species-area relationship. J Biogeogr 27:17–26.

Lopez G, Elmgren R (1989) Feeding depths and organic absorption for the deposit feeding benthic amphipods Pontoporera affinis and Pontoporeia femorata. Limnol Oceanogr 34:982–991.

Lopez GR, Levinton JS (1987) Eclogy of deposit-feeding animals in marine sediments. Q Rev Biol 62:235–260.

Manzetti S, Stenersen JHV (2010) A critical view of the environmental condition of the Sognefjord. Mar Pollut Bull 60:2167–2174.

Mcgill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. 21:178-185.

McGovern M, Poste AE, Oug E, Renaud PE, Trannum HC (2020) Riverine impacts on benthic biodiversity and functional traits: A comparison of two sub-Arctic fjords. Estuar Coast Shelf Sci 240:106774.

Meyer HK, Roberts EM, Mienis F, Rapp HT (2020) Drivers of megabenthic community structure in one of the world's deepest silled-fjords, Sognefjord (western Norway). Front Mar Sci 7: 393.

Micheli F, Halpern BS (2005) Low functional redundancy in coastal marine assemblages. Ecol Lett 8:391–400.

Mileikovsky SA (1971) Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. Mar Biol Int J Life Ocean Coast Waters 10:193–213.

Mills EL (1969) The community concept in marine zoology, with comments on continua and instability in some marine communities: A review. J Fish Res Board Canada 26:1415–1428.

Mitchelson-Jacob G, Sundby S (2001) Eddies of Vestfjorden, Norway. Cont Shelf Res 21:1901–1918.

Mittelbach GG, Schemske DW (2015) Ecological and evolutionary perspectives on community assembly. Trends Ecol Evol 30:241–247.

Mori AS, Isbell F, Seidl R (2018) β-Diversity, community assembly, and ecosystem functioning. Trends Ecol Evol 33:549–564.

Murina V, Sorensen J (2004) Marine worms of the phylum Sipuncula in Faroese waters. Fróðskaparrit 51:280–291.

Myksvoll MS, Jung K, Albretsen J, Sundby S (2014) Norwegian coastal cod subpopulations. 71:957–969.

Myksvoll MS, Sundby S, Ådlandsvik B, Vikebø FB (2011) Retention of coastal cod eggs in a fjord caused by interactions between egg buoyancy and circulation pattern. Mar Coast Fish 3:279–294.

Naeem S (1998) Species redundancy and ecosystem reliability. Conserv Biol 12:39–45.

Nagelkerken I, Connell SD (2015) Global alteration of ocean ecosystem functioning due to increasing human CO2 emissions. Proc Natl Acad Sci U S A 112:13272–13277.

Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. Front Ecol Environ 5:429–436.

Norling K, Rosenberg R, Hulth S, Grémare A, Bonsdorff E (2007) Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. 332:11–23.

North CA, Lovvorn JR, Kolts JM, Brooks ML, Cooper LW, Grebmeier JM (2014) Deposit-feeder diets in the Bering Sea : potential effects of climatic loss of sea ice-related microalgal blooms. Ecol Appl 24:1525–1542.

Nygren A, Parapar J, Pons J, Meißner K, Bakken T, Kongsrud JA, et al. (2018) A mega-cryptic species complex hidden among one of the most common annelids in the North East Atlantic. PLoS One 13:1–37.

Orrock JL, Watling JI (2010) Local Community size mediates ecological drift and competition in metacommunities. Proc R Soc B Biol Sci 277:2185–2191.

Ottersen G, Bogstad B, Yaragina NA, Stige LC, Vikebø FB, Dalpadado P (2014) A review of early life history dynamics of Barents Sea cod (Gadus morhua). ICES J Mar Sci 71:2064–2087.

Oxtoby LE, Budge SM, Iken K, O'Brien DM, Wooller MJ (2016) Feeding ecologies of key bivalve and polychaete species in the Bering Sea as elucidated by fatty acid and compound-specific stable isotope analyses. Mar Ecol Prog Ser 557:161–175.

Palumbi SR, Sandifer PA, Allan JD, Beck MW, Fautin DG, Fogarty MJ, et al. (2009) Managing for ocean biodiversity to sustain marine ecosystem services. Front Ecol Environ 7:204–211.

Payne CM, Allen JA (1991) The morphology of deep-sea Thyasiridae (Mollusca: Bivalvia) from the Atlantic Ocean. Philos Trans - R Soc London, B 334:481–562.

Petryashov V V., Vassilenko S V., Voronkov AY, Sirenko BI, Smirnov A V., Smirnov IS (2013) Biogeographical analysis of the Chukchi Sea and adjacent waters based on fauna of some macrobenthos taxa. Invertebr Zool 10:49–68.

Rao Y, Cai L, Chen B, Chen X, Zheng L, Lin S (2020) How do spatial and environmental factors shape the structure of a coastal macrobenthic community and meroplanktonic larvae cohort? Evidence from Daya Bay. Mar Pollut Bull 157:111242.

Ravelo AM, Bluhm BA, Foster N, Iken K (2020) Biogeography of epibenthic assemblages in the central Beaufort Sea. Mar Biodivers 50:8.

Renaud PE, Løkken TS, Jørgensen LL, Berge J, Johnson BJ (2015) Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. Front Mar Sci 2:31.

Renaud PE, Sejr MK, Bluhm BA, Sirenko B, Ellingsen IH (2015) The future of Arctic benthos: Expansion, invasion, and biodiversity. Prog Oceanogr 139:244–257.

Rice DL, Rhoads DC (1989) Early diagenesis of organic matter and the nutritional value of sediment. In: Ecology of Marine Deposit Feeders. Springer, New York, NY, pp 114–123.

Rice J, Arvanitidis C, Borja A, Frid C, Hiddink JG, Krause J, et al. (2012) Indicators for sea-floor integrity under the european marine strategy framework directive. Ecol Indic 12:174–184.

Richoux NB, Vermeulen I, Froneman PW (2014) Fatty acid profiles reveal temporal and spatial differentiation in diets within and among syntopic rocky shore suspension-feeders. Mar Ecol Prog Ser 495:143–160.

Ricklefs RE (2007) History and diversity: Explorations at the intersection of ecology and evolution. Am Nat 170:S56–S70.

Rosenberg R, Hellman B, Lundberg A (1996) Benthic macrofaunal community structure in the Norwegian Trench, deep Skagerrak. J Sea Res 35:181–188.

Rossi F, Baeta A, Marques JC (2015) Stable isotopes reveal habitat-related diet shifts in facultative deposit-feeders. J Sea Res 95:172–179.

Scipione MB (2013) Do studies of functional groups give more insight to amphipod biodiversity. Crustaceana 86:955–1006.

Silberberger MJ, Renaud PE, Buhl-Mortensen L, Ellingsen IH, Reiss H (2019) Spatial patterns in sub-Arctic benthos: multiscale analysis reveals structural differences between community components. Ecol Monogr 89:e01325.

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.

Silberberger MJ, Renaud PE, Kröncke I, Reiss H (2018) Food-web structure in four locations along the European shelf indicates spatial differences in ecosystem functioning. Front Mar Sci 5:119.

Skagseth Ø, Slotte A, Stenevik EK, Nash RDM (2015) Characteristics of the Norwegian coastal current during years with high recruitment of Norwegian spring spawning herring (*Clupea harengus* L.). PLoS One 10:1–17.

Skreslet S, Espinasse M, Olsen K, Espinasse BD (2020) Variable predator–prey relations in zooplankton overwintering in subarctic fjords. Polar Res 39:1–17.

Skreslet S, Olsen K, Chelak M, Eiane K (2015) NE Atlantic zooplankton wintering in fjord habitats responds to hemispheric climate. J Plankton Res 37:773–789.

Skreslet S, Olsen K, Mohus Å, Tande KS (2000) Stage-specific habitats of *Calanus finmarchicus* and *Calanus helgolandicus* in a stratified northern Norwegian fjord. ICES J Mar Sci 57:1656–1663.

Smith F (2001) Historical regulation of local species richness across a geographic region. Ecology 82:792–801.

Snelgrove PVR, Butman CA (1994) Animal sediment relationships revisited – cause versus effect. Oceanogr Mar Biol 32:111–177.

Snelgrove PVR, Henry Blackburn T, Hutchings PA, Alongi DM, Frederick Grassle J, Hummel H, et al. (1997) The importance of marine sediment biodiversity in ecosystem processes. Ambio 26:578–583.

Snelgrove PVR, Soetaert K, Solan M, Thrush S, Wei CL, Danovaro R, et al. (2018) Global carbon cycling on a heterogeneous seafloor. Trends Ecol Evol 33:96–105.

Strong JA, Andonegi E, Bizsel KC, Danovaro R, Elliott M, Franco A, et al. (2015) Marine biodiversity and ecosystem function relationships: The potential for practical monitoring applications. Estuar Coast Shelf Sci 161:46–64.

Sweetman AK, Witte U (2008) Macrofaunal response to phytodetritus in a bathyal Norwegian fjord. Deep Res Part I Oceanogr Res Pap 55:1503–1514.

Syvitski JPM, Burrell DC, Skei JM (1987) Fjords: processes and products. Springer, New York, NY.

Taranger GL, Karlsen Ø, Bannister RJ, Glover KA, Husa V, Bjørn A, et al. (2015) Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. ICES J Mar Sci 72:997–1021.

Thomsen E, Vorren TO (1986) Macrofaunal palaeoecology and stratigraphy in late quaternary shelf sediments off Northern Norway. Palaeogeogr Palaeoclimatol Palaeoecol 56:103–150.

Thorson G (1966) Some factors influencing the recruitment and establishment of marine benthic communities. Netherlands J Sea Res 3:267–293.

Tilman D, Isbell F, Cowles JM (2014) Biodiversity and ecosystem functioning. Annu Rev Ecol Evol Syst 45:471–493.

Van Der Linden P, Patrício J, Marchini A, Cid N, Neto JM, Marques JC (2012) A biological trait approach to assess the functional composition of subtidal benthic communities in an estuarine ecosystem. Ecol Indic 20:121–133.

Warwick RM (2014) Meiobenthos and macrobenthos are discrete entities and not artefacts of sampling a size continuum: Comment on Bett (2013). Mar Ecol Prog Ser 505:295–298.

Wassmann P, Svendsen H, Keck A, Reigstad M (1996) Selected aspects of the physical oceanography and particle fluxes in fjords of northern Norway. J Mar Syst 8:53–71.

Webb C, Ackerly DD, Mcpeek MA, Donoghue MJ (2002) Phylogenies and community ecology. Annu Rev Ecol Syst 33:475–505.

Weinert M, Mathis M, Kröncke I, Pohlmann T, Reiss H (2021) Climate change effects on marine protected areas: Projected decline of benthic species in the North Sea. Mar Environ Res 163:105230.

Wesławski JM, Kendall MA, Włodarska-Kowalczuk M, Iken K, Kedra M, Legezynska J, et al. (2011) Climate change effects on Arctic fjord and coastal macrobenthic diversity-observations and predictions. Mar Biodivers 41:71–85.

White CA, Woodcock SH, Bannister RJ, Nichols PD (2019) Terrestrial fatty acids as tracers of finfish aquaculture waste in the marine environment. Rev Aquac 11:133–148.

Whitlatch RB (1980) Patterns of resource utilization and coexistence in marine intertidal deposit-feeding communities. J Mar Res 38:743–765.

Wigham BD, Galley EA, Smith CR, Tyler PA (2008) Inter-annual variability and potential for selectivity in the diets of deep-water Antarctic echinoderms. Deep Res Part II Top Stud Oceanogr 55:2478–2490.

Wilson JB (1999) Guilds, functional types and ecological groups. Oikos 86:507–522.

Wilson W (1990) Competition and predation in marine soft-sediment communities. Annu Rev Ecol Syst 21:221–241.

Witte U, Aberle N, Sand M, Wenzhöfer F (2003) Rapid response of a deep-sea benthic community to POM enrichment: An in situ experimental study. Mar Ecol Prog Ser 251:27–36.

Wlodarska-kowalczuk M, Pearson TH, Kendall MA (2005) Benthic response to chronic natural physical disturbance by glacial sedimentation in an Arctic fjord. Mar Ecol Prog Ser 303:31–41.

Włodarska-Kowalczuk M, Renaud PE, Węsławski JM, Cochrane SKJ, Denisenko SG (2012) Species diversity, functional complexity and rarity in Arctic fjordic versus open shelf benthic systems. Mar Ecol Prog Ser 463:73–87.

Włodarska-Kowalczuk M, Węsawski JM, Kotwicki L (1998) Spitsbergen glacial bays macrobenthos - A comparative study. Polar Biol 20:66–73.

Woodin SA, Volkenborn N, Pilditch CA, Lohrer AM, Wethey DS, Hewitt JE, et al. (2016) Same pattern, different mechanism: Locking onto the role of key species in seafloor ecosystem process. Sci Rep 6:1–11.

Worm B, Karez R (2002) Competition, Coexistence and Diversity on Rocky Shores. In: Competition and Coexistence. Ecological Studies , Vol . 161. Springer, Berlin, Heidelberg, pp 133–163.

Wu RSS, Shin PKS (1997) Sediment characteristics and colonization of soft-bottom benthos: A field manipulation experiment. Mar Biol 128:475–487.

Zaborska A, Włodarska-Kowalczuk M, Legeżyńska J, Jankowska E, Winogradow A, Deja K (2018) Sedimentary organic matter sources, benthic consumption and burial in west Spitsbergen fjords – Signs of maturing of Arctic fjordic systems? J Mar Syst 180:112–123.

Paper I

This article was published in *Estuarine, Coastal and Shelf Science*, 225, Èric Jordà Molina, Marc J. Silberberger, Valentin Kokarev, Henning Reiss, *Environmental drivers of benthic community structure in a deep sub-arctic fjord system*, 106239, Copyright Elsevier (2019).

Estuarine, Coastal and Shelf Science 225 (2019) 106239

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Environmental drivers of benthic community structure in a deep sub-arctic fjord system

Èric Jordà Molina[a], Marc J. Silberberger[a,b,*], Valentin Kokarev[a], Henning Reiss[a]

[a] Faculty of Biosciences and Aquaculture, Nord University, 8049, Bodø, Norway
[b] Institute of Oceanology Polish Academy of Sciences, Powstańców Warszawy 55, 81-712, Sopot, Poland

ARTICLE INFO

Keywords:
Infauna
Macrofauna
Sill
Deep multibasin fjord
Tysfjord
Norway

ABSTRACT

Fjords are unique geomorphological features that are found globally along (previously) glaciated coasts. They are characteristic for the entire Norwegian coast, where growing human populations and economic development increasingly impact the associated fjord ecosystems, and accordingly basic knowledge about ecosystem structure and functioning is needed. Knowledge about benthic systems within deep basins (over 400 m) of sub-Arctic fjords is currently missing and it remains questionable whether our understanding of similarly deep temperate fjords or shallower sub-arctic fjords is directly transferable to such systems. This study aims to investigate the patterns of soft-bottom benthic communities within a northern Norwegian deep multibasin fjord system and relate them to the prevailing environmental conditions, following a sampling strategy of many-sites with one-sample each. Here we show that oxygen content of the water and organic matter gradients in the sediment, structure the benthic communities of the fjord reflecting the main basins. We found that the community of the deepest basin (> 700 m) of this sub-Arctic fjord is similar to the community just outside of Tysfjord at the same depth but differ from other communities within the fjord. Furthermore, the deep basin community reflects deep communities of temperate fjords and the deep Skagerrak. The community within the innermost basin is well adapted to periodic hypoxia with low quality or degraded food supply. Our results demonstrated that fjord specific multibasin topography and the corresponding environmental factors are important drivers of ecological processes, which resulted in distinct benthic communities in each of the three basins. The management of such heterogeneous fjord ecosystems should take an adaptive approach and apply measures that take the differences of these benthic communities into account.

1. Introduction

Norway has one of the longest coastlines in the world, which extends from temperate regions in the South to an Arctic climate close to the Norwegian-Russian border in the North. This coastline is characterized by fjords that play a key role in coastal environments. In general, fjords are estuaries with high rates of sedimentation which makes them important sites for carbon sequestration (Faust et al., 2017) and they provide nursery grounds for marine fish species as well as feeding areas for migratory birds (McLusky and Elliott, 2004). Furthermore, fjords are marine ecosystems where various anthropogenic activities take place, such as fish farming, industry, tourism, or fisheries.

Today, Arctic and sub-Arctic fjord ecosystems are under strong pressure by the ongoing climate change, since the temperature rises particularly fast at high latitudes (Kaplan and New, 2006). Consequently many fish species have been reported to extend their range further North over the last years (Berge et al., 2015; Perry et al., 2005). Similarly, responses of macrofauna were observed with some benthic species increasing their distribution range further North, thereby increasing the species richness in northern Norway (Narayanaswamy et al., 2010). However, these observations are restricted to offshore regions of the continental shelf and climate change is likely to affect coastal ecosystems differently. Expected increase in freshwater runoff and inputs of terrestrial derived organic matter (Frigstad et al., 2013) are likely to alter coastal ecosystems with potential impact on benthic communities. Accumulation of organic matter of both terrestrial and anthropogenic origin can significantly alter the structure of macrofaunal assemblages in the basins of fjords (Johansen et al., 2018; Pearson and Rosenberg, 1978; Zaborska et al., 2018).

Previous studies have shown that depth and bottom topography, especially, the presence of silled basins play an important role for the

---

[*] Corresponding author. Institute of Oceanology Polish Academy of Sciences, Powstańców Warszawy 55, 81-712, Sopot, Poland.
E-mail address: marcs@iopan.pl (M.J. Silberberger).

https://doi.org/10.1016/j.ecss.2019.05.021
Received 7 January 2019; Received in revised form 23 May 2019; Accepted 25 May 2019

distribution of benthic communities in northern Norwegian fjords (Holte, 1998; Holte et al., 2005, 2004; Larsen, 1997). Although not direct environmental drivers of benthic community structure, depth and bottom topography are important surrogates which reflect other environmental variables (*e.g.* temperature, light regime, vertical flux) that have direct effects on benthic communities (Drewnik et al., 2016; McArthur et al., 2010). In general, basins of silled fjords are perceived as more stable environments since they are less affected by oceanographical fluctuations (Renaud et al., 2007; Syvitski et al., 1987). However, isolation of basins from adjacent sea areas can result in oxygen deficiency, which leads to lower species diversity (Holte et al., 2005). Most of the data on sub-Arctic silled fjords macrobenthic communities come from relatively shallow basins, while there is still no well-grounded knowledge on the soft-bottom benthic communities inhabiting the deepest depositional sub-Arctic fjord basins (> 400 m depth) that are characteristic for the coast of Nordland county. The benthic communities of some of the deepest western Norwegian fjords such as Hardangerfjord (max. depth: 890 m) and Sognefjord (max. depth: 1308 m) have been investigated to some extent (Husa et al., 2014; but see Manzetti and Stenersen, 2010), revealing a species poor and low abundant community in the deepest part of the Hardanger basin. It remains, however, questionable whether a similar diversity pattern occurs in deep sub-Arctic fjords, including Tysfjord, the deepest fjord of northern Norway with a maximum depth of 725 m.

This is in contrast to the known ecological importance of this fjord, which contains a genetically isolated population of the European lobster (*Homarus gammarus*) (Jørstad and Farestveit, 1999) as well as reef-forming sponges and cold water corals (David Cothran, personal communication 2017). Furthermore, Tysfjord served as an important overwintering region for herring from 1986 through 2005 (Røttingen et al., 1994), which sustained a dense population of killer whales preying on the herring (Nøttestad and Axelsen, 1999). In this regard, it is well documented that the ecosystem has experienced radical changes in recent years. Large aggregations of overwintering Norwegian spring spawning herring and associated whales have not been observed in Tysfjord since 2006 (Jourdain and Vongraven, 2017).

Since a high number of human activities are developing rapidly in northern Norway together with the ongoing climate change, it is important to gain profound knowledge of the structure and dynamics of seafloor communities especially within depositional deep basins and thereby provide a basis for a sustainable ecosystem-based management of deep sub-Arctic fjords. Thus, this study aims to investigate the patterns in the distribution of soft-bottom benthic communities within a northern Norwegian deep multibasin fjord system. Specifically, we (i) assess the soft-bottom benthic communities along a head to mouth transect of Tysfjord, (ii) describe the benthic community structure within the fjord and compare this structure among the different basins, and (iii) relate faunal structure to the prevailing environmental conditions.

2. Material and methods

2.1. Study area

Tysfjord, the deepest fjord in Northern Norway, is located in Norland county and comprised the study domain (Fig. 1). Its main basin has a length of 29 km in north-south orientation with a maximum depth of 725 m and possesses multiple connections to secondary fjords in the southern and eastern margin of the fjord. The main basin is delimitated in the north by the 280 m deep Korsnes sill and in the south by the 300 m deep Helland sill. Hellmofjord, the longest secondary fjord of the Tysfjord system, has a length of 31 km and is a direct extension of the main basin in the south, prolonging the total length of the system to approximately 60 km. Hellmofjord has a maximum width of 1 km and contains two deep basins, the middle basin with a depth of 375 m and the 455 m deep innermost basin, which are separated by the shallow Musken sill (depth: 60 m; Fig. 1).

Tysfjord is a sub-arctic fjord (in the sense of: ice-free fjords north of the Arctic circle) that experiences pronounced seasonal variations in temperature and salinity (Brkljacic et al., 2016). The temperature of the surface water over the deep basin varies between approximately 4 °C in winter and a maximum of 15 °C in summer. The salinity of the surface water ranges from approximately 33 in winter to 25 in summer. The deep water of the deep basin, however, is characterized by a very stable temperature (7.3 °C) and salinity (35.1–35.2) year-round. The main catchment area of Tysfjord lies towards the south and east and accordingly most runoff from land enters the secondary fjords, thereby creating a salinity gradient in the surface water that increases from the secondary fjords to the main basin.

2.2. Sampling and sample processing

The sampling campaign was conducted between the 22nd and the 26th May 2017 on board RV *Tanteyen*. A Van Veen grab (0.1 m^2) was used to collect samples at 35 stations along the North-South axis of the fjord system, including the three basins as well as two stations outside the fjord system (Fig. 1). A sampling strategy of many-sites, one-sample was chosen as it allows to best identify the main gradient structure. According to Schweiger et al. (2016), such a sampling approach is recommended for our study where a high level of systematic error (*e.g.* spatial autocorrelation, unaccountable additional environmental drivers) has to be expected. Such a sampling approach is untraditional and not widely used in benthic ecology. However, van Son et al. (2016) and Silberberger et al. (2019) have demonstrated that it is well suited to identify the main gradient structure of benthic community composition and relate this structure to environmental gradients, which were the main objectives of our study.

For each grab sample, measurements of pH and Redox potential (mV) were recorded from the surface layer of the sediments using electronic probes (EcoSense® pH10A Pen Tester & EcoSense® ORP15A ORP Temperature Pen Tester 11). The upper 5 cm and 2 cm of the sediment were sampled with a syringe (2.5 cm diameter) and stored at − 20 °C until analyzed for granulometry and total organic matter, respectively. Consecutively, macrofauna was collected by washing of the sample over a sieve (mesh size: 1 mm). Macrofauna was preserved with 4% formaldehyde buffered with borax for later taxonomic identification. The mesh size of 1 mm was chosen in accordance with the ICES recommendation for descriptive surveys (Rumohr, 2009), despite the possibility that minute individuals may get lost, since it has been shown that the general patterns of the infaunal community structure is well represented by this mesh size (Thompson et al., 2003).

In addition, 23 CTD casts were deployed along the transect to measure temperature [°C], salinity, dissolved oxygen [mg/l], fluorescence [μg/l] and density [kg/l] of the complete water column (Fig. 1).

In the lab, all macrofauna was collected from the samples under a stereo microscope and identified to the lowest taxonomic level possible. Names of all taxa follow the World Register of Marine Species (WoRMS Editorial Board, 2018).

The granulometry samples were wet washed through a cascade of sieves (2000 μm; 1000 μm; 500 μm; 250 μm; 125 μm; 63 μm) and each fraction was dried for 24 h at 90 °C. The effluent (< 63 μm) was collected into a bucket and left for at least 48 h and up to 1 week to settle. Once the water was clear from particles, the excess water was decanted and the content dried for 24 h at 90 °C. After the drying, the weights of the individual size fractions were determined and introduced to the software GRADISTAT version 8.0 (Blott and Pye, 2001) in order to calculate the mud content [%] (< 63 μm), sand content [%] (63–2000 μm), and the textural group for each sample based on the Folk and Ward (1957) ternary classification in terms of mud, sand and gravel.

The organic matter content was approximated by loss on ignition at 520 °C (Heiri et al., 2001). Large fauna and organic particles were

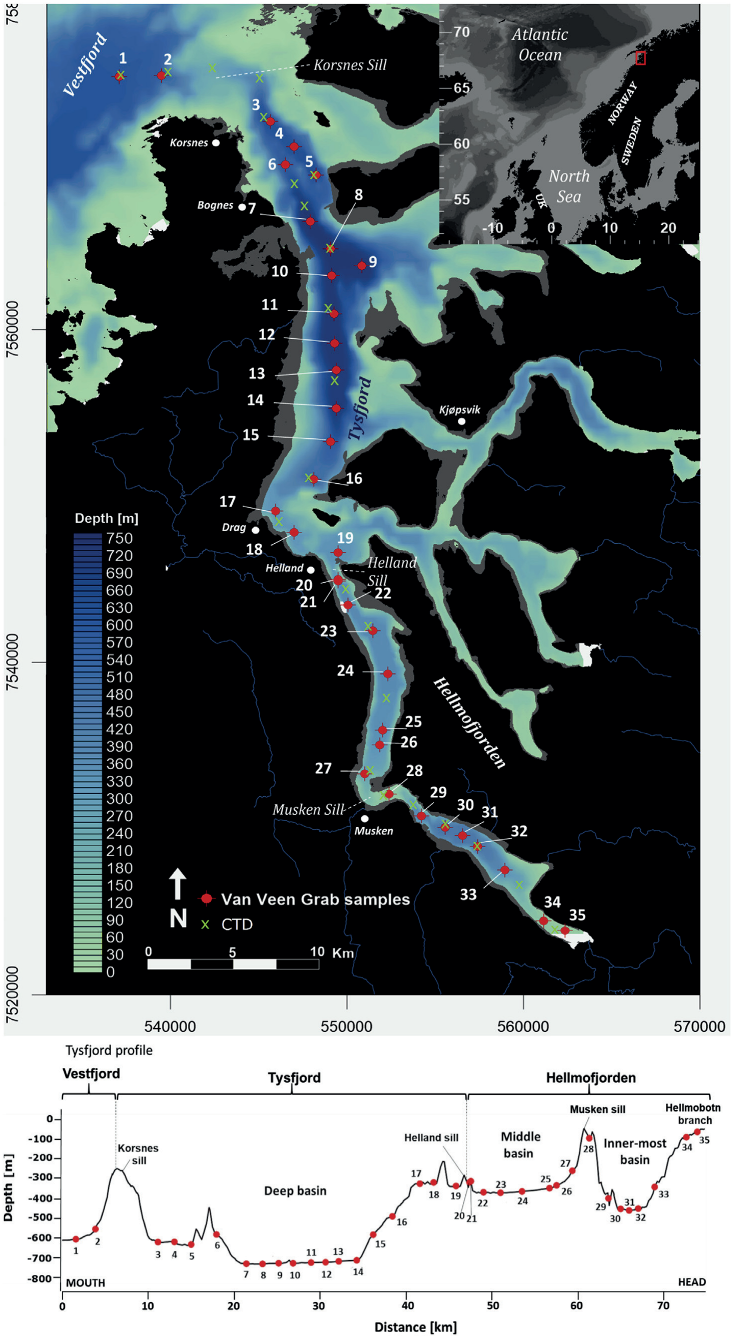


Fig. 1. Study region. *top*: Map of Tysfjord, benthos stations indicated in red, CTD stations indicated in green; *bottom*: depth profile of the sampled transect, benthos stations indicated in red. Main basins and sills are labeled. *Note*: The depicted depth profile follows the benthos stations through the fjord and accordingly the traveled distance exceeds the total length of the fjord. The order of stations number 5 and 6 was assigned according to a ridge that runs parallel to stations 4 and 5, separating them from station 6. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

removed prior to the combustion of the sample for 5 h.

2.3. Statistical analysis

All statistical analyses were performed in R, version 3.5.1 (R Development Core Team, 2018), making use of methods included in the ade4 (Dray and Dufour, 2007; Thioulouse et al., 2011), vegan (Oksanen et al., 2018), and labdsv packages (Roberts, 2016).

All colonial organisms were removed from the faunal data, which was subsequently subjected to a Hellinger transformation. The Hellinger transformation is defined as $y'_{ij} = \sqrt{\frac{y_{ij}}{y_{i+}}}$, where y_{ij} is the abundance of species j at site i and y_{i+} is the total abundance at site i. This transformation was chosen to make the data suitable for Euclidean-based methods and to give a low weight to rare species, which are often encountered randomly in blind sampling in aquatic environments, especially when a sampling strategy without replication is chosen (Legendre and Gallagher, 2001).

We used Unweighted Pair Grouping Method with Arithmetic-mean (UPGMA) clustering to identify faunal communities within the fjord. Following the methods described by Borcard et al. (2018) we used fusion level values, multiscale bootstrap resampling, and species fidelity analysis to identify the optimal number of clusters. We used nonmetric multidimensional scaling (nMDS) to validate the obtained sample clusters.

The identified community clusters were then characterized using univariate diversity measures (number of taxa, total abundance, the Shannon index ($H'_{\log e}$ & $H'_{\log 2}$) (Shannon, 1948), Hurlbert rarefaction (ES100) (Hurlbert, 1971), Pielou's evenness (J) (Pielou, 1966)). The Shannon index was calculated with two different bases to allow for better comparison with existing literature. Furthermore, we used a combination of three different approaches to identify key species of every cluster: Indicator value indices (IndVal) (Dufrêne and Legendre, 1997), species contribution analysis (SCA) (van Son and Halvorsen, 2014), and the most abundant taxa of each cluster. The IndVal method is aimed to identify combinations of species that can be used to discriminate a group of samples from all other samples in the analysis. SCA, however, is used to identify species that contribute most to the difference between two groups of samples, disregarding all other samples in the data set. In contrast, the most abundant taxa in a group of samples disregard all other samples entirely. Key species were then identified by combined assessment of the results of all three methods, because each method individually is biased by the amount of samples they take into account.

We used variation partitioning to identify the importance of individual environmental parameters in structuring the faunal community. Therefore, all environmental variables were assigned to three sets of environmental variables: (1) bottom water characteristics, (2) sediment characteristics, and (3) depth (Table 1). Bottom water characteristics, which were based on CTD measurements, were assigned so that the measurements of the closest CTD cast was used for each grab sample. Prior to the variation partitioning, each set of environmental variables was individually subjected to a forward selection using a series of constrained and partially constrained redundancy analysis (RDA) with a double stopping criterion (Blanchet et al., 2008), to avoid overestimation of the explained variation. In this approach, variables are added to the model in order of decreasing explanatory power until no variable adds significantly to the explanatory power or until the adj.R^2 exceeds that of the full model. Following the variable selection, RDA was used to partition the variation in the faunal data set on the three sets of selected environmental variables and all combinations of them (Borcard et al., 1992; Peres-Neto et al., 2006).

Finally, we used a non-parametric Kruskal-Wallis test (Kruskal and Wallis, 1952) and its corresponding post-hoc comparisons (with Holm correction) to compare all environmental variables selected by the forward selection between the previously identified community clusters (Borcard et al., 2018).

Table 1
All sets of explanatory environmental variables included in the analysis. Variables selected by the forward selection are printed in bold.

Set	Environmental variable
Bottom water characteristics	**O_2 in bottom water [mg/l]** **Salinity of bottom water** **Temperature of bottom water [°C]**
Sediment characteristics	**Mud content [%]** Textural group pH of the sediment Redox potential of the sediment [mV] **Organic matter in the sediment [%]**
Depth	**Depth [m]**

3. Results

3.1. Environmental setting

The CTD measurements revealed a colder desalinated layer of water from the surface down to around 100 m depth throughout the whole fjord (Fig. 2). Beneath this upper layer, water masses differed between the basins. The water outside the Korsnes sill (*i.e.* outside the fjord) was characterized by a temperature of 7.6 °C, a salinity of 35.25, and was well oxygenated (> 8 mgO_2/l). Temperature, salinity, and the oxygen contend decreased gradually from the Korsnes sill towards the Middle basin, where values between 7.4 and 7.5 °C for temperature, 35 for salinity, and 7 mgO_2/l were measured. At the Musken sill, however, the water mass characteristics changed more drastically towards the innermost basin, which was characterized by colder water (6.6 °C) with lower salinity (34.75) and lower oxygen content (between 4 and 6 mgO_2/l) (Fig. 2).

Among the sediment characteristics, mud content showed a high variability with values between 3.8% (stn. 28) and 92.8% (stn. 7). In general, a pattern of high mud content in basins and a low mud content at sills and shallow stations was found. A similar pattern was observed for organic matter content in sediments with values ranging from 0.74% at the Musken Sill to 7.2% in the Deep Basin (Fig. 2).

3.2. Faunal community

After removal of all colonial organisms, we found 199 different taxa (152 species) representing eight different phyla (supplement 1). 111 of these taxa were rare, *i.e.* represented by three or less individuals. The bivalve *Kelliella miliaris* was the most abundant species representing 23.4% of all individuals in this study, followed by the polychaete *Heteromastus filiformis* (6.0%), and the bivalves *Mendicula ferruginosa* (5.5%), *Parathyasira equalis* (5.0%), and *Genaxinus eumyarius* (4.1%).

The UPGMA clustering identified five distinct community clusters (Fig. 3a), including three main clusters that contained 32 stations. These three main clusters (cluster A, B, and D) separated the fjord community almost exactly according to the three main basins. Cluster A included all samples from the deep basin together with the stations outside the Korsnes sill (stn. 1 and 2) and station 22 (Fig. 3b). Cluster B contained the stations from the mid-region of the fjord, which includes the Middle basin and the region around the Helland sill. Cluster D included all stations from the innermost basin. The remaining three stations were particularly shallow (~100 m depth) and were assigned to the other two clusters, which represent the Musken sill (cluster C) and the two innermost stations (Cluster E). The nMDS analysis supported the identified community clusters (Fig. 3c). The three main clusters were separated from each other along the first ordination axis, while stations of the clusters C and E were also separated along the second axis. The latter two clusters are not described in more detail below because of too low sample size.

The communities of the three main clusters showed distinct

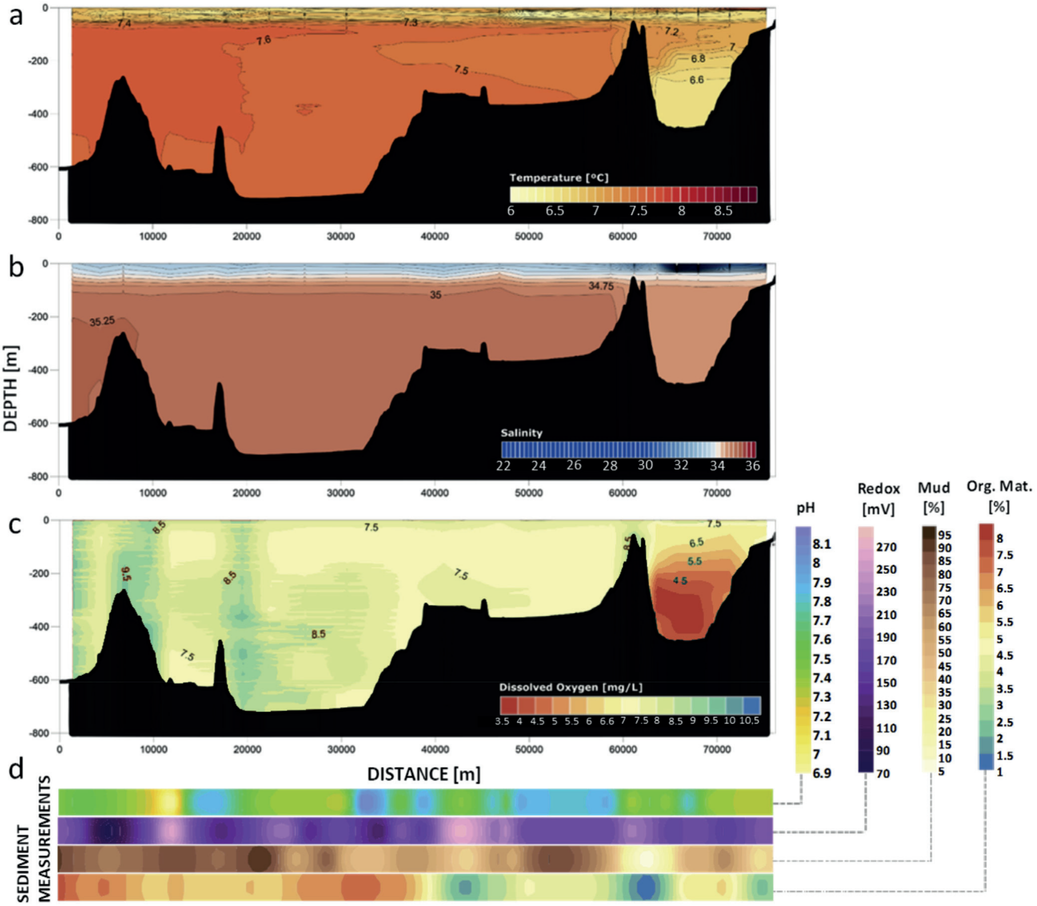


Fig. 2. Results of the CTD casts along the fjord transect showing (a) Temperature [°C], (b) Salinity and (c) Dissolved Oxygen [mg/l], and (d) the results for the sediment parameters showing from top to bottom pH, Redox potential [mV], Mud content [%], and Organic Matter content [%].

diversity characteristics (Table 2). Shannon diversity as well as the average number of species per sample, clearly identified cluster B as the most diverse community within the fjord basins. Cluster A was characterized by a lower evenness than the other clusters, which was primarily caused by the extreme dominance of *K. miliaris* in this part of the fjord (Fig. 4). Cluster D, in contrast, was characterized by an overall low diversity due to a particularly low number of taxa.

According to the relative contribution to the total abundance, IndVal and SCA, we identified *K. miliaris*, *Paradiopatra fiordica*, and *Spiochaetopterus typicus* as the characteristic taxa of the faunal community associated with cluster A (Fig. 4 and Table 2). The community associated with cluster B, however, appeared to be characterized rather by its high diversity than by any typical species. In contrast to all other clusters, no species contributed with more than 10% to the total abundance in cluster B (Fig. 4) and the most abundant species were also common in other parts of the fjord. However, with regard to the results of IndVal, SCA and the most abundant species, we found that the co-occurrence of the bivalves *K. miliaris*, *M. ferruginosa*, *Thyasira obsoleta* and the polychaete *H. filiformis* characterized this cluster. In contrast, the community associated with samples from cluster D was clearly characterized by the bivalve *P. equalis.* Even though, the polychaetes *H. filiformis* and *Terebellides stroemii* contributed each with over 10% of the total abundance in cluster D, IndVal did not identify them as good indicator species for this cluster, which was also confirmed by the SCA.

3.3. Environmental driver of community structure

Forward selection of environmental variables identified all three sets of environmental variables to significantly explain some structure within the Hellinger transformed faunal data. All variables were selected for the bottom water characteristics and depth, only mud content and the organic matter content were selected for the sediment characteristics (Table 1). The variation partitioning identified the bottom water characteristics as the set of environmental variables that individually explained the largest fraction of the variation in the community (0.34), while depth and sediment characteristics were able to explain 0.21 and 0.17, respectively (Fig. 5). Only a small part of the explained variation was shared by bottom water and sediment characteristics (0.06) and accordingly these two sets can be considered as independent from each other. With regard to depth, the variation

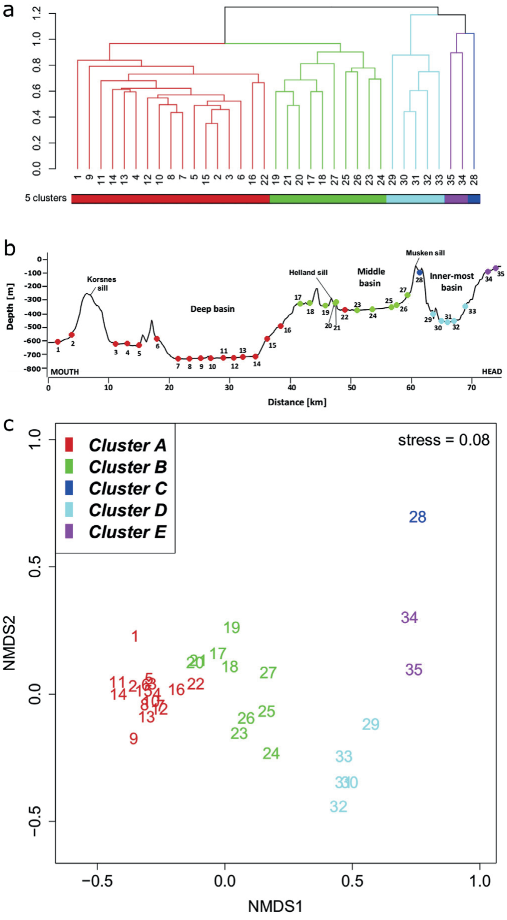


Fig. 3. Structure of the Hellinger transformed abundance data. (a) Dendrogram of the UPGMA clustering, (b) cluster affiliation of each sample along the fjord transect, and (c) plot of the nMDS ordination are shown. The identified sample clusters are indicated by different colors. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

partitioning showed that a small part of the variation explained by the bottom water characteristics was also accounted for by the depth (0.09), but also that the majority of this variation was independent from depth (0.25). The sediment characteristics on the other side shared the majority of the variation they could explain with depth (0.13).

When all the selected environmental variables were analyzed individually, it became obvious that the overlap in explanatory power of depth and sediment characteristic was caused by the organic matter content. The organic matter content reflects the depth almost exactly and separated the community of cluster A from all other clusters (Fig. 6). The strong explanatory power of the bottom water characteristics, however, is a mix of all three variables included in the analysis and clearly separated the innermost fjord cluster D from clusters A and B.

4. Discussion

The benthic community structure of the sub-Arctic Tysfjord clearly reflects the multibasin structure of the fjord. Our study suggests that the basin specific species assemblages are caused by the limited deep-water exchange of the innermost basin and the organic matter accumulation in the basins. We found bivalve and polychaete species in high abundances throughout the Tysfjord basin communities. In particular the deep and middle basin were characterized by a dominance of bivalves (Fig. 4; cluster A and B). Such a high dominance of bivalves is not known from other silled northern Norwegian fjords, where an overall prevalence of polychaetes has been described (Holte, 1998; Holte et al., 2005; Larsen, 1997; Oug, 2000). In general, the benthic communities in Tysfjord seem to differ from previously described silled basin communities. For instance, the tube-building polychaetes *Galathowenia oculata* and *Maldane sarsi* seemed to be indicative of silled basin communities in many locations (Holte, 1998; Larsen, 1997; Oug, 2000), while both species were virtually absent in Tysfjord. The abundances of *M. sarsi* can be very high (up to 12 000 ind./m^2) in shallow silled basins (Holte, 2001). Studying three sub-Arctic silled basins subject to organic discharges and oxygen minima of 2–3.5 mg/l, Holte et al. (2005) showed that *M. sarsi, G. oculata* and *Owenia fusiformis*, along with *Parathyasira equalis* and *Prionospio cirrifera*, showed higher preferences towards deeper basins. Both *M. sarsi* and oweniid polychaetes are functionally important for carbon transport between surface and deeper layers of sediment and vice versa, and their presence can be a sign of a “mature community” (Zaborska et al., 2018). Their absence in Tysfjord in any significant amount implies different benthic functioning compared to shallower silled basins. In contrast, the community of the innermost basin of Tysfjord resembled the deeper basin of Rombacken (311–350 m deep stations) in the neighboring Ofotfjord system more closely, where Larsen (1997) found *Heteromastus filiformis*, *Prionospio cirrifera* and thyasirid bivalves dominating the community, while oweniid and maldanid polychaetes were absent. In shallower parts of Rombacken, however, these families were a common component of the benthic communities. Accordingly, basin depth seems to be an important property of northern Norwegian fjords.

4.1. Depth related community structure

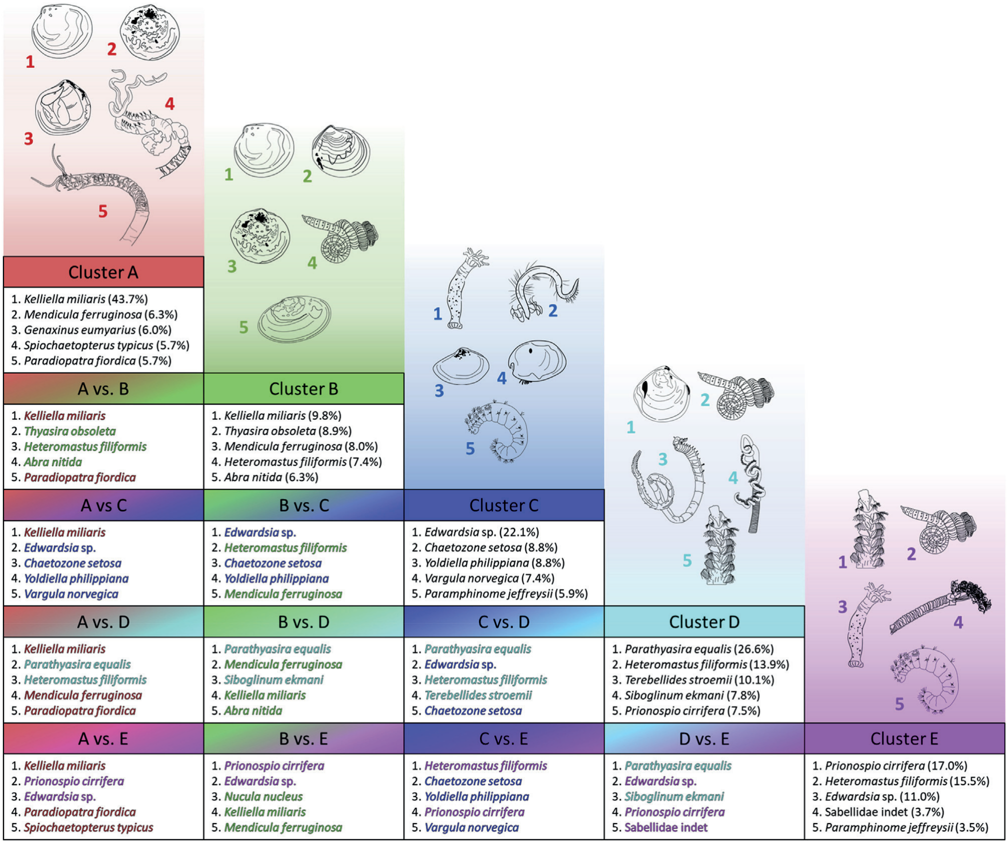
Although we report total infaunal abundances throughout the Tysfjord system that seem to vary unrelated to the sampled depth gradient (Table 2), a separation in deep (depth $>$ 400 m; cluster A and D) and shallow (depth $<$ 400 m; cluster B) basin community clusters became apparent regarding the applied diversity measures. The shallow community cluster showed an average $H'_{(\log 2)}$ over 4.4 and an ES100 of 27, while the $H'_{(\log 2)}$ of the deep basin and the inner-most basin was 3.2 and the ES100 below 20. Furthermore, the less divers deeper communities seem to be more dominated by individual taxa, while the shallower middle basin diversity falls within the typical range reported for boreal and sub-Arctic fjords (Holte et al., 2005).

The relatively low diversity of the deep communities in Tysfjord resemble the pattern described for the deepest fjords in southern Norway, Hardangerfjord and Sognefjord (Fauchald, 1974, 1972). With high contribution of *Kelliella miliaris, Paradiopathra fiordica* (Husa et al., 2014), and *Spiochaetopterus typicus* (Rygg and Skei, 1997) the deep benthic communities of Hardangerfjord are very similar to the community in the deep basin of Tysfjord. According to Fauchald (1974), the basins of these deep fjords are generally poorer in species than other off-shore regions with similar depths. However, Rosenberg et al. (1996), identified a characteristic deep faunal assemblage ($>$ 400 m) with a lower species richness than at shallower regions ($<$ 400 m) in the Norwegian Trench (maximum depth 700 m). They reported *Spiochaetopterus bergensis*, *Genaxinus eumyarius*, and *Kelliella miliaris* as characteristic species of the deep Skagerrak community. Accordingly, the deep Skagerrak community resembles the community of the deepest

Table 2

Summary of the characteristics of the identified sample clusters. The number of samples contributing to each cluster is given together with the average abundance, the average number of taxa per sample, the total number of taxa in the cluster, the average Shannon index ($H'_{(\log e)}$ & $H'_{(\log 2)}$), Pielou's Evenness (J), Hulbert rarefaction (ES100), and species identified by the IndVal method of Dufrêne and Legendre (1997). *Note*: The total number of species in each cluster are reported as general information and should not be directly compared between clusters due to the different sample numbers.

	Cluster A	Cluster B	Cluster C	Cluster D	Cluster E
Number of stations	17	10	1	5	2
Average abundance [ind./m^2]	1468	1772	680	1152	2445
Average number of species per sample	25.7	39.9	27	18	42.5
Total number of species in cluster	96	119	27	42	64
$H'_{(\log e)}$	2.2	3.0	2.9	2.2	2.9
$H'_{(\log 2)}$	3.2	4.4	4.2	3.2	4.3
J	0.70	0.84	0.87	0.77	0.79
ES100	19	27	24	15	27
IndVal species	*Paradiopatra fiordica* *Kelliella miliaris* *Spiochaetopterus typicus*	*Nephtys hystricis* *Onchnesoma steenstrupii steenstrupii* *Nucula nucleus* *Mendicula ferruginosa*	-	*Parathyasira equalis*	-



Cluster A

1. *Kelliella miliaris* (43.7%)
2. *Mendicula ferruginosa* (6.3%)
3. *Genaxinus eumyarius* (6.0%)
4. *Spiochaetopterus typicus* (5.7%)
5. *Paradiopatra fiordica* (5.7%)

Cluster B

1. *Kelliella miliaris* (9.8%)
2. *Thyasira obsoleta* (8.9%)
3. *Mendicula ferruginosa* (8.0%)
4. *Heteromastus filiformis* (7.4%)
5. *Abra nitida* (6.3%)

Cluster C

1. *Edwardsia* sp. (22.1%)
2. *Chaetozone setosa* (8.8%)
3. *Yoldiella philippiana* (8.8%)
4. *Vargula norvegica* (7.4%)
5. *Paramphinome jeffreysii* (5.9%)

Cluster D

1. *Parathyasira equalis* (26.6%)
2. *Heteromastus filiformis* (13.9%)
3. *Terebellides stroemii* (10.1%)
4. *Siboglinum ekmani* (7.8%)
5. *Prionospio cirrifera* (7.5%)

Cluster E

1. *Prionospio cirrifera* (17.0%)
2. *Heteromastus filiformis* (15.5%)
3. *Edwardsia* sp. (11.0%)
4. Sabellidae indet (3.7%)
5. *Paramphinome jeffreysii* (3.5%)

A vs. B

1. ***Kelliella miliaris***
2. ***Thyasira obsoleta***
3. ***Heteromastus filiformis***
4. ***Abra nitida***
5. ***Paradiopatra fiordica***

A vs C

1. ***Kelliella miliaris***
2. ***Edwardsia* sp.**
3. ***Chaetozone setosa***
4. ***Yoldiella philippiana***
5. ***Vargula norvegica***

B vs. C

1. ***Edwardsia* sp.**
2. ***Heteromastus filiformis***
3. ***Chaetozone setosa***
4. ***Yoldiella philippiana***
5. ***Mendicula ferruginosa***

A vs. D

1. ***Kelliella miliaris***
2. ***Parathyasira equalis***
3. ***Heteromastus filiformis***
4. ***Mendicula ferruginosa***
5. ***Paradiopatra fiordica***

B vs. D

1. ***Parathyasira equalis***
2. ***Mendicula ferruginosa***
3. ***Siboglinum ekmani***
4. ***Kelliella miliaris***
5. ***Abra nitida***

C vs. D

1. ***Parathyasira equalis***
2. ***Edwardsia* sp.**
3. ***Heteromastus filiformis***
4. ***Terebellides stroemii***
5. ***Chaetozone setosa***

A vs. E

1. ***Kelliella miliaris***
2. ***Prionospio cirrifera***
3. ***Edwardsia* sp.**
4. ***Paradiopatra fiordica***
5. ***Spiochaetopterus typicus***

B vs. E

1. ***Prionospio cirrifera***
2. ***Edwardsia* sp.**
3. ***Nucula nucleus***
4. ***Kelliella miliaris***
5. ***Mendicula ferruginosa***

C vs. E

1. ***Heteromastus filiformis***
2. ***Chaetozone setosa***
3. ***Yoldiella philippiana***
4. ***Prionospio cirrifera***
5. ***Vargula norvegica***

D vs. E

1. ***Parathyasira equalis***
2. ***Edwardsia* sp.**
3. ***Siboglinum ekmani***
4. ***Prionospio cirrifera***
5. **Sabellidae indet**

Fig. 4. Results of the species contribution analysis (SCA). The five most abundant taxa for each cluster are given with their relative contribution to the total abundance within the cluster. Pairwise comparisons give the 5 taxa contributing most to the difference between the cluster pair. Colors indicate the cluster with the higher abundance for the respective taxon. Drawings by Èric Jordà Molina according to organisms in the present study. Only, *Heteromastus filiformis* was drawn according to a photo by Fredrik Pleijel and *Prionospio cirrifera* was re-drawn from Maciolek (1985). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

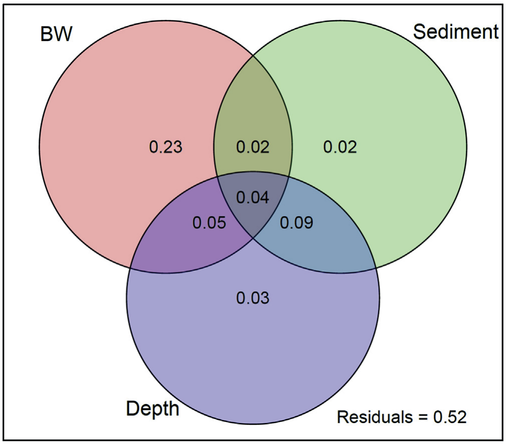


Fig. 5. Venn diagram showing the results of the variation partitioning. The explained fraction of the total variation in the Hellinger transformed abundance data is given for all three sets of environmental variables and all combinations of them. Bottom water properties (BW) includes the variables salinity, temperature, and oxygen. Sediment properties (Sediment) includes the variables organic matter content and mud content. Depth includes the sampling depth. The residuals, *i.e.* the unexplained variation, is indicated.

basin in Tysfjord very closely (Fig. 4). Rosenberg et al. (1996) suggested that the main structuring factors for the communities in the deep Skagerrak were the sediment characteristics, sediment transport and accumulation rates. The variation partitioning in our study showed that the majority of the variation in the community data that was accounted for by the depth could also be explained by the sediment properties. Particularly the organic matter content followed the depth gradient in our study, which suggests that the observed depth related diversity pattern could be largely driven by the organic matter enrichment within the deep basins.

A similar depth separation in deep and shallow communities with deep communities being more dominated by a few very abundant species has been reported for sub-Arctic offshore regions (Silberberger et al., 2019). There, however, the identified boundary between the communities lies around 800 m depth, which coincides with the boundary between Atlantic and Arctic water masses. No such water mass boundary occurs around 400 m depth in Tysfjord and accordingly the drivers of the observed depth related diversity pattern seem to differ between offshore regions and deep shelf regions (fjord basins/Norwegian trench).

Furthermore, our study identified a clear distinction between the three shallowest stations and all deep communities in the fjord. Such a separation between shallow (~100 m) and basin communities has previously been observed during environmental monitoring in a north Norwegian fjord (Helland et al., 1994) and should be expected in general due to the stronger seasonal variations in temperature and salinity in the upper 100–150 m of all fjords in the area (Brkljacic et al., 2016) and very different sedimentary conditions (Fig. 2).

4.2. Oxygen limitation

We identified bottom water properties as the environmental variables that could explain most of the community structure in the Tysfjord system. In particular, the clear difference between the water mass in the innermost basin and the rest of the fjord. The colder temperature of about 6.5 °C observed in this basin indicates that its deep water is retained by the shallow Musken sill for longer periods and that deep-water renewal is an episodic event. Accordingly, we observed reduced oxygen concentration of about 4 mg/l within the innermost basin in May, a concentration below which a reduction in species numbers has been reported (Reish, 1971). In addition, we expect a continuous decrease in oxygen concentrations throughout the summer until the thermohaline stratification weakens in autumn (Diaz and Rosenberg, 1995).

It has been shown that shallow sills inhabit communities with low diversities in the basins behind the sills in southern Norwegian fjords (Buhl-Jensen, 1986; Buhl-Mortensen and Høisæter, 1993). Buhl-Mortensen and Høisæter (1993) mentioned that lack of oxygen was never an issue in their study system, but acknowledged that restricted water exchange of deep water was an important driver of the community structure. They report that oxygen concentrations were always above 2 ml/l (≈2.85 mg/l). It is well known that deep water stagnation in fjord basins can lead to a reduction in dissolved oxygen (Inall and Gillibrand, 2010). In the most extreme, anoxia can lead to a complete defaunation of the seafloor. Values lower than 1–2 mg/l of dissolved oxygen are considered critical, but hypoxic conditions (< 3 mg/l) can also cause changes in faunal assemblages (Diaz and Rosenberg, 1995). However, several studies suggest that changes in species composition can be induced with even higher oxygen concentrations of 2–6 mg/l (Molvær et al., 2007; Reish, 1971; Wu, 2002).

The five numerically dominant taxa in the innermost basin (compare Fig. 4) have all been reported as common species in hypoxic environments (Diaz and Rosenberg, 1995; Hourdez and Weber, 2005; Keuning et al., 2011; Leppäkoski, 1971). Besides their tolerance to low oxygen condition, the members of the community in the inner-most basin are also characterized by their affinity to oligotrophic conditions or low-quality food sources. Two of the most abundant species, the bivalve *P. equalis* and the polychaete *Siboglinum ekmani* possess symbiotic chemoautotrophic bacteria that can provide them with at least a considerable part of their nutrition (Dufour, 2005; Keuning et al., 2011; Southward et al., 1986, 1981), even though the genus *Parathyasira* is known to vary considerably in their symbiont density among and within species. Zanzerl and Dufour (2017), however, demonstrated that specimens of *Parathyasira* without symbionts formed deep pedal tracts, which they interpret as an adaptation to deep pedal feeding in combination with symbiont farming along the burrow walls. The polychaete *H. filiformis* is believed to sustain itself by utilizing a combination of deep buried low quality particulate organic carbon and dissolved organic carbon in the sediment (Clough and Lopez, 1993).

4.3. Organic matter of the seafloor

In addition to bottom water properties, we found total organic matter as an important driver of community structure. This gradient is directly reflecting depth (Fig. 6) and indicates the accumulation of organic material in the basins. It is, however, likely that our results underestimate the role of the available organic matter, since we had no information about organic matter quality to include in our analysis. Deep fjord basins can have several potential sources of carbon. In northern Norwegian fjords, the spring bloom is known to occur in early spring (March to April) with low rates of pelagic primary production throughout the rest of the year, when increasing sedimentation of organic matter is associated with local periods of increased river run-off or resuspension at greater depths (Wassmann et al., 1996). However, besides seasonal pulses of sedimentation, there is strong interannual variation of organic matter vertical fluxes that depends on combined biological (*e.g.* grazing of zooplankton) and physical processes (*e.g.* wind-induced advection); as a result, particulate organic matter reaches the bottom mainly in the form of larger fecal pellets and detritus (Lutter et al., 1989; Reigstad et al., 2000; Wassmann et al., 1996). Another potential carbon source to deep basins of fjords can be macroalgal detritus (Renaud et al., 2015). Although the contribution of different carbon sources to the basins of Tysfjord is unknown, the

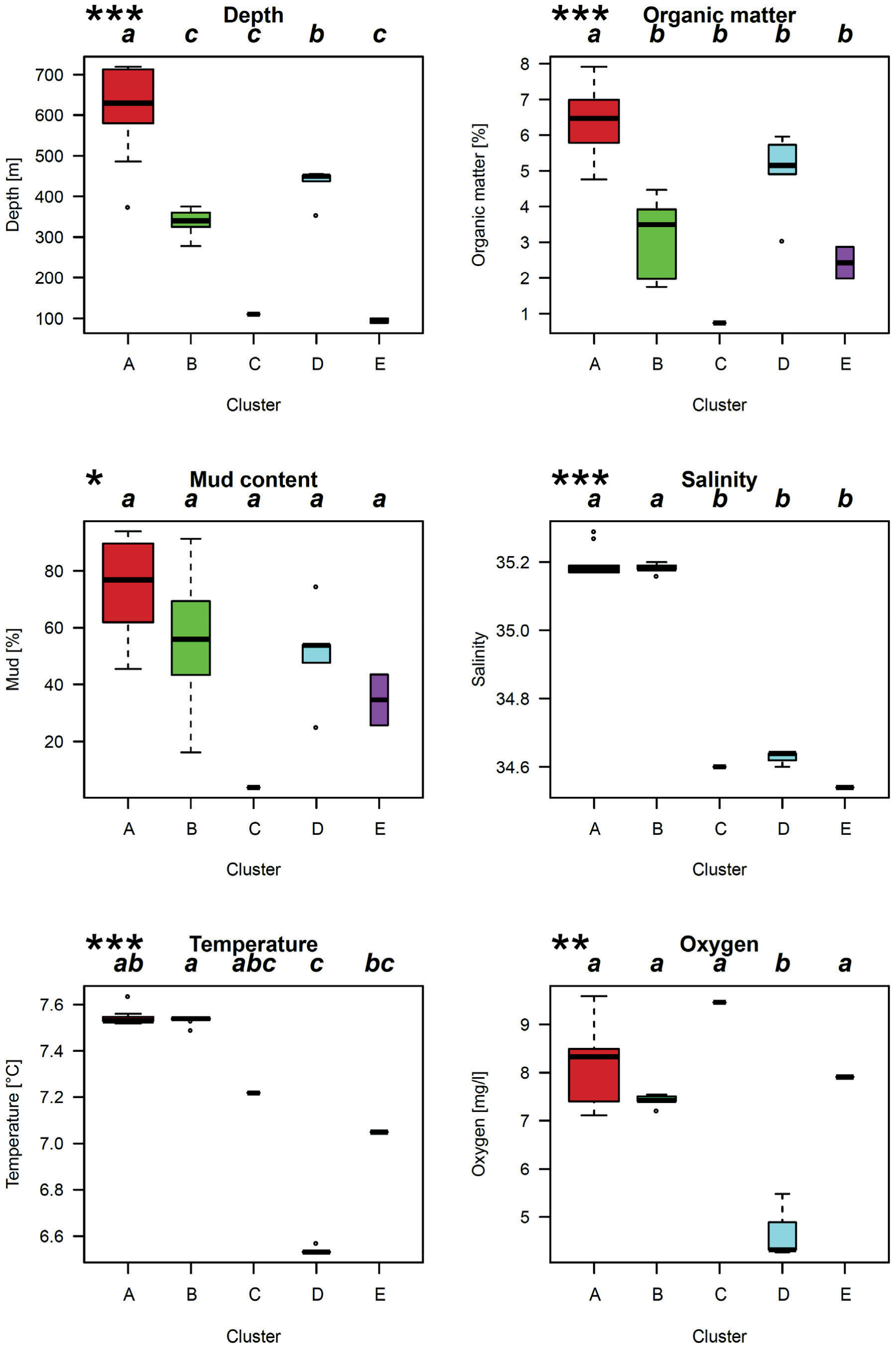


Fig. 6. Box plots for all environmental variables selected by the forward selection procedure. Stars indicate the significance of the differences among groups for each environmental variable, according to Kruskal–Wallis test. Letters indicate results of the post-hoc comparison. Groups with the same letter are not significantly different.

geomorphology and water mass distribution indicate a general pattern. The deep sills and the seemingly continuously exchanged water of the deep and middle basin indicate that advection of mesozooplankton from Vestfjorden and their production of fecal pellets are probably an important source of organic matter that reaches these basins (Reigstad et al., 2000; Wassmann et al., 1996). Surface sediment chemistry, however, suggest that the importance of advection from Vestfjorden on sedimentary processes in Tysfjorden decreases with distance from the fjord opening (Faust et al., 2017). Furthermore, the shallow Musken sill seems to restrict shelf water advection into the innermost basin and accordingly the relatively high values of organic matter content suggest accumulation of refractory organic matter that is not directly accessible to macrofauna (Zaborska et al., 2018). This is confirmed by observed large particles of terrestrial organic material in samples from the innermost basin (personal observation È. Jordà Molina). Such a nature of the organic matter in the innermost basin corresponds well with the feeding modes of the dominant species at this location (described above).

4.4. General diversity patterns

Studies from temperate and arctic fjord systems have shown that species diversity decreases from the open shelf to the outer part of fjords and even further towards the inner part (Buhl-Jensen, 1986; Buhl-Mortensen and Høisæter, 1993; Włodarska-Kowalczuk et al., 2012). It might seem inviting to assume a common driver behind such a general pattern, but the before mentioned studies related their observations to different environmental drivers, like sill depth, sedimentation from glaciers, or sediment carbon content.

For our study region, Silberberger et al. (2019) reported an average Shannon index ($H'_{\log\ e} = 3.18$) and evenness ($J = 0.88$) for infaunal macrofauna samples that were collected with the same gear as in the present study from offshore waters of the Lofoten-Vesterålen region down to a depth of 800 m. Accordingly, the species diversity of samples from clusters B, C and E (Table 2; shallower than 400 m) fall within the same range as the continental shelf. Only the deep basin and the innermost basin show a reduced species diversity compared to the shelf. Since these two basins are representing the outer and inner part of the fjord, we cannot confirm an outer-inner gradient of species diversity in Tysfjord. Decreased species diversity seems rather to occur towards environmental extremes (*e.g.* oxygen limitation, depth, organic enrichment), which are often, but not necessarily, found towards the inner part of the fjord.

In conclusion, our study has demonstrated that the fjord specific topography and the corresponding environmental drivers are the main forcing drivers of ecological processes. Particularly, the multibasin topography has a strong influence on hydrology and sedimentation processes, which leads to formation of distinct communities in basins isolated by sills. Accordingly, it is difficult to infer a general and universal pattern to describe ecological processes in fjords. The environmental management of fjord systems in turn, need to take this heterogeneity on small spatial scales into account to adapt their approaches and measures accordingly. This is, however, only possible if monitoring programs are able to identify this heterogeneity. We suggest that an increased application of a sampling approach of many-sites one-sample could improve the ecosystem-based management. This approach is widely applicable to study benthic community structure in relation to environmental gradients, what has been documented in a pollution gradient in the Oslofjord (van Son et al., 2016), to identify fine-scale spatial structure in sandy shelf sediments (Silberberger et al., 2019), and to identify the community structure throughout an entire fjord system (this study).

Nonetheless, we demonstrated that deep sub-Arctic fjord communities resemble communities of other deep regions of the northern European continental shelf (including fjords). Thus, we suggest that functioning of similar fjord systems might be inferred from each other across climate zones in northern Europe, while spatial proximity alone does not permit for such a comparison.

Specifically, we observed a clear distinction between benthic communities in shallow regions of the fjord and the basins. Furthermore, we found a distinct diversity drop below 400 m depth, which raises questions about the environmental monitoring of aquaculture farms in Norwegian fjords. While the corresponding sampling guidelines acknowledge the need to monitor close-by fjord basins, the evaluation of the environmental status is based on the same scale of diversity indices as in the shallow areas (Standard Norge, 2016). This application of the same diversity goals for shallow and deep habitats of the fjord contradicts our observed community structure.

Acknowledgements

The authors want to thank M. Krogstad and M. McGovern for help during the fieldwork and C. Steffensen for help with the grain-size analysis. An earlier version of the original research in this paper appeared in the first author's master thesis. Thanks to Mike Elliott and the four reviewers for their valuable comments to improve the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2019.05.021.

References

Berge, J., Heggland, K., Lønne, O.J., Cottier, F., Hop, H., Gabrielsen, G.W., Nøttestad, L., Misund, O.A., 2015. First records of Atlantic mackerel (Scomber scombrus) from the Svalvard Archipelago, Norway, with possible explanations for the extension of its distribution. Arctic 68, 54–61. https://doi.org/10.14430/arctic4455.

Blanchet, G., Legendre, P., Borcard, D., 2008. Forward selection of spatial explanatory variables. Ecology 89, 2623–2632. https://doi.org/10.1890/07-0986.1.

Blott, S.J., Pye, K., 2001. Gradistat: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surf. Process. Landforms. https://doi.org/10.1002/esp.261.

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045–1055.

Borcard, D., Gillet, F., Legendre, P., 2018. Numerical Ecology with R. Springer-Verlag, New York.

Brkljacic, M.S., Gitmark, J., Johnsen, T.M., Norli, M., Dahl-Hansen, G.A., 2016. Marin Overvåking Nordland 2013-2015. Undersøkelser Av Hydrografi, Planteplankton, Hardbunnsorganismer Og Bløtbunnsfauna I 6 Fjorder I Nordland. NIVA Rapport Nr. Norsk institutt for vannforskning, Oslo 6993-2016.

Buhl-Jensen, L., 1986. The benthic amphipod fauna of the west-Norwegian continental shelf compared with the fauna of five adjacent fjords. Sarsia 71, 193–208. https://doi.org/10.1080/00364827.1986.10419690.

Buhl-Mortensen, L., Høisæter, T., 1993. Mollusk fauna along an offshore fjord gradient. Mar. Ecol. Prog. Ser. 97, 209–224.

Clough, L.M., Lopez, G.R., 1993. Potential carbon sources for the head-down deposit-feeding polychaete Heteromastus filiformis. J. Mar. Res. 51, 595–616. https://doi.org/10.1357/0022240933224052.

Diaz, R., Rosenberg, R., 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanogr. Mar. Biol. Annu. Rev. https://doi.org/10.1021/je700185m.

Dray, S., Dufour, A.-B., 2007. The ade4 package: implementing the duality diagram for ecologists. J. Stat. Softw. https://doi.org/10.18637/jss.v022.i04.

Drewnik, A., Węsławski, J.M., Włodarska-Kowalczuk, M., Łącka, M., Promińska, A., Zaborska, A., Gluchowska, M., 2016. From the worm's point of view. I: environmental settings of benthic ecosystems in Arctic fjord (Hornsund, Spitsbergen). Polar Biol. 39, 1411–1424. https://doi.org/10.1007/s00300-015-1867-9.

Dufour, S.C., 2005. Gill anatomy and the evolution of symbiosis in the bivalve family thyasiridae. Biol. Bull. 208, 200–212. https://doi.org/10.2307/3593152.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366. [0345:SAAIST]2.0.CO;2. https://doi.org/10.1890/0012-9615(1997)067.

Fauchald, K., 1972. Some polyghaetous annelids from the deep basins in Sognefjorden, Western Norway. Sarsia 49, 89–106. https://doi.org/10.1080/00364827.1972.10411211.

Fauchald, K., 1974. Deep-water errant polychaetes from hardanger-Fjorden, western Norway. Sarsia 57, 1–31. https://doi.org/10.1080/00364827.1974.10411268.

Faust, J.C., Scheiber, T., Fabian, K., Vogt, C., Knies, J., 2017. Geochemical characterisation of northern Norwegian fjord surface sediments: a baseline for further paleo-environmental investigations. Cont. Shelf Res. 148, 104–115. https://doi.org/10.1016/J.CSR.2017.08.015.

Folk, R.L., Ward, W.C., 1957. Brazos River bar [Texas]; a study in the significance of grain size parameters. J. Sediment. Res. https://doi.org/10.1306/74D70646-2B21-11D7-8648000102C1865D.

Frigstad, H., Andersen, T., Hessen, D.O., Jeansson, E., Skogen, M., Naustvoll, L.J., Miles, M.W., Johannessen, T., Bellerby, R.G.J., 2013. Long-term trends in carbon, nutrients and stoichiometry in Norwegian coastal waters: evidence of a regime shift. Prog. Oceanogr. 111, 113–124. https://doi.org/10.1016/j.pocean.2013.01.006.

Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. J. Paleolimnol. 25, 101–110. https://doi.org/10.1023/A:1008119611481.

Helland, A., Rygg, B., Sørensen, K., 1994. Ranfjorden 1992-1993. Hydrografi, Sedimenterende Materiale, Bunnsedimenter Og Bløtbunnsfauna. NIVA Rapport Nr. 3087. Norsk institutt for vannforskning, Oslo.

Holte, B., 1998. The macrofauna and main functional interactions in the sill basin sediments of the pristine holandsfjord, Northern Norway, with autecological reviews for some key-species. Sarsia 83, 55–68. https://doi.org/10.1080/00364827.1998.10413669.

Holte, B., 2001. Possible ecological effects from maldanid (annelida, polychaeta) "superdominance" in a small North Norwegian sill system. Ophelia 55, 69–75. https://doi.org/10.1080/00785236.2001.10409474.

Holte, B., Oug, E., Cochrane, S., 2004. Depth-related benthic macrofaunal biodiversity patterns in three undisturbed north Norwegian fjords. Sarsia 89, 91–101. https://doi.org/10.1080/00364820410003496.

Holte, B., Oug, E., Dahle, S., 2005. Soft-bottom fauna and oxygen minima in sub-arctic north Norwegian marine sill basins. Mar. Biol. Res. 1, 85–96. https://doi.org/10.1080/17451000510019033.

Hourdez, S., Weber, R.E., 2005. Molecular and functional adaptations in deep-sea hemoglobins. J. Inorg. Biochem. 99, 130–141. https://doi.org/10.1016/J.JINORGBIO.2004.09.017.

Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52, 577–586. https://doi.org/10.2307/1934145.

Husa, V., Kutti, T., Ervik, A., Sjøtun, K., Hansen, P.K., Aure, J., 2014. Regional impact from fin-fish farming in an intensive production area (Hardangerfjord, Norway). Mar. Biol. Res. 10, 241–252. https://doi.org/10.1080/17451000.2013.810754.

Inall, M.E., Gillibrand, P.A., 2010. The physics of mid-latitude fjords: a review. Geol. Soc. London, Spec. Publ. 344 (17) LP – 33.

Johansen, P.-O., Isaksen, T.E., Bye-Ingebrigtsen, E., Haave, M., Dahlgren, T.G., Kvalø, S.E., Greenacre, M., Durand, D., Rapp, H.T., 2018. Temporal changes in benthic macrofauna on the west coast of Norway resulting from human activities. Mar. Pollut. Bull. 128, 483–495. https://doi.org/10.1016/J.MARPOLBUL.2018.01.063.

Jørstad, K.E., Farestveit, E., 1999. Population genetic structure of lobster (Homarus gammarus) in Norway, and implications for enhancement and sea-ranching operation. Aquaculture 173, 447–457. https://doi.org/10.1016/S0044-8486(98)00475-X.

Jourdain, E., Vongraven, D., 2017. Humpback whale (Megaptera novaeangliae) and killer whale (Orcinus orca) feeding aggregations for foraging on herring (Clupea harengus) in Northern Norway. Mamm. Biol. 86, 27–32. https://doi.org/10.1016/J.MAMBIO.2017.03.006.

Kaplan, J.O., New, M., 2006. Arctic climate change with a 2 ∘C global warming: timing, climate patterns and vegetation change. Clim. Change 79, 213–241. https://doi.org/10.1007/s10584-006-9113-7.

Keuning, R., Schander, C., Kongsrud, J.A., Willassen, E., 2011. Ecology of twelve species of Thyasiridae (Mollusca: Bivalvia). Mar. Pollut. Bull. 62, 786–791. https://doi.org/10.1016/j.marpolbul.2011.01.004.

Kruskal, W.H., Wallis, W.A., 1952. Use of ranks in one-criterion variance analysis. J. Am. Stat. Assoc. https://doi.org/10.1080/01621459.1952.10483441.

Larsen, L.-H., 1997. Soft-bottom macro invertebrate fauna of North Norwegian coastal waters with particular reference to sill-basins. Part one: bottom topography and species diversity BT - interactions and Adaptation Strategies of Marine Organisms. Hydrobiologia 355, 101–113.

Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280. https://doi.org/10.1007/s004420100716.

Leppäkoski, E., 1971. Benthic recolonization of the Bornholm basin. Thalassia Jugosl. 7, 171–179.

Lutter, S., Taasen, J.P., Hopkins, C.C.E., Smetacek, V., 1989. Phytoplankton dynamics and sedimentation processes during spring and summer in Balsfjord, Northern Norway. Polar Biol. 10. https://doi.org/10.1007/BF00239156.

Maciolek, N.J., 1985. A revision of the genus Prionospio Malmgren, with special emphasis on species from the Atlantic Ocean, and new records of species belonging to the genera Apoprionospio Foster and Paraprionospio Caullery (Polychaeta, Annelida, Spionidae). Zool. J. Linn. Soc. 84, 325–383. https://doi.org/10.1111/j.1096-3642.1985.tb01804.x.

Manzetti, S., Stenersen, J.H.V., 2010. A critical view of the environmental condition of the Sognefjord. Mar. Pollut. Bull. 60, 2167–2174. https://doi.org/10.1016/j.marpolbul.2010.09.019.

McArthur, M.A., Brooke, B.P., Przeslawski, R., Ryan, D.A., Lucieer, V.L., Nichol, S., McCallum, A.W., Mellin, C., Cresswell, I.D., Radke, L.C., 2010. On the use of abiotic surrogates to describe marine benthic biodiversity. Estuar. Coast Shelf Sci. 88, 21–32. https://doi.org/10.1016/J.ECSS.2010.03.003.

McLusky, D.S., Elliott, M., 2004. The Estuarine Ecosystem: Ecology, Threats and Management, third ed. ed. Oxford University Press.

Molvær, J., Eikrem, W., Magnusson, J., Pedersen, A., Tjomsland, T., 2007. The OSPAR Comprehensive Procedure for the Norwegian West Coast - Eutrophication Status. NIVA Rapport Nr. Norsk institutt for vannforskning, Oslo, pp. 5474.

Narayanaswamy, B.E., Renaud, P.E., Duineveld, G.C.A., Berge, J., Lavaleye, M.S.S., Reiss, H., Brattegard, T., 2010. Biodiversity trends along the western European margin. PLoS One 5. https://doi.org/10.1371/journal.pone.0014295.

Norge, Standard, 2016. Miljøovervåking av bunnpåvirkning fra marine akvakulturanlegg. Norsk Standard 9410, 2016.

Nøttestad, L., Axelsen, B.E., 1999. Herring schooling manoeuvres in response to killer whale attacks. Can. J. Zool. 77, 1540–1546. https://doi.org/10.1139/cjz-77-10-1540.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2018. Vegan: community ecology package. R Packag. version 2 5-2.

Oug, E., 2000. Soft-bottom macrofauna in the high-latitude ecosystem of Balsfjord, northern Norway: species composition, community structure and temporal variability. Sarsia 85, 1–13. https://doi.org/10.1080/00364827.2000.10414551.

Pearson, T.H., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Annu. Rev. 16, 229–311.

Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87, 2614–2625. https://doi.org/10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO:2.

Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine Fishes. Science (80-.) 308 (1912) LP – 1915.

Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. J. Theor. Biol. https://doi.org/10.1016/0022-5193(66)90013-0.

R Development Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Reigstad, M., Wassmann, P., Ratkova, T., Arashkevich, E., Pasternak, A., Øygarden, S., 2000. Comparison of the springtime vertical export of biogenic matter in three northern Norwegian fjords. Mar. Ecol. Prog. Ser. 201, 73–89. https://doi.org/10.3354/meps201073.

Reish, D.J., 1971. Effect of pollution abatement in Los Angeles harbours. Mar. Pollut. Bull. 2, 71–74. https://doi.org/10.1016/0025-326X(71)90226-8.

Renaud, P.E., Włodarska-Kowalczuk, M., Trannum, H., Holte, B., Węsławski, J.M., Cochrane, S., Dahle, S., Gulliksen, B., 2007. Multidecadal stability of benthic community structure in a high-Arctic glacial fjord (van Mijenfjord, Spitsbergen). Polar Biol. 30, 295–305. https://doi.org/10.1007/s00300-006-0183-9.

Renaud, P.E., Løkken, T.S., Jørgensen, L.L., Berge, J., Johnson, B.J., 2015. Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. Front. Mar. Sci. 2, 1–15. https://doi.org/10.3389/fmars.2015.00031.

Roberts, D.W., 2016. Package ' labdsv .' R Packag. ver. 1.8–0. https://doi.org/10.1021/es103092a.See.

Rosenberg, R., Hellman, B., Lundberg, A., 1996. Benthic macrofaunal community structure in the Norwegian Trench, deep skagerrak. J. Sea Res. 35, 181–188. https://doi.org/10.1016/S1385-1101(96)90745-5.

Røttingen, I., Foote, K.G., Ruse, I., Ona, E., 1994. Acoustic Abundance Estimation of Wintering Norwegian Spring Spawning Herring, with Emphasis on Methodological Aspects. ICES CM 1994/(B + D + G + H, pp. 1.

Rumohr, H., 2009. Soft-bottom Macrofauna: Collection, Treatment, and Quality Assurance of Samples. vol. 43 ICES Techniques in Marine Environmental Sciences No.

Rygg, B., Skei, J., 1997. Tiltaksorienterte Miljøundersøkelser I Sørfjorden Og Hardangerfjorden 1996. Delrapport 2: Sedimenter Og Bløtbunnfauna, NIVA-Rapport 3733. Norsk institutt for vannforskning.

Schweiger, A.H., Irl, S.D.H., Steinbauer, M.J., Dengler, J., Beierkuhnlein, C., 2016. Optimizing sampling approaches along ecological gradients. Methods Ecol. Evol. 7, 463–471. https://doi.org/10.1111/2041-210X.12495.

Shannon, C.E., 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27, 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x.

Silberberger, M.J., Renaud, P.E., Buhl-Mortensen, L., Ellingsen, I.H., Reiss, H., 2019. Spatial patterns in sub-Arctic benthos: multiscale analysis reveals structural differences between community components. Ecol. Monogr. 89. https://doi.org/10.1002/ecm.1325.

Southward, A.J., Southward, E.C., Dando, P.R., Rau, G.H., Felbeck, H., Flügel, H., 1981. Bacterial symbionts and low 13C/12C ratios in tissues of Pogonophora indicate unusual nutrition and metabolism. Nature 293, 616.

Southward, A.J., Southward, E.C., Dando, P.R., Barrett, R.L., Ling, R., 1986. Chemoautotrophic function of bacterial symbionts in small Pogonophora. J. Mar. Biol. Assoc. U. K. 66, 415–437. https://doi.org/10.1017/S0025315400043046.

Syvitski, J.P.M., Burrell, D.C., Skei, J.M., 1987. Fjords : Processes and Products. Springer, New York.

Thioulouse, J., Dray, S., Dufour, A.-B., Siberchicot, A., Jombart, T., Pavoine, S., 2011. Multivariate Analysis of Ecological Data with Ade4, Carme. Springer.

Thompson, B.W., Riddle, M.J., Stark, J.S., 2003. Cost-efficient methods for marine pollution monitoring at Casey Station, East Antarctica: the choice of sieve mesh-size and taxonomic resolution. Mar. Pollut. Bull. 46, 232–243. https://doi.org/10.1016/S0025-326X(02)00366-1.

van Son, T.C., Halvorsen, R., 2014. Multiple parallel ordinations: the importance of choice of ordination method and weighting of species abundance data. Sommerfeltia 37, 1–37. https://doi.org/10.2478/som-2014-0001.

van Son, T.C., Halvorsen, R., Bakke, T., 2016. Sampling effort required to recover the main gradients in marine benthic species composition. Mar. Ecol. 37, 329–335. https://doi.org/10.1111/maec.12281.

Wassmann, P., Svendsen, H., Keck, A., Reigstad, M., 1996. Selected aspects of the physical oceanography and particle fluxes in fjords of northern Norway. J. Mar. Syst. 8, 53–71. https://doi.org/10.1016/0924-7963(95)00037-2.

WoRMS Editorial Board, 2018. World register of marine species (WoRMS). https://doi.org/10.14284/170.

Wu, R.S.S., 2002. Hypoxia: from molecular responses to ecosystem responses. Mar. Pollut. Bull. 45, 35–45. https://doi.org/10.1016/S0025-326X(02)00061-9.

Włodarska-Kowalczuk, M., Renaud, P., Węsławski, J., Cochrane, S., Denisenko, S., 2012. Species diversity, functional complexity and rarity in Arctic fjordic versus open shelf benthic systems. Mar. Ecol. Prog. Ser. 463, 73–87. https://doi.org/10.3354/meps09858.

Zaborska, A., Włodarska-Kowalczuk, M., Legeżyńska, J., Jankowska, E., Winogradow, A., Deja, K., 2018. Sedimentary organic matter sources, benthic consumption and burial in west Spitsbergen fjords – signs of maturing of Arctic fjordic systems? J. Mar. Syst. 180, 112–123. https://doi.org/10.1016/J.JMARSYS.2016.11.005.

Zanzerl, H., Dufour, S.C., 2017. The burrowing behaviour of symbiotic and asymbiotic thyasirid bivalves. J. Conchol. 42, 299–308.

Paper II

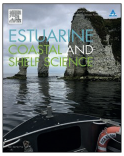
This article was published in *Estuarine, Coastal and Shelf Science*, 252, Valentin Kokarev, Mathieu Tachon, Marthe Austad, Maeve McGovern, Henning Reiss, *Strong macrobenthic community differentiation among sub-Arctic deep fjords on small spatial scales*, 107271, Copyright Elsevier (2021).

Estuarine, Coastal and Shelf Science 252 (2021) 107271

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: http://www.elsevier.com/locate/ecss



Strong macrobenthic community differentiation among sub-Arctic deep fjords on small spatial scales

Valentin Kokarev[a,*], Mathieu Tachon[a], Marthe Austad[b], Maeve McGovern[c,d], Henning Reiss[a]

[a] *Faculty of Biosciences and Aquaculture, Nord University, 8049, Bodø, Norway*
[b] *Aqua Kompetanse AS, 7770, Flatanger, Norway*
[c] *Norwegian Institute for Water Research (NIVA), Oslo, Norway*
[d] *Department of Arctic Marine Biology, UiT: The Arctic University of Norway, Tromsø, Norway*

ARTICLE INFO

Keywords:
Saltfjord
Skjerstadfjord
Sørfolda
Vestfjord
Norwegian coast
Infauna
Macrofauna
Organic matter

ABSTRACT

Fjords play an important role in carbon cycling and sequestration, but the burial of organic matter in sediments strongly depends on the composition of macrobenthic communities. We studied three deep, sub-Arctic fjords located in northern Norway to assess the community differentiation of neighbouring fjords and the underlying environmental drivers. The fjords have relatively deep depositional basins (370–570 m), but they differ in sill depth and water exchange. In all fjords studied, the silty sediments were characterised by organic matter of mostly marine origin. We found that each basin was inhabited by a distinct benthic community, with pronounced differences in total abundance, biomass and species diversity. Only in one fjord (Skjerstadfjord), with a shallow sill, a slight mouth-to-head pattern of the community was found. The strong differentiation of macrobenthos among different fjords seems not to be directly associated with environmental drivers such as organic matter input, water masses or depth.

1. Introduction

The Norwegian coastline is characterised by a high number of fjords – deep estuaries that were created or modified by glaciers. There are considerable differences among fjords in terms of their geomorphology; differences in sill depth can affect many of the processes in these coastal systems, including water exchange with adjacent systems (Syvitski et al., 1987). Apart from geomorphology, the geographic setting is also of particular importance. For instance, sub-Arctic silled fjords of northern Norway (located above the Arctic circle) differ from the fjords located at lower latitudes in having more frequent episodes of deep water exchange due to reduced stratification, higher tidal amplitude and, generally, deeper sills (Wassmann et al., 1996; Larsen, 1997; Holte et al., 2005). Even geomorphologically different fjords, located in close vicinity to each other, can have similar patterns in vertical export of organic matter to the seafloor (Reigstad et al., 2000). Sediments of sub-Arctic fjords are often characterised by low input of terrestrial organic matter compared to Arctic and boreal fjords (Faust and Knies, 2019; Włodarska-Kowalczuk et al., 2019). The phytoplankton growth season north of the Arctic circle is only 6–7 months compared to 9–12 months along the southern Norwegian coast, which results in lower yearly primary production (Eilertsen and Degerlund, 2010). Such contrasting differences in environmental settings can potentially result in very different ecosystem components among fjords at different latitudes, including macrofauna. Data on macrobenthic communities of sub-Arctic fjords are scarce and usually from fjords with relatively shallow basins (Larsen, 1997; Holte, 1998; Oug, 2000; Holte et al., 2005). There are even less data on the soft-bottom macrobenthic communities inhabiting the deep basins and almost no information exists on the spatial structure within and among sub-Arctic fjords (but see Jordà Molina et al., 2019). Fjords in the Vestfjord region are particularly interesting considering the high rates of marine organic matter burial observed in their basins compared to those of boreal and Arctic fjords (Faust and Knies, 2019). High marine productivity in the Vestfjord basin, sustained by inflow of nutrient-rich Atlantic waters and upwelling along its steep walls, can lead to advection of organic matter into neighbouring fjords, where burial and remineralization rates on the seafloor depend, in part, on macrobenthic community composition (Zaborska et al., 2018; Włodarska-Kowalczuk et al., 2019). Thus, knowledge on macrobenthic communities is essential to understand carbon cycling in these systems, as well as to monitor and predict the effects of an expanding aquaculture industry in Norwegian coastal waters – another source of allochthonous

---

* Corresponding author.
E-mail address: valentin.kokarev@nord.no (V. Kokarev).

https://doi.org/10.1016/j.ecss.2021.107271
Received 30 July 2020; Received in revised form 4 February 2021; Accepted 9 February 2021

organic matter in fjords (Husa et al., 2014; Johansen et al., 2018).

In general, fjord communities are considered impoverished in terms of biodiversity compared to adjacent open sea areas (Buhl-Mortensen, 1996; Buhl-Mortensen and Høisæter, 1993; Włodarska-Kowalczuk et al., 2012). Apart from environmental drivers such as enhanced sedimentation from river/glacier runoff, possible periods of hypoxia etc., reduction in species richness can be caused by smaller habitat area and its homogeneity (Yang et al., 2015; Scheiner et al., 2011). In this sense, comparisons among fjord basins and their inhabitants are of particular interest. Fjords, located in direct vicinity of each other, share the same pool of species, yet each basin can still be perceived as an independent habitat due to its relative isolation by the sill at the fjord entrance. Thus, it can be assumed that neighbouring fjords with similar environmental settings should have similar macrofaunal composition. However, stochastic events such as the timing of the arrival of species into a community can potentially lead to community divergence (Chase, 2003, 2007; Fukami, 2015). Considering the above, we studied the macrofaunal communities and environmental conditions of several sub-Arctic fjord basins to assess the degree of differentiation of inhabitant macrobenthic communities. Our specific research questions were 1) how similar are closely situated sub-Arctic fjord systems in their benthic community composition and 2) what environmental conditions correlate with these biological patterns?

2. Materials and methods

2.1. Study area and sampling design

We sampled three sub-Arctic fjords from two fjord systems located at 67° N in Nordland, northern Norway (Fig. 1). The Saltfjord-Skjerstadfjord and Folda systems are located approximately 40 km from each other, and are separated by relatively deep sills (220–260 m) from the adjacent Vestfjord. Saltfjord is the shallowest of the three fjords studied (max. depth 380 m), and is connected to the deeper Skjerstadfjord (max. depth 540 m) by the shallow and narrow strait 'Saltstraumen', which is only 26 m deep. Saltstraumen is a hydrologically active area, through which significant amounts of water enters Skjerstadfjord forced by tidal currents (Eliassen et al., 2001). The third studied fjord is Sørfolda (max. depth 560 m), a southern branch of the Folda fjord system, located to the north of Saltfjord-Skjerstadfjord.

All three of these sub-Arctic fjords remain ice-free throughout the year but experience seasonal variation in surface water temperature and salinity associated with river runoff (Skreslet et al., 2000; Myksvoll et al., 2011). However, the bottom water in Saltfjord shows almost no seasonal variation in salinity and temperature (ranging between 34.5 and 35.5, and 6–7.8 °C, respectively) (Skreslet et al., 2000; Busch et al., 2014). Similar bottom water properties were recorded for Sørfolda (34.7–34.9 and 6.6–6.9 °C; Aure and Pettersen, 2004). Bottom water masses in Skjerstadfjord also display little variation across different seasons, but overall are colder (4–4.9 °C) and less saline (33.5–33.9) than with Saltfjord and Sørfolda (Skreslet, 2002; Busch et al., 2014). The oxygen concentration in bottom water is usually above 5.5 ml/L in all three basins (Skreslet et al., 2000; Skreslet, 2002; Aure and Pettersen, 2004). All three fjords are anthropogenically impacted to some degree because of their close proximity to two relatively big cities (Bodø and Fauske) and their industrial facilities. In addition, salmon farming is widespread in this region with several fish farms located in both Skjerstadfjord and Sørfolda. However, for this study, no sampling occurred within 1 km of fish farms.

The sampling campaign was carried out in two periods: April–June 2013 (Saltfjord and Skjerstadfjord) and May 2015 (Sørfolda) from the research vessel "Tanteyen". The sampling was arranged in three transects along the mouth-to head axis of each fjord (Fig. 1). In Saltfjord and Sørfolda, stations outside the main basin were also included (S10, S11 and S12 for the former and F1 and F2 in the latter). Two 0,1 m^2 Van Veen grab samples were taken at each sampling station. Coordinates and

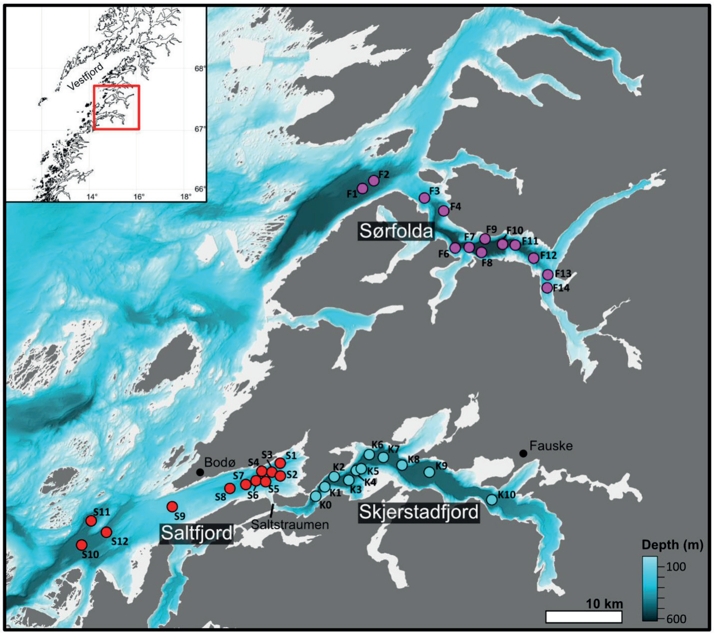


Fig. 1. Map of the study area. Stations denoted the following: S – Saltfjord transect (red), K – Skjerstadfjord transect (blue), F – Sørfolda transect (purple). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

related information for all the stations are available in Supplementary Table 1.

2.2. Collection of fauna

The grab samples were sieved on a 1 mm mesh and fixed with 4% formaldehyde buffered with borax. While the 1 mm mesh retains smaller total abundances than smaller mesh sizes, it is suitable for describing general patterns of macrobenthic distribution (Thompson et al., 2003; Somerfield et al., 2018). In the lab, animals were sorted from sediments, identified to the lowest taxon possible, counted, weighed (wet weight) to the nearest 0.1 mg, and stored in 70% ethanol. All polychaetes were weighted without tubes. However, for Sørfolda stations, a calculated mean of 1 mg per *Spiochaetopterus typicus* individual (based on specimens weighted without a tube) was used as a conversion factor from abundance to biomass to facilitate the sample processing. Colonial (e.g. colonial cnidarians, Bryozoa), meiobenthic taxa (e.g. copepods, nematodes, ostracods) and larger suprabenthic taxa (e.g. Mysida, decapod shrimps) were excluded from the analysis. The two replicate grab samples were combined in statistical analyses to remove the effects of fine-scale patchiness. The complete faunal list is available in Supplementary Table 2.

2.3. Sediment samples

Surface sediment subsamples were taken with a spoon from one of the grab samples at each station for granulometry (approximately the top 5 cm) and organic matter (approximately the top 2 cm) analyses. The samples were stored at −20 °C before being processed further. Samples for granulometry were wet washed through a cascade of sieves (1000 μm, 500 μm, 250 μm, 125 μm, 63 μm). All fractions were dried at 100 °C and weighed. The <63 μm fraction was collected in a bucket and left in a cool place to settle for several days prior to decantation and drying. The percent contribution of each fraction was calculated for each sample.

The samples for organic matter analysis were dried at 60 °C, ground with a mortar and pestle and acidified with 2N hydrochloric acid to remove inorganic carbon. Stable isotope analysis and concentration measurements of nitrogen and organic carbon were performed simultaneously with a THERMO/Finnigan MAT V isotope ratio mass spectrometer, coupled to a THERMO Flash EA 1112 elemental analyser via a THERMO/Finnigan Conflo IV- interface in the stable isotope laboratory of the Museum für Naturkunde, Berlin. Stable isotope ratios are expressed in the conventional delta notation ($\delta^{13}C/\delta^{15}N$) relative to VPDB (Vienna PeeDee Belemnite standard) and atmospheric nitrogen. Percent of terrigenous organic matter (% C_{terr}) was estimated based on $\delta^{13}C_{org}$ signature using a simple mixing model with end-member values of −19.3‰ and −26.5‰ for marine and terrigenous organic matter, respectively (Faust and Knies, 2019). We used percent of total organic carbon (TOC), C:N ratio (weight), % of terrigenous organic matter (% C_{terr}) and $\delta^{15}N$ to characterize quantity and origin of organic matter in sediments.

2.4. CTD data

In May 2015, CTD measurements of temperature, salinity and oxygen were carried out at selected stations in each fjord to characterize bottom water masses of the silled basins. No CTD data were available for the year 2013 when the benthos was sampled in Saltfjord and Skjerstadfjord.

2.5. Modelling of water exchange between Saltfjord and Skjerstadfjord

The effects of a shallow sill on the hydrodynamic regime of the Saltfjord-Skjerstadfjord fjord system were further investigated using the hydrodynamic unstructured grid Finite Volume Community Ocean Model (FVCOM; Chen et al., 2007). The model domain extended from the northernmost part of Meløy municipality to the south, to the northernmost part of Steigen municipality to the north. The model was run along a vertical transect of about 18 km crossing through Saltstraumen with forcing fields for 2013. The model was set up with a grid in which cell size ranged from around 1 km in the open ocean, down to nearly 10 m in narrow straits (e.g. Saltstraumen), and which consisted of 34 vertical sigma layers.

2.6. Statistical analysis of community data

All statistical analyses were performed in R (version 3.6.1; using the packages pvclust, vegan and labdsv; R Development Core Team, 2019) and Primer 7 (Clarke and Gorley, 2015). Species abundances were used for multivariate analyses and to calculate diversity indices. Abundances were preferred over biomass for better comparability with existing literature as the majority of papers on fjords in the region use abundances to describe macrobenthic communities. Prior to multivariate analyses, data were standardized by station to reduce the effect of differences in total abundance among stations due to sampling year (see section 4.2), and subsequently square root transformed in order to reduce the role of dominant species (Clarke et al., 2014). Bray-Curtis coefficients (Bray and Curtis, 1957) were used to calculate the dissimilarity matrix. We used Unweighted Pair Grouping Method with Arithmetic-mean (UPGMA) clustering to identify the main patterns in the community data. The optimal number of clusters was identified with multiscale bootstrap resampling using a modified “pvclust()” function for the Bray-Curtis dissimilarity matrix from the pvclust R package (Github 2019) as well as species fidelity analysis following the methods described in Borcard et al. (2018). The results were verified using non-metric multidimensional scaling (nMDS).

Abundance, biomass, species number per station (S), expected number of species per 25 individuals (ES (25)); Shannon index (H’, to a log base of both 2 and e, for better comparison with existing literature), Pielou’s evenness (J′) and average taxonomic distinctness (Δ*) were used as univariate characteristics of the identified clusters (Clarke et al., 2014). Furthermore, we used Species Indicator values (IndVal) (Dufrêne and Legendre, 1997) to identify indicator species for each cluster. Species were clustered together using index of association: a similarity index, that is calculated as a Bray-Curtis index based on species abundances standardised across samples with values ranging from 0 (perfect “negative” association) to 100 (perfect “positive” association”) (Clarke et al., 2014).

2.7. Variation partitioning

The relationship between the species data set and measured environmental variables as well as sampling locations was investigated using variation partitioning (Borcard et al., 2018). Three groups of explanatory variables were used: depth (included water depth only), fjord (factor variable with three levels which corresponded to three sampling locations: Saltfjord, Skjerstadfjord and Sørdolda) and sediment (% TOC, %N, $\delta^{13}C$, $\delta^{15}N$, C:N and % of three granulometric fractions: 125 μm, 63 μm and <63 μm). No hydrological parameters were used because none were measured directly for every station. Although stations S12, S11, S10, F1, F2 are located outside their respective fjords, they were considered as a part of the sampling location since the benthic fauna did not significantly differ between the stations inside the sill basin and adjacent outer stations for both Saltfjord and Sørfolda (see below). Prior to variation partitioning, three groups of factor variables were separately subjected to forward selection based on adjusted R^2 with significance level as stopping criteria. We used dbRDA (McArdle and Anderson, 2001) based on Bray-Curtis dissimilarities derived from standardized square root transformed abundance data both for forward selection and variation partitioning. The variables depth, fjord, $\delta^{15}N$, and C:N ratio were selected for the partitioning. In addition, we performed variation partitioning for each fjord separately with two groups of variables, depth and sediment, to identify any patterns associated with environmental drivers within fjords that can be potentially masked by joint analysis. The results of forward selection are available in Supplementary Table 3.

3. Results

3.1. Environmental setting

The granulometry analysis revealed that the mud fraction (silt and clay, <63 μm) was dominating the sediment composition and the size fractions below 250 μm contributed with more than 90% of the sediment at most stations of all fjords (Fig. 2A–C). While the fraction of 63–125 μm consisted mostly of very fine sand, the 125–250 μm fraction was usually dominated by uniform mud aggregates rather than sand particles (Fig. 2D). The exception was station S9, located on the sill of Saltfjord, with no aggregates and coarser sediment. No apparent gradient in granulometry from outer to inner stations was found for any of the three fjords.

All fjords were dominated by marine organic matter (% C_{terr} ranged from 11.4 to 47%) with C:N ratios of less than 10 (4.5–9.5) and $\delta^{15}N$ in the ranging from 4.3 to 6.6‰ (Fig. 3). TOC was strongly correlated with the percentage of nitrogen in the sediments of Sørfolda ($r = 0.99$, $p < 0.001$) and Saltfjord ($r = 0.87$, $p < 0.001$) indicating that most of the nitrogen is of organic origin. While this was not the case for Skjerstadfjord as a whole ($r = 0.28$, $p > 0.05$), a strong linear relationship was revealed when stations from the anterior part of the fjord (K0–K5) were excluded ($r = 1.00$, $p < 0.001$).

The amount of organic matter differed among the basins of the three sampled fjords and their adjacent basins (Fig. 3). The TOC values were on average higher in Sørfolda with an average of 1.7% and a maximum of 2.7%, while in Saltfjord and Skjerstadfjord, TOC rarely exceeded 1.5% (Fig. 3). TOC was higher in the Saltfjord basin compared to stations located outside of the basin (S10-12). This trend was accompanied by an increase in terrigenous organic matter and C:N ratio as well as a decrease in $\delta^{15}N$. Skjerstadfjord showed an increase in terrigenous organic matter towards the inner part (up to 47%), which was also accompanied by increase in C:N ratio. However, the increase in TOC was not very pronounced in the inner part of Skjerstadfjord. Also, in Skjerstadfjord, the lowest $\delta^{15}N$ values were observed (mean 5.2‰ versus 5.6‰ and 5.8‰ for Saltfjord and Sørfolda, respectively). No obvious trends in terms of organic matter content or quality were found along the fjord axis in Sørfolda. In general, C:N significantly correlated with % C_{terr} ($r = 0.61$, $p < 0.001$) and negatively with $\delta^{15}N$ ($r = -0.39$, $p < 0.05$).

Based on the CTD data, bottom water masses were similar among Saltfjord, Sørfolda, and stations in the adjacent basins (Table 1), indicating regular inflow of warm and saline waters into these fjords. Bottom water masses in Skjerstadfjord were colder and less saline. All basins were generally well oxygenated with oxygen saturation over 65%.

The typical circulation patterns and water exchanges between Saltfjord and Skjerstadfjord based on the FVCOM are shown in Fig. 4. During rising tides, more saline and denser surface water from Saltfjord flows over the sill and then down to deeper levels in Skjerstadfjord, where the water has approximately the same density. The advection of surface water from Saltfjord into the greater depths of Skjerstadfjord, together with further vertical mixing, are the main processes contributing to the deep water renewal of Skjerstadfjord. During falling tides, the less saline and lighter surface water from Skjerstadfjord flows over the sill and then mixes with the surface waters of Saltfjord. Thus, water flow from Skjerstadfjord into Saltfjord is limited to the upper water layers.

3.2. Faunal data

Based on the results of the UPGMA clustering, multiscale bootstrap resampling and species fidelity analysis, we identified five clusters in the faunal data (Fig. 5A). These clusters approximately corresponded to sampling location. The exception was the sill station S9 in Saltfjord, which was more similar to the stations in Sørfolda than to those in the Saltfjord. Stations K0 and K1, located close to Saltstraumen, formed a different cluster (cluster "A") than the other Skjerstadfjord stations (cluster "B") based on species fidelity analysis. However, the "approximately unbiased" (AU) p-values, identified by multiscale bootstrap resampling for clusters A and B, were only 0.68 and 0.83, respectively, indicating that clusters A and B are quite similar. This was supported by nMDS ordination (Fig. 5B), showing that all clusters clearly formed their own groups, except for clusters A and B, which were not well separated from each other. The varying level of dissimilarity among stations of cluster C was a consequence of low total abundance per station (mostly below 100 individuals), thus leading to a greater influence of rare species.

While many of the dominant species were shared among the clusters, e.g. the polychaete *Heteromastus filiformis*, which was present in high

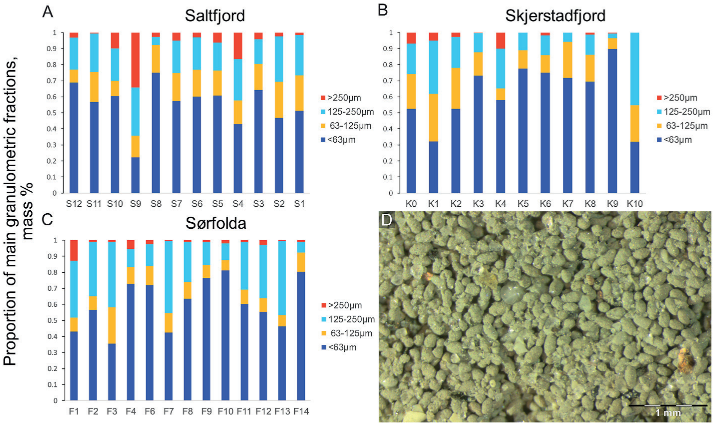


Fig. 2. Results of granulometry for three fjords: A Saltfjord, B Skjerstadfjord, C Sørfolda. For each station, the contribution of the three main fractions are shown: >250 μm, 125–250 μm, 63–125 μm and <63 μm. D: a macrophotograph of the 125 μm fraction from station F3, showing the high abundance of uniformly shaped mud aggregates. Stations are ordered in the direction from outer fjord to inner fjord.

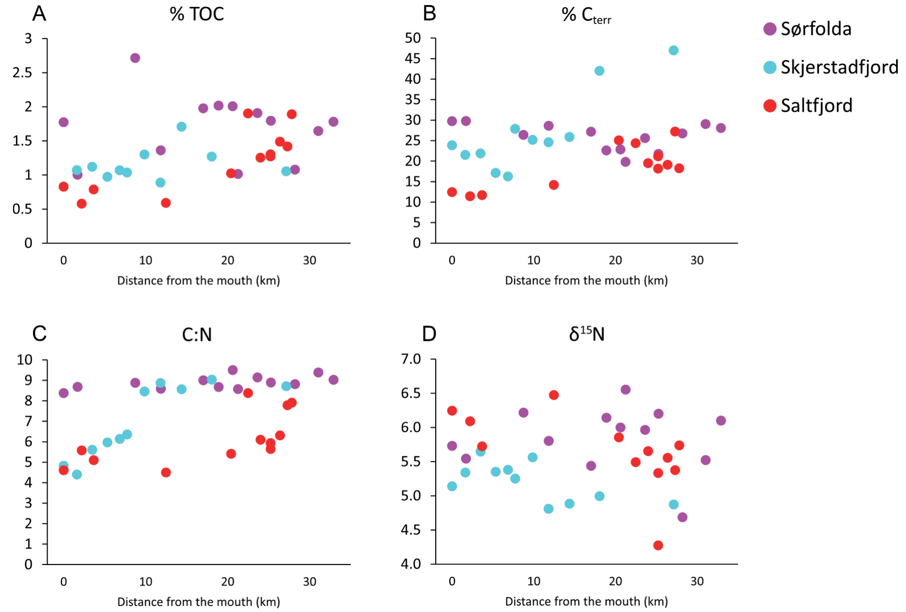


Fig. 3. Characteristics of organic matter in surface sediments: A, % of total organic carbon (% TOC); B, % of terrigenous organic matter (% C_{terr}); C, C:N ratio and D, δ^{15}N (‰).

Table 1
Bottom water parameters in May 2015 (*station located outside of the Saltfjord basin).

	Station	Depth (m)	Salinity	Temperature (°C)	Oxygen (%)	Oxygen (mg/L)
Saltfjord	S12*	458	35.4	7.2	84.4	8.0
	S8	368	35.3	7.3	77.3	7.3
	S5	377	35.3	7.3	79.6	7.4
Skjerstadfjord	K0	521	33.8	4.9	71.0	7.1
	K5	506	33.8	4.9	71.0	7.1
	K9	372	33.8	4.9	73.4	7.4
Sørfolda	F2	502	35.4	7.0	74.2	7.1
	F7	519	35.3	7.0	68.3	6.4
	F11	535	35.3	7.0	67.7	6.4
	F12	456	35.3	7.0	68.4	6.4
	F14	350	35.3	7.0	70.9	6.7

abundances in all fjords (Fig. 6, Table 2), each fjord was also characterized by a high number of unique taxa with a maximum of 46 taxa only found in Sørfolda (Table 2).

Skjerstadfjord clusters A and B were very similar in terms of dominant species based on both abundance and biomass (Table 2). The polychaetes *Heteromastus filiformis*, *Paramphinome jeffreysii* and *Ceratocephale loveni,* as well as the echinoderms *Brisaster fragilis* and *Ctenodiscus crispatus,* were the most dominant taxa in both groups. The large size of these two echinoderm species led to a much higher observed biomass in Skjerstadfjord compared to the other sampling locations. The polychaete *Galathowenia oculata*, a dominant species in cluster A, contributed little to the total abundance in cluster B, where the bivalve *Parathyasira equalis* was abundant. Moreover, cluster A had higher abundance and diversity (except taxonomic distinctness) and possessed a higher number of unique taxa than cluster B (Fig. 7, Table 2). The lower average taxonomic distinctness of cluster A indicates that the higher diversity in this cluster compared to cluster B is associated with closely related (mainly polychaete) species.

Saltfjord cluster C was characterised by the lowest abundance and overall low diversity, but the highest average taxonomic distinctness (Fig. 7). The latter was due to the highly dominant sipunculid *Onchnesoma steenstrupii,* which is phylogenetically distinct from other species within this cluster (Table 2). The highest diversity values were recorded for Saltfjord cluster D, which consisted of a single station located at the sill (S9), where 15 taxa were exclusively found (Table 2). While the benthic community at this station showed higher similarity with Sørfolda stations than with any of the other Saltfjord stations (Fig. 5), it was similar to Saltfjord cluster C in that *O. steenstrupii* was among the most abundant species.

All Sørfolda stations were grouped together within a single cluster E. These stations had higher abundance and diversity compared to clusters A, B, and C (Fig. 7). Among the dominant species was *Thyasira obsoleta,* which was completely absent in the other clusters (Fig. 6). The dominance of the polychaetes *Spiochaetopterus typicus*, *Heteromastus filiformis* and the bivalve *Kelliella miliaris* was similar to cluster D (Table 2). In general, the benthic assemblage of cluster E was the most distinct in terms of species composition based on 46 unique taxa as well as several indicator species, identified by the IndVal routine (Table 2).

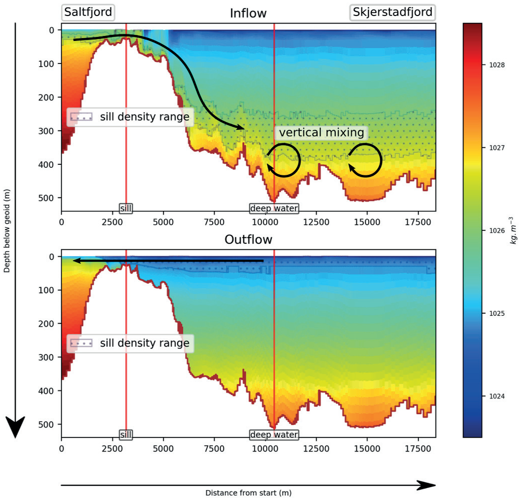


Fig. 4. Seawater density along Saltstraumen, modelled for the 1st June 2013 during both the rising tide (top) and the falling tide (bottom). The shaded area highlights the depth of the water masses which have a density that falls within the density range of the water flowing over the sill.

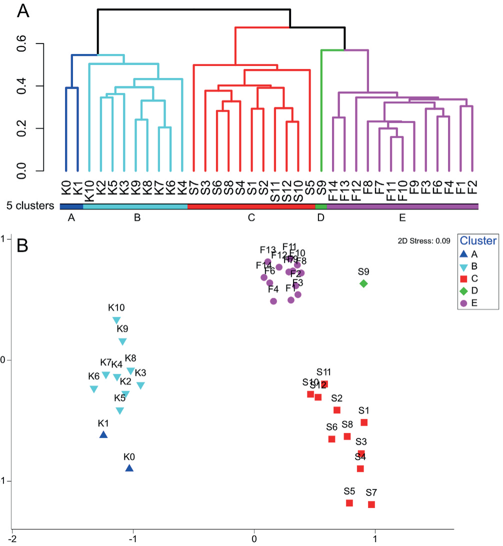


Fig. 5. The results of UPGMA clustering (A) and nMDS ordination diagram (B) based on Bray-Curtis dissimilarity matrix calculated from square root-transformed standardized species abundance data. Cluster A = Skjerstadfjord/Saltstraumen, Cluster B = Skjerstadfjord, Cluster C = Saltfjord and adjacent basin, Cluster D = Saltfjord sill, Cluster E = Sørfolda and adjacent basin.

3.3. Variation partitioning

Results of variation partitioning showed that more than half of the variation in the data set can be explained by the factor Fjord (0.57) (Fig. 8A). This was expected since the identified clusters were fjord specific. All of the factor groups were significant in explaining the variation in the species data set. For the sediments, only two variables were selected by forward selection: C:N ratio and δ^{15}N. Interestingly, depth and sediment appeared to be independent of each other, but most of their explained variation could also be explained by the sampling location. Nevertheless, the majority of the variation explained by fjord was unrelated to depth and sediment characteristics, indicating that neither are the main environmental drivers responsible for differences in community structure among the fjords. The within-fjord variation was mainly associated with sediment variables for Saltfjord and Skjerstadfjord, while Depth was more important for Sørfolda (Fig. 8B–D). Interestingly, different sediment variables were selected by forward selection for different fjords: δ^{15}N for Saltfjord, C:N and δ^{13}C for Skjerstadfjord and δ^{13}C for Sørfolda. The faunal dataset in Skjerstadfjord was more constrained by environmental variables than the other two fjords (0.34 of variation explained versus 0.17 and 0.18 in Saltfjord and Sørfolda, respectively).

4. Discussion

The deep basins (>350m) of the three sampled fjords were characterised by stable water masses and, in general, homogeneous sediments, reflecting their depositional character for mainly marine organic matter. In general, deep depositional sites show more degraded food supply compared to shallower coastal areas, which has a pronounced effect on macrofaunal composition (Dauwe et al., 1998). We found that each fjord basin was inhabited by a distinct benthic community, despite their close vicinity to each other and exchange with adjoining waters. This stands in contrast to adjacent deep fjords of western Norway, where community structure varies with distance to offshore waters, rather than to a specific basin (Buhl-Mortensen, 1996; Buhl-Mortensen and Høisæter, 1993). These findings may indicate that different processes are structuring macrobenthos in deep sub-Arctic and boreal fjords.

4.1. Sediment characteristics and organic matter sources

There were no pronounced differences in sediment particle size distributions among the fjords, however, organic matter properties differed among the studied basins. In general, TOC, % of C_{terr} (based on $\delta^{13}C_{org}$), C:N and δ^{15}N were in accordance with previous findings for the Vestfjord region (Faust and Knies, 2019). In all fjords studied, C:N ratios never reached values above 10, which is indicative of predominantly marine origin for organic matter (Rullkötter, 2006), and were significantly correlated with % of C_{terr}. However, δ^{15}N values appeared to change independently from these two parameters. The low δ^{15}N and high values of C_{terr} observed for the inner part of the basin in Skjerstadfjord are likely related to higher terrigenous input compared to outer parts of the basin, a pattern observed for fjords worldwide (Smeaton et al., 2017; Hinojosa et al., 2014; Sepúlveda et al., 2011). δ^{15}N values for Skjerstadfjord sediments sampled close to Saltstraumen might not reflect the organic matter sources of nitrogen because of the high inorganic nitrogen content in this part of the fjord. Interestingly, Sørfolda showed higher levels of terrestrial input than Saltfjord but also relatively high δ^{15}N values. However, δ^{15}N values can vary depending on the abundance of fresh phytoplankton or various fractionation processes in sediments (Silberberger et al., 2018; Robinson et al., 2012). In sub-Arctic fjords close to Tromsø (northern Norway, 69°N), organic matter fluxes and their composition depend on advection of water masses from the open coastal zone, and zooplankton abundance, showing strong seasonal and interannual variation, while fjord morphology and sill depth are of minor importance for the flux (Wassmann et al., 1996; Reigstad et al., 2000). Since sampling in Sørfolda was carried out two years after Saltfjord/Skjerstadfjord, interannual differences in the spring bloom production and the settlement of organic matter could have affected the patterns observed in this study.

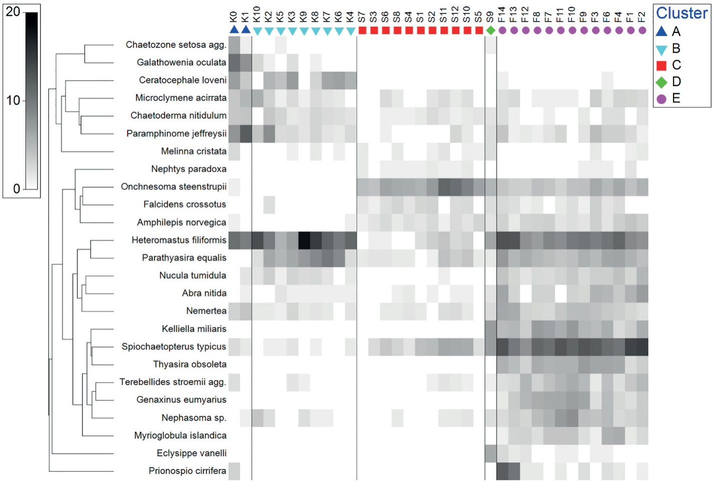


Fig. 6. Shade plot of square root transformed abundances (per 0.2 m^2) for the 25 most abundant species. Species grouped using UPGMA clustering based on index of association. Cluster A = Skjerstadfjord/Saltstraumen, Cluster B = Skjerstadfjord, Cluster C = Saltfjord and adjacent basin, Cluster D = Saltfjord sill, Cluster E = Sørfolda and adjacent basin.

Table 2
Dominant species based on abundance, biomass, IndVal species and number of unique taxa. Cluster A = Skjerstadfjord/Saltstraumen, Cluster B = Skjerstadfjord, Cluster C = Saltfjord and adjacent basin, Cluster D = Saltfjord sill, Cluster E = Sørfolda and adjacent basin. *- species listed in Supplement Table 2.

	Skjerstadfjord		Saltfjord		Sørfolda
	Cluster A	Cluster B	Cluster C	Cluster D	Cluster E
Dominant species based on total cluster abundance (% of total cluster abundance)	*Paramphinome jeffreysii* (19.74)	*Heteromastus filiformis* (48.72)	*Onchnesoma steenstrupii* (50.00)	*Kelliella miliaris* (13.28)	*Spiochaetopterus typicus* (23.63)
	Heteromastus filiformis (19.64)	*Parathyasira equalis* (15.80)	*Spiochaetopterus typicus* (15.26)	*Spiochaetopterus typicus* (13.01)	*Heteromastus filiformis* (16.20)
	Galathowenia oculata (16.62)	*Ceratocephale loveni* (8.37)	*Parathyasira equalis* (4.87)	*Heteromastus filiformis* (10.84)	*Parathyasira equalis* (4.80)
	Ceratocephale loveni (5.67)	*Paramphinome jeffreysii*(4.51)	*Falcidens crossotus* (3.80)	*Eclysippe vanelli* (10.03)	*Kelliella miliaris* (4.67)
	Chaetozone setosa agg. (3.78)	*Microclymene acirrata* (2.26)	*Heteromastus filiformis* (3.80)	*Onchnesoma steenstrupii* (7.05)	*Thyasira obsoleta* (4.66)
Dominant species based on total cluster biomass (% of total cluster biomass)	*Brisaster fragilis* (48.53)	*Brisaster fragilis* (40.42)	*Brissopsis lyrifera* (81.17)	*Chirimia biceps* (41.48)	*Brisaster fragilis* (20.87)
	Astarte crenata (20.54)	*Ctenodiscus crispatus* (32.19)	*Psilaster andromeda* (2.82)	*Nephtys hystricis*(5.95)	*Sipunculus norvegicus* (19.05)
	Ctenodiscus crispatus (6.95)	*Polyphysia crassa* (13.90)	*Onchnesoma steenstrupii* (2.50)	*Abra nitida* (5.50)	*Terebellides stroemii agg.* (7.79)
	Paraedwardsia arenaria (4.46)	*Ceratocephale loveni* (2.68)	*Nemertea* (1.68)	*Ampelisca cf. amblyops* (4.1)	*Ophiura sarsii* (7.33)
	Notomastus latericeus (3.60)	*Notomastus latericeus* (1.44)	*Parathyasira equalis* (1.59)	*Pista bansei* (3.87)	*Parathyasira equalis* (6.13)
IndVal species	*Paraedwardsia arenaria*	*Parathyasira.equalis*	*Onchnesoma steenstrupii* *Eulalia tjalfiensis*	*Eclysippe vanelli* *Laonice sarsi* *Cuspidaria lamellosa* *Onchnesoma squamatum* *Kelliella miliaris*	*Mendicula ferruginea* *Thyasira obsoleta* *Genaxinus eumyarius* *Myrioglobula islandica* *Abyssoninoe sp.* *Paradoneis eliasoni* *Augeneria sp.* *Eriopisa elongata*
Total number of taxa	68 79	51	53 90	65	123
Number of unique taxa* (Present only in a particular cluster/fjord)	17 32	3	7 23	15	46

Nevertheless, the fjords described here are dominated by marine organic matter, as are other fjords in the Vestfjord region, as a result of high marine productivity in the area (Faust and Knies, 2019). The relatively low contribution of terrigenous organic matter to the organic matter pool in the sediment seems to be characteristic of many sub-Arctic fjords due to low river runoff and scarce vegetation (Faust and Knies, 2019; Włodarska-Kowalczuk, 2019). Nonetheless, based on these qualitative characteristics of organic matter and TOC content, it can be concluded that sources of organic matter differed slightly among and within the three studied fjords, with higher terrestrial input in Sørfolda compared

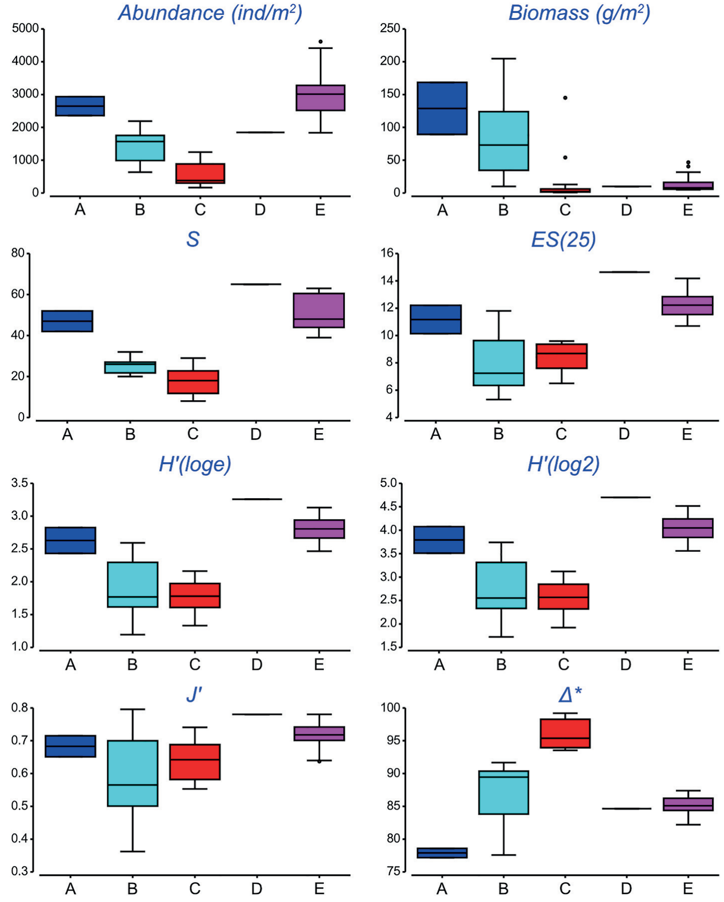


Fig. 7. Univariate characteristics of identified clusters: Abundance (individuals per square meter), Biomass (gram wet weight per square meter), number of species per station (S), expected number of species per 25 individuals ES(25), Shannon index (H′) Pielou's evenness (J′) and average taxonomic distinctness (Δ*). Cluster A = Skjerstadfjord/Saltstraumen, Cluster B = Skjerstadfjord, Cluster C = Saltfjord and adjacent basin, Cluster D = Saltfjord sill, Cluster E = Sørfolda and adjacent basin.

to Saltfjord, and increasing terrestrial input towards the inner part of the basin in Skjerstadfjord.

In general, sediments were dominated by the mud (silt and clay) fraction (<63 μm). Moreover, we observed a high percentage of mud aggregates in the sand fraction (125–250 μm), especially in Sørfolda. The aggregates were preserved in the samples following the gentle wet-sieving technique used. Similar uniformly shaped aggregates were described from the Palos Verdes shelf margin in South California, which were considered to be a result of sediment "pelletization" caused by benthic fauna, mainly capitellid polychaetes (Drake et al., 2002). This could be the case also for the fjord basins in this study since the capitellid *Heteromastus filiformis* was one of the most dominant species in all communities observed. Pellet deposition by head-down feeding *H. filiformis* can significantly alter sediment characteristics by enhancing the vertical transport of carbon from deeper sediment layers to the surface and the degradation of refractory organic matter (Neira and Höpner, 1994; Wild et al., 2005). Pelletization also leads to faster sedimentation of the particles after resuspension altering the near-bottom sediment transport (Drake et al., 2002). Thus, the pellet aggregates observed in this study suggest strong modification of fjord sediments by the benthic fauna, while the consequences of such "pelletization" for sediment biogeochemistry and carbon sequestration are yet to be understood.

4.2. Faunal composition and community structure

All the fjords in this study were characterised by a distinct macrobenthic community, while the community patterns within each basin along the fjord axis were not very pronounced. Skjerstadfjord was the only fjord that showed a further clustering within the fjord, with two clusters separating the community of the entrance region from the rest of the fjord. Moreover, variation partitioning suggested a stronger environmental forcing in Skjerstadfjord indicating a pronounced effect of organic matter quality on the benthic community structure. However, variation among fjords seems to be controlled not only by organic matter quality or depth, which is discussed in section 4.3.

Saltfjord and Sørfolda have similar sill depths around 250 m as well as bottom water temperature and salinity, which suggests similar water exchange with the adjacent Vestfjord. However, the two benthic communities in these fjords were significantly different. The Saltfjord basin

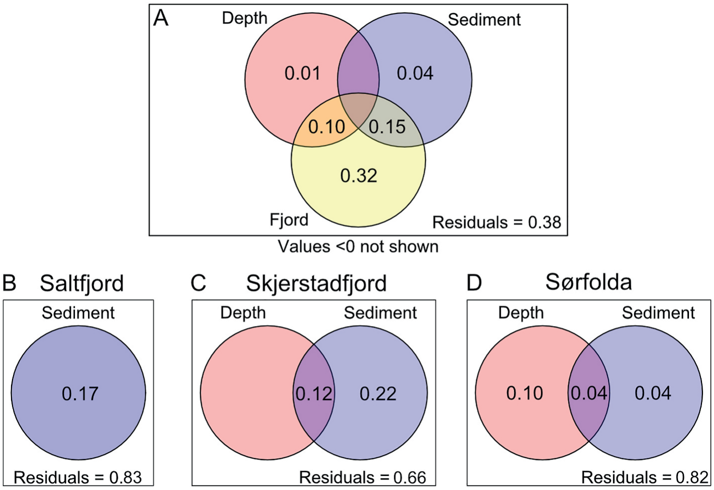


Fig. 8. Venn diagram showing the results of variation partitioning: A – all fjords, B – Saltfjord, C – Skjerstadfjord, D – Sørfolda. Numbers indicate the proportion of variation explained (Adjusted R^2) independently and jointly by three groups of factors: Depth, Fjord and Sediment.

community (most stations of cluster C) was characterised by relatively low total abundances (<1000 ind./m^2) and a high dominance of the sipunculid worm *Onchnesoma steenstrupii,* a species that represented half of all the individuals in this cluster. Infaunal sipunculids are surface deposit feeders (Cutler, 1994), while the second most abundant polychaete species *Spiochaetopterus typicus* can switch from suspension feeding to surface deposit feeding (Jumars et al., 2015). The mode of feeding of the most abundant species implies a high dependence of this community on organic matter settling from the water column. The dominance of *O. steenstrupii* in benthic communities has rarely been reported, except of a region in the western Mediterranean (800 m) with consistent organic matter supply (Mamouridis et al., 2011). Marine valleys in the Lofoten-Vesterålen region are also dominated by *O. steenstrupii* (Silberberger et al., 2019). It is a species sensitive to pollution (Rygg &Norling, 2013), and it is absent from areas with high organic input from fish farms, even when present in the surrounding community (Kutti et al., 2007).

O. steenstrupii and *S. typicus* were present in the Sørfolda basin at all stations. However, in Sørfolda, the benthic community was generally more abundant and diverse, and the higher total abundance in Sørfolda could potentially be linked to the interannual differences: several stations, revisited in Saltfjord in 2015, showed higher abundance (average 2820 ind/m^2), which falls into the range of abundances for Sørfolda in this study, while *S. typicus* and *O. steenstrupii* were still the two most abundant species similar to 2013 (data not included in the present study). Probably, both communities with high contribution of surface-deposit and suspension feeders rely on organic matter which is advected from Vestfjord, however, such advection events are subject to interannual variability (Wassmann et al., 1996; Reigstad et al., 2000). High dominance of the genus *Spiochaetopterus* as well as abundant thyasirid bivalves and *Kelliella miliaris* makes this community very similar to the communities found in the Norwegian Trench (Skagerrak), where similar C:N and slightly higher TOC values were observed, which suggests similar organic input between the two habitats (Rosenberg et al., 1996). Bulk sediment characteristics differed slightly between Sørfolda and Saltfjord, with indications of lower terrigenous organic matter input in Saltfjord. However, sediment factors explained a relatively low proportion of variance in the dataset.

The macrofaunal community of Skjerstadfjord also differed significantly from the two other fjords, and was characterised by intermediate levels of total abundance, biomass and diversity compared to Saltfjord and Skjerstadfjord. In addition, a spatial structuring of the communities within the fjord basin was observed. The stations close to the Saltstraumen strait (cluster A), were characterised by a higher total abundance and diversity than the other stations in Skjerstadfjord (cluster B). Furthermore, the community of cluster A had a high contribution of the tube-dwelling polychaete *Galathowenia oculata* compared to cluster B and to the other fjords in this study. *G. oculata* forms dense populations in several silled basins in northern Norway but does not usually occur at depths exceeding 200 m (Larsen, 1997; Holte, 1998; Oug, 2000; McGovern et al., 2020). *G. oculata* selectively feeds on surface detritus particles (Bamber, 1984). Thus, its high abundances can be indicative of strong bentho-pelagic coupling in this hydrodynamically active region of the fjord. Some other distinguishing species of this cluster were the large suspension feeding bivalve *Astarte crenata* and burrowing anthozoans from the family Edwardsiidae, which are also known to feed on food captured in the water column (Daly et al., 2012). This contrasts with cluster B, where none of the dominant species are known to feed on the sediment surface or overlaying water layer. These differences are likely related to the dynamic environmental conditions close to Saltstraumen, where water masses from Saltfjord are advected into Skjerstadfjord by tidal currents (Fig. 4). Denser surface waters from Saltfjord sink to the deeper layers of Skjerstadfjord, enhancing bentho-pelagic coupling at the fjord entrance. Thus, higher sedimentation rates of advected organic matter and its resuspension can be expected compared to the rest of the fjord, supporting a more diverse and abundant community. However, there was no observed increase in the TOC values at these stations, which can be explained by effective utilisation of high-quality organic matter by the benthos consisting of both surface and sub-surface deposit feeders (Zaborska et al., 2018). This is corroborated by the high abundance of the omnivorous polychaete *Paramphinome jeffreysii* in cluster A, which indicates an opportunistic response to an increase in organic matter in deep waters (Bannister et al., 2014; Gunton et al., 2015).

The dominance of sub-surface deposit feeding species such as the bivalve *Parathyasira equalis* and the polychaete *Heteromastus filiformis* in the benthic community of Skjerstadfjord (cluster B) is very similar to the community of the innermost basin of the Tysfjord multi-basin system

(Jordà Molina et al., 2019). Although both basins in Skjerstadfjord and Tysfjord have a relatively shallow sill, 26 and 60 m respectively, their hydrological conditions are considerably different. While the Skjerstadfjord basin seems to be well oxygenated by the strong tidal driven currents, this is not the case for Tysfjord's innermost basin, where relatively low oxygen concentrations (saturation <50%) were observed (Jordà Molina et al., 2019). Although present in all three fjords, *P. equalis* and *H. filiformis* probably become the most abundant species in conditions where the supply of fresh organic matter is limited. Thus, it can be concluded that the absence of surface-deposit and suspension feeders among the most abundant species is a distinguishing characteristic of cluster B. Populations of subsurface deposit feeders are less dependent on fluxes of fresh pelagic organic matter (Rice and Rhoads, 1989). It seems that the structuring factor for Skjerstadfjord is the distance from Saltstraumen, which corresponds with a decrease in pelagic organic matter input to the sediment. Interestingly, the increase in terrestrial input towards the inner part of the fjord had no pronounced effect on the community structure, likely due to the low bioavailability of terrestrial organic matter compared to marine.

4.3. Fjord-specific communities

In our study, we identified fjord-specific communities that significantly differed in their structure. The majority of the variation in the macrofaunal community structure that could be explained by depth or sediment characteristics was also associated with sampling location, as shown by results of variation partitioning. However, that shared variation accounted for less than half of the variation explained by the factor "Fjord". Considering the high level of local endemism (number of species absent from nearby fjords) found in our study, it can be assumed that the three communities of the three basins represent completely different benthic assemblages, which formed or developed independently. In line with this finding, basin-specific communities were also described for the Tysfjord multi-basin system further north (Jordà Molina et al., 2019). Thus, distinct fjord, or even basin communities, appear to be a characteristic feature for macrobenthic assemblages of fjords in this sub-Arctic region.

There were two major events that have influenced the structure of macrobenthic communities along the shelf of northern Norway: deglaciation of troughs and subsequent inflow of warm Atlantic water about 10 kyr BP, which resulted in the replacement of Arctic with boreal species (Thomsen and Vorren, 1986). Presumably, similar events at a comparable time scale occurred when the modern communities of the Vestfjord region started to develop. Water mass properties are an important factor structuring macrofaunal distribution, as benthic communities can change with inflow of warmer water masses, even on much shorter (decadal) time scales (Kędra et al., 2010). Temperature not only directly influences particular aspects of species biology such as growth and reproduction, but also interspecific relationships, which can drive local-scale community shifts (Kordas et al., 2011). Thus, the relative hydrological isolation of Skjerstadfjord, where the shallow sill limits the influence of Atlantic water masses on the macrobenthic communities and retains colder water masses in the fjord, might be a strong driver for a distinct community.

In contrast, the pronounced differences in community structure between Saltfjord and Sørfolda remains unclear, especially since the deep sills should enable sufficient water exchange with coastal water masses. However, different communities can also establish in similar environments as a result of stochastic processes during community assembly, e.g. the order of species colonizing the habitat (priority effects; Chase, 2003; Fukami, 2015). Considering that these two communities presumably started developing at the same time in the same region and shared an available pool of species, the priority effects might be a potential reason for community differentiation that should be explored further. Previous studies on boreal and Arctic fjords suggest that the reduced diversity compared to the offshore pool of species can be a result of specific environmental conditions in the fjord systems, e.g. reduced habitat complexity, higher fluxes of organic matter and sedimentation from glaciers (Buhl-Mortensen and Høisæter, 1993; Włodarska-Kowalczuk et al., 2012). While we have no data on the species pool from adjacent waters to compare to, we suggest that the subset of species present in these fjords forms not only as a result of environmental filtering of the fauna, but also because of stochastic processes which lead to variation among fjords with similar environmental conditions.

4.4. Conclusion

Strong macrobenthic community differentiation among closely situated deep fjords is only partially correlated with environmental conditions, of which water exchange with surrounding waters is of particular importance. We suggest that stochastic processes during community assembly could be an additional driver of the observed pattern. If stochastic processes result in different communities in fjords with similar environmental settings, no typical macrobenthic community can be described for sub-Arctic fjords as many combinations of functionally similar species can be drawn from the pool of species. For instance, the proportion of surface to subsurface deposit feeders is probably maintained by the supply of organic matter to the seafloor, but species composition even within each trophic guild can be different among different fjords. However, knowledge on the variation among different fjords is meagre, which comprises not only spatial patterns, but also temporal variability of macrobenthic communities and their functional aspects. This knowledge would be necessary before any general conclusion about the isolation and differentiation of benthic communities in sub-Arctic fjords can be drawn.

Author statement

Valentin Kokarev: Conceptualization, Investigation, Formal analysis, Writing - Original Draft, Writing - Review & Editing. **Mathieu Tachon**: Investigation, Formal analysis, Writing - Review & Editing. **Marthe Austad:** Investigation, Writing - Review & Editing. **Maeve McGovern:** Investigation, Writing - Review & Editing. **Henning Reiss:** Conceptualization, Investigation, Writing - Review & Editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The authors would like to thank Egor Gaidukov for field work and preliminary processing of Saltfjord and Skjerstadfjord samples. The authors are also grateful to Morten Krogstad for help during the fieldwork and Arunima Sen, Marc Silberberger and Eivind Oug for valuable suggestions to the manuscript. The analysis of sediment organic matter was possible thanks to Ulrich Struck (Museum für Naturkunde, Berlin). The study was funded by Nord University. Finally, we acknowledge the valuable comments of the anonymous reviewers.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2021.107271.

References

Aure, J., Pettersen, R., 2004. Miljøundersøkelser i Norske fjorder 1975–2000 [Environmental investigations in Norwegian fjords 1975–2000.] Fisken Havet 8, 1–176 (In Norwegian).

Bamber, R.N., 1984. The utilization of fly ash by two tube-building polychaetes. J. Exp. Mar. Biol. Ecol. 81 (2), 107–113. https://doi.org/10.1016/0022-0981(84)90001-7.

Bannister, R.J., Valdemarsen, T., Hansen, P.K., Holmer, M., Ervik, A., 2014. Changes in benthic sediment conditions under an Atlantic salmon farm at a deep, well-flushed coastal site. Aquacult. Environ. Interact. 5 (1), 29–47.

Borcard, Daniel, Gillet, François, Legendre, Pierre, 2018. Numerical Ecology with R. Springer.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27, 325–349. https://doi.org/10.2307/1942268.

Buhl-Mortensen, L., 1996. Amphipod fauna along an offshore-fjord gradient. J. Nat. Hist. 30 (1), 23–49. https://doi.org/10.1080/00222939600770031.

Buhl-Mortensen, L., Høisæter, T., 1993. Mollusc fauna along an offshore-fjord gradient. Marine ecology progress series. Oldendorf 97 (3), 209–224.

Busch, K.E.T., Iversen, K.R., Nashoug, B.F., Kiele, M.R., Gitmark, J., Remen, V., Velvin, R., Krogstad, M., 2014. Miljøundersøkelse Av Skjerstadfjorden. SALT report nr, p. 1006 (In Norwegian).

Chase, J.M., 2003. Community assembly: when should history matter? Oecologia 136 (4), 489–498.

Chase, J.M., 2007. Drought mediates the importance of stochastic community assembly. Proc. Natl. Acad. Sci. Unit. States Am. 104 (44), 17430–17434.

Chen, C., et al., 2007. A finite-volume numerical approach for coastal ocean circulation studies: comparisons with finite difference models. J. Geophys. Res. Atmos. 112 https://doi.org/10.1029/2006JC003485.

Clarke, K.R., Gorley, R.N., 2015. Getting Started with PRIMER V7. PRIMER-E: Plymouth. Plymouth Marine Laboratory.

Clarke, K.R., Gorley, R.N., Somerfield, P.J., Warwick, R.M., 2014. Change in Marine Communities: an Approach to Statistical Analysis and Interpretation. Primer-E Ltd.

Cutler, E.B., 1994. The Sipuncula: Their Systematics, Biology, and Evolution. Cornell University Press.

Daly, Marymegan, Perissinotto, Renzo, Laird, Megan, Dyer, David, Todaro, Antonio, 2012. Description and ecology of a new species of edwardsia de Quatrefages, 1842 (anthozoa, actiniaria) from the st lucia estuary, South Africa. Mar. Biol. Res. 8 (3), 233–245. https://doi.org/10.1080/17451000.2011.617757.

Dauwe, B.P.H.J., Herman, P.M.J., Heip, C.H.R., 1998. Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. Mar. Ecol. Prog. Ser. 173, 67–83.

Drake, D.E., Eganhouse, R., McArthur, W., 2002. Physical and chemical effects of grain aggregates on the Palos Verdes margin, southern California. Continent. Shelf Res. 22 (6–7), 967–986. https://doi.org/10.1016/S0278-4343(01)00115-7.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366. https://doi.org/10.1890/0012-9615, 1997.

Eilertsen, H.C., Degerlund, M., 2010. Phytoplankton and light during the northern high-latitude winter. J. Plankton Res. 32 (6), 899–912.

Eliassen, Inge K., Yngve, Heggelund, Magne, Haakstad, 2001. A numerical study of the circulation in Saltfjorden, Saltstraumen and Skjerstadfjorden. Continent. Shelf Res. 21 (15), 1669–1689. https://doi.org/10.1016/S0278-4343(01)00019-X.

Faust, J.C., Knies, J., 2019. Organic matter sources in North Atlantic fjord sediments. G-cubed 20, 2872–2885. https://doi.org/10.1029/2019GC008382.

Fukami, T., 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. Annu. Rev. Ecol. Evol. Syst. 46, 1–23.

Github. http://raw.github.com/nielshanson/mp_tutorial/master/taxonomic_analysis/code/pvclust_bcdist.R. (Accessed 4 November 2019).

Gunton, L.M., Neal, L., Gooday, A.J., Bett, B.J., Glover, A.G., 2015. Benthic polychaete diversity patterns and community structure in the Whittard Canyon system and adjacent slope (NE Atlantic). Deep Sea Res. Oceanogr. Res. Pap. 106, 42–54.

Hinojosa, J.L., Moy, C.M., Stirling, C.H., Wilson, G.S., Eglinton, T.I., 2014. Carbon cycling and burial in New Zealand's fjords. G-cubed 15, 4047–4063. https://doi.org/10.1002/2014gc005433.

Holte, B., 1998. The macrofauna and main functional interactions in the sill basin sediments of the pristine holandsfjord, Northern Norway, with autecological reviews for some key-species. Sarsia 83, 55–68. https://doi.org/10.1080/00364827.1998.10413669.

Holte, B., Oug, E., Dahle, S., 2005. Soft-bottom fauna and oxygen minima in sub-arctic north Norwegian marine sill basins. Mar. Biol. Res. 1, 85–96. https://doi.org/10.1080/17451000510019033.

Husa, V., Kutti, T., Ervik, A., Sjøtun, K., Hansen, P.K., Aure, J., 2014. Regional impact from fin-fish farming in an intensive production area (Hardangerfjord, Norway). Mar. Biol. Res. 10 (3), 241–252.

Johansen, P.O., Isaksen, T.E., Bye-Ingebrigtsen, E., Haave, M., Dahlgren, T.G., Kvalø, S. E., et al., 2018. Temporal changes in benthic macrofauna on the west coast of Norway resulting from human activities. Mar. Pollut. Bull. 128, 483–495.

Jordà Molina, È., Silberberger, M.J., Kokarev, V., Reiss, H., 2019. Environmental drivers of benthic community structure in a deep sub-arctic fjord system. Estuar. Coast Shelf Sci. 225, 106239.

Jumars, P.A., Dorgan, K.M., Lindsay, S.M., 2015. Diet of worms emended: an update of polychaete feeding guilds. Annu. Rev. Mar. Sci. 7, 497–520.

Kędra, M., Włodarska-Kowalczuk, M., Węsławski, J.M., 2010. Decadal change in macrobenthic soft-bottom community structure in a high Arctic fjord (Kongsfjorden, Svalbard). Polar Biol. 33 (1), 1. https://doi.org/10.1007/s00300-009-0679-1.

Kordas, R.L., Harley, C.D., O'Connor, M.I., 2011. Community ecology in a warming world: the influence of temperature on interspecific interactions in marine systems. J. Exp. Mar. Biol. Ecol. 400 (1–2), 218–226.

Kutti, T., Hansen, P.K., Ervik, A., Høisæter, T., Johannessen, P., 2007. Effects of organic effluents from a salmon farm on a fjord system. II. Temporal and spatial patterns in infauna community composition. Aquaculture 262 (2–4), 355–366.

Larsen, L.H., 1997. Soft-bottom macro invertebrate fauna of North Norwegian coastal waters with particular reference to sill-basins. Part one: bottom topography and species diversity. In: Interactions and Adaptation Strategies of Marine Organisms. Springer, Dordrecht, pp. 101–113.

Mamouridis, V., Cartes, J.E., Parra, S., Fanelli, E., Salinas, J.S., 2011. A temporal analysis on the dynamics of deep-sea macrofauna: influence of environmental variability off Catalonia coasts (western Mediterranean). Deep Sea Res. Oceanogr. Res. Pap. 58 (4), 323–337.

McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290–297. https://doi.org/10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2.

McGovern, M., Poste, A., Oug, E., Renaud, P.E., Trannum, H.C., 2020. Riverine impacts on benthic biodiversity and functional traits: a comparison of two sub-Arctic fjords. Coast. Shelf Sci. 106774. Estuarine.

Myksvoll, Mari S., Sundby, Svein, Ådlandsvik, Bjørn, Vikebø, Frode B., 2011. Retention of coastal cod eggs in a fjord caused by interactions between egg buoyancy and circulation pattern. Mar. Coast. Fish. 3 (1), 279–294. https://doi.org/10.1080/19425120.2011.595258.

Neira, Carlos, Höpner, Thomas, 1994. The role of Heteromastus filiformis (Capitellidae, Polychaeta) in organic carbon cycling. Ophelia 39 (1), 55–73. https://doi.org/10.1080/00785326.1994.10429902.

Oug, Eivind, 2000. Soft-bottom macrofauna in the high-latitude ecosystem of Balsfjord, northern Norway: species composition, community structure and temporal variability. Sarsia 85 (1), 1–13. https://doi.org/10.1080/00364827.2000.10414551.

R Development Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Reigstad, M., Wassmann, P., Ratkova, T., Arashkevich, E., Pasternak, A., Øygarden, S., 2000. Comparison of the springtime vertical export of biogenic matter in three northern Norwegian fjords. Mar. Ecol. Prog. Ser. 201, 73–89. https://doi.org/10.3354/meps201073.

Rice, D.L., Rhoads, D.C., 1989. Early diagenesis of organic matter and the nutritional value of sediment. Ecology of Marine Deposit Feeders. Springer, New York, NY, pp. 59–97.

Robinson, R.S., Kienast, M., Albuquerque, A.L., Altabet, M., Contreras, S., Holz, R.D., Yang, J.Y., 2012. A review of nitrogen isotopic alteration in marine sediments. Paleoceanography 27, PA4203. https://doi.org/10.1029/2012pa002321.

Rosenberg, R., Hellman, B., Lundberg, A., 1996. Benthic macrofaunal community structure in the Norwegian Trench, deep Skagerrak. J. Sea Res. 35 (1–3), 181–188.

Rullkötter, J., 2006. Organic matter: the driving force for early diagenesis. In: Schulz, H. D., Zabel, M. (Eds.), Marine Geochmistry, second ed. Springer, Berlin Heidelberg New York, pp. 125–168. https://doi.org/10.1007/3-540-32144-6_4.

Rygg, B., Norling, K., 2013. Norwegian Sensitive Index (NSI) for Marine Macro Invertebrates, and an Update of Indicator Species Index (ISI). NIVA report SNO 6475-2013. 48 s.

Scheiner, S.M., Chiarucci, A., Fox, G.A., Helmus, M.R., McGlinn, D.J., Willig, M.R., 2011. The underpinnings of the relationship of species richness with space and time. Ecol. Monogr. 81 (2), 195–213.

Sepúlveda, J., Pantoja, S., Hughen, K.A., 2011. Sources and distribution of organic matter in northern Patagonia fjords, Chile (∼ 44–47 S): a multi-tracer approach for carbon cycling assessment. Continent. Shelf Res. 31 (3–4), 315–329.

Silberberger, M.J., Renaud, P.E., Kröncke, I., Reiss, H., 2018. Food-web structure in four locations along the European shelf indicates spatial differences in ecosystem functioning. Front. Mar. Sci. 5, 119. https://doi.org/10.3389/fmars.2018.00119.

Silberberger, M.J., Renaud, P.E., Buhl-Mortensen, L., Ellingsen, I.H., Reiss, H., 2019. Spatial patterns in sub-Arctic benthos: multiscale analysis reveals structural differences between community components. Ecol. Monogr. 89 (1), e01325 https://doi.org/10.1002/ecm.1325.

Skreslet, S., 2002. Miljøundersøkelse i Skjerstadfjorden. I. Resultater fra måleprogrammet. Avdeling for fiskeri- og naturfag, Høgskolen i Bodø. HBO-rapport 2/2002. (In Norwegian).

Skreslet, S., Olsen, K., Mohus, Å., Tande, K.S., 2000. Stage-specific habitats of Calanus finmarchicus and Calanus helgolandicus in a stratified northern Norwegian fjord. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 57 (6), 1656–1663.

Smeaton, C., Austin, W.E.N., 2017. Sources, sinks, and subsidies: terrestrial carbon storage in mid-latitude fjords. J. Geophys. Res.: Biogeosciences 122, 2754–2768. https://doi.org/10.1002/2017jg003952.

Somerfield, P.J., Dashfield, S.L., Warwick, R.M., 2018. The structure and organisation of integral marine benthic communities in relation to sieve mesh size. J. Exp. Mar. Biol. Ecol. 502, 164–173.

Syvitski, J.P.M., Burrell, D.C., Skei, J.M., 1987. Fjords: Processes and Products. Springer-Verlag, New York, p. 379.

Thompson, B.W., Riddle, M.J., Stark, J.S., 2003. Cost-efficient methods for marine pollution monitoring at Casey Station, East Antarctica: the choice of sieve mesh-size and taxonomic resolution. Mar. Pollut. Bull. 46 (2), 232–243.

Thomsen, E., Vorren, T.O., 1986. Macrofaunal palaeoecology and stratigraphy in late Quaternary shelf sediments off Northern Norway. Palaeogeogr. Palaeoclimatol. Palaeoecol. 56 (1–2), 103–150.

Wassmann, P., Svendsen, H., Keck, A., Reigstad, M., 1996. Selected aspects of the physical oceanography and particle fluxes in fjords of northern Norway. J. Mar. Syst. 8 (1–2), 53–71.

Wild, C., Røy, H., Huettel, M., 2005. Role of pelletization in mineralization of fine-grained coastal sediments. Mar. Ecol. Prog. Ser. 291, 23–33.

Włodarska-Kowalczuk, M., Renaud, P.E., Węsławski, J.M., Cochrane, S.K., Denisenko, S. G., 2012. Species diversity, functional complexity and rarity in Arctic fjordic versus open shelf benthic systems. Mar. Ecol. Prog. Ser. 463, 73–87.

Włodarska-Kowalczuk, M., Mazurkiewicz, M., Górska, B., Michel, L.N., Jankowska, E., Zaborska, A., 2019. Organic carbon origin, benthic faunal consumption and burial in sediments of northern Atlantic and Arctic fjords (60-81 0N). J. Geophys. Res.: Biogeosciences 124. https://doi.org/10.1029/2019JG005140.

Yang, Z., Liu, X., Zhou, M., Ai, D., Wang, G., Wang, Y., et al., 2015. The effect of environmental heterogeneity on species richness depends on community position along the environmental gradient. Sci. Rep. 5 (1), 1–7.

Zaborska, A., Włodarska-Kowalczuk, M., Legeżyńska, J., Jankowska, E., Winogradow, A., Deja, K., 2018. Sedimentary organic matter sources, benthic consumption and burial in west Spitsbergen fjords – signs of maturing of Arctic fjordic systems? J. Mar. Syst. 180, 112–123. https://doi.org/10.1016/J.JMARSYS.2016.11.005.

Paper III

Combining species and biological trait composition to assess macrobenthic community assembly in deep sub-Arctic fjords

Valentin Kokarev[1*], Eivind Oug[2] and Henning Reiss[1]

[1] Faculty of Biosciences and Aquaculture, Nord University, 8049 Bodø, Norway

[2] Norwegian Institute for Water Research (NIVA), Oslo, Norway

[*]Corresponding author: valentin.kokarev@nord.no

Abstract

Ecosystem properties, such as functioning and stability, are often linked to biodiversity. At small scales, biodiversity is determined by community assembly of local communities. Biodiversity can be perceived from a taxonomic point of view as the number and relative abundances of species coexisting in a local community and from a functional point of view as the range of functional niches occupied by these species. Biological traits expressed by species might serve as a proxy between the two approaches as they are related to resource use and, consequently, a functional niche of a species. There is a major gap in knowledge on macrobenthic diversity and community assembly in deep sub-Arctic fjords that limits our understanding of ecosystem processes in these depositional habitats. We studied eight deep (>290 m) sub-Arctic basins in northern Norway to assess the community differentiation of neighbouring fjords based on species and biological trait composition. There was a significant difference in macrobenthic community structure between shallow-silled and deep-silled fjords, which were characterised by distinct bottom water masses. Moreover, further differentiation was observed among fjords with similar levels of water exchange with surrounding waters on a basin scale. Biological trait composition revealed that, generally, basins with a shallow sill have a higher proportion of deep-dwelling subsurface deposit feeding fauna, indicating differences in benthic functioning. We suggest that differentiation on a basin scale with regard to species composition results from stochastic community assembly, low connectivity among basins, and particularly presence of dispersal barriers, such as a shallow sill, while water exchange with surrounding waters mediates organic matter fluxes to the seafloor and, consequently, the functional structure of macrobenthos.

1 Introduction

Understanding the processes underlying species composition and abundance within ecological communities is one of the fundamental problems in ecology. Fjord basin species communities could serve as models for studying community assembly in marine macrobenthos as the borders of this habitat are well-defined due to enclosure by land and presence of sills at the fjord mouth, which can limit exchange processes with the offshore environment. Several environmental drivers, such as organic enrichment, hypoxia and enhanced sedimentation from river/glacier runoff, have been documented to influence macrobenthic communities within fjord ecosystems (e.g. Pearson and Rosenberg, 1978; Diaz and Rosenberg, 1995; Wlodarska-Kowalczuk and Pearson, 2004; McGovern et al., 2020). The above-mentioned environmental drivers often cause instability and lead to habitat deterioration, reflected in decreased species diversity of fjord communities compared to the open shelf (Włodarska-Kowalczuk et al., 2012). Habitat deterioration can create unfavourable abiotic conditions for some of the potential benthic colonizers leading to the absence of these species in the community, a process often referred to as “environmental filtering” (Kraft et al., 2015). Apart from environmental filtering, many factors can potentially influence species richness, including environmental heterogeneity, biotic interactions and dispersal limitations (Brown et al., 2016; Scheiner et al., 2011; Hart et al., 2017). Accordingly, several hypotheses were proposed to explain the reduced diversity of fjord communities compared to offshore habitats: more homogenous sediment composition, competitive dominance of opportunistic species due to higher organic matter content and limited dispersal due to a shallow sill (Buhl-Mortensen and Hoisaeter, 1993). Fjords, particularly with deep basins, are often regarded as subsets of deep-sea fauna or “mini-oceans” (Brattegard, 1980). Therefore, fjord basins might be perceived as smaller deep-sea patches, where, potentially, species richness is more influenced by isolation and stochastic processes such as disturbance and population dynamics compared to larger habitats (“small island effects”; Lomolino, 2000). Such a view, for instance, is in accordance with data from a deep-fjord system in New Zealand, where basin-scale processes including disturbance and local connectivity were identified as major drivers (Brewin et al., 2011).

While the majority of studies focus on local diversity, among-fjord variation in species composition might be critical to understand biodiversity organization and assembly of these communities (Mori et al., 2018), but such data are largely lacking. Geomorphology of fjords suggests that community patches, or local communities, can correspond to basin topography. Therefore, closely situated basins can be considered a metacommunity, an approach recently proposed for studying macrobenthic communities (Corte et al., 2018). A metacommunity can be defined as a set of local communities connected via dispersal of multiple potentially interacting species (Leibold et al., 2004; Heino et al., 2015). In such a framework, the importance of local processes such as environmental filtering and competitive exclusion on community assembly is mediated by dispersal. Particularly high dispersal might result in the homogenization of local communities (Mouquet and Loreau, 2003). In fjord systems, the connectivity of neighbouring patches is constrained not only by dispersal abilities of species, but also by sill depth, as it limits water exchange, and consequently potential exchange of larvae and adults. In smaller and isolated habitats, niche-based processes such as environmental filtering and competitive exclusion can be overridden by stochastic processes such as fluctuations in population size (ecological drift) (Orrock and Watling, 2010; Chase and Myers, 2011;). High variation in community composition among environmentally similar sites can also be established due to differences in colonization history in habitats with low disturbance and a rich regional pool of species (“priority effects”; Chase, 2003; Fukami, 2015). This is particularly interesting, as species turn-over among closely situated fjords in New Zealand was related to habitat age (time it became available for colonization), indicating the importance of historical processes on community assembly (Smith, 2001). Thus, in fjords, where disturbance events such as enhanced sedimentation or hypoxia are absent, species community assembly might be dominated by stochastic, rather than deterministic processes.

Biological traits, expressed by species, are important to understand the link between functional and taxonomic structure of local communities as they provide information on resource use of species. Functional composition might be less driven by dispersal limitations compared to species composition, providing a different view on community assembly; moreover, traits associated with dispersal abilities can be incorporated in the analysis (Fukami et al., 2005; Weiher et al., 2011). In macrobenthic ecology, biological traits related to morphology, behaviour and life history are used to assess community functional structure (e.g. Bremner et al., 2006; Degen et al., 2018). Species with similar traits belong to the same functional guild, i.e. group of ecologically similar species that utilise resources in similar ways (Götzenberger et al., 2012). Resource partitioning and competition can be expected to be the highest among species from the same functional guild. The distribution of species among functional guilds further allows is related to functional redundancy, an attribute that expresses to which degree different species perform similar functions in a community. High functional redundancy is generally considered as insurance for maintained ecosystem functioning in cases of biodiversity loss (Naeem, 1998; Walker et al., 1999; Diaz and Cabido, 2001; Bellwood et al., 2003; Hooper et al., 2005). High redundancy would indicate that ecosystem functions are robust to environmental change or in case of perturbations, are able to revert to previous states (resilience). Low functional redundancy, on the other side, implies a risk that functions get lost in cases of species losses, but at the same time might ensure higher adaptability to changed environmental conditions (Diaz and Cabido, 2001). Determining the relationships between taxonomic diversity and functional diversity can be used as proxies to assess functional redundancy and susceptibility of community functioning to species loss (Micheli and Halpern, 2005).

Sub-Arctic fjords in the Vestfjord region are generally deep, in most cases rather narrow, and more or less separated from the coastal waters outside by sills of varying depths. Studies of the benthic macrofauna have shown that the distribution of the communities is largely restricted to a specific fjord/basin (Jordà Molina et al., 2019; Kokarev et al., 2021). These communities have pronounced differences in structure and composition. Basins with shallower sills are characterised by colder and less saline bottom water masses, indicating restricted water exchange, while biological data indicates that inhabiting communities might be more adapted to degraded food supply (Jordà Molina et al., 2019; Kokarev et al., 2021). Macrobenthic communities in basins with sufficient water exchange and similar bottom water masses shared some dominant species but still differed in their structure, and this among-basin variation cannot be sufficiently explained by differences in measured sediment parameters or topography (depth) (Kokarev et al., 2021). In the present study, we further explore macrobenthos of sub-Arctic fjords on a larger dataset by combining species and trait composition. The main objective is to assess how biological characteristics and functional attributes, in particular, can contribute to explaining differences among basin communities. The objective included addressing the following questions: do fjords with different species compositions also differ in biological trait composition (dominant functional guilds); and what is the functional redundancy (number of species with similar traits) of these communities? The present study will contribute to understanding the scale of community assembly in fjord species communities, and consequently, ecosystem functioning in fjords (Mori et al., 2018).

2 Materials and methods

2.1 Study area

In our study, we used data for eight sub-Arctic fjord basins located in the Vestfjord region, northern Norway (Figure 1, Table 1, Supplementary Table 1). The fjords in the area are characterised by relatively deep basins, stable bottom water masses throughout a year and fine-grained sediments with organic matter of mainly marine origin, although some increases in terrestrial organic matter input are observed in more inland basins (Faust and Knies, 2019; Kokarev et al., 2021).

The studied fjords were divided into two categories based on sill depth at the entrance of the fjord basins. Deep-silled (> 200 m) basins (Saltfjord, Sørfolda, Tysfjord deep, Tysfjord middle) are characterised by bottom water temperatures >7° C and salinity >35 indicating regular inflow of Atlantic water masses (Table 1). Shallow-silled basins (Skjerstadfjord, Nordfjord, Mistfjord, Tysfjord innermost) were distinguished by lower temperatures and salinities, indicating a limited water exchange. However, relatively low oxygen saturation was observed only in Tysfjord innermost basin, indicating that in some fjords with shallow sills the bottom water renewal is a more episodic event. In Skjerstadfjord, another fjord with a shallow sill, the bottom water layer is regularly supplied with surface waters from Saltfjord on rising tide due to turbulent mixing of inflowing water and density differences (Kokarev et al., 2021). Contrary, basin water renewal in Mistfjord happens at decadal intervals (Skreslet et al., 2020). Stations located just outside several basins (Saltfjord; Sørfolda; Tysfjord) were treated as a part of the concerning fjord basin as community structure did not significantly differ from the main basin communities (Jordà Molina et al., 2019; Kokarev et al., 2021).

2.2 Collection of fauna

Samples were collected by an 0.1 m^2 Van Veen grab. The grab samples were sieved on a 1 mm mesh on board and subsequently fixed with 4% formaldehyde buffered with borax. In the lab, animals were sorted, identified to the lowest taxon possible, counted, weighed (wet weight) to the nearest 0.1 mg, and stored in 70% ethanol. No biomass data were available for Nordfjord as some larger animals were dissected upon collection for fatty acid and stable isotope analysis as part of a separate study. The complete species list is available as Supplementary Table 2.

2.3 Biological traits

For analysis of trait composition and functional diversity, species were assigned to seven traits using a fuzzy coding approach (Table 2). Six traits representing morphology and behaviour (‘Adult life habit’, ‘Mobility’, ‘Body design’, ‘Feeding habit’, ‘Normal adult size’ and ‘Position in sediment’) and subdivided into 29 categories (modalities) were used to describe functional guilds of benthic invertebrates. One trait (‘Larval type’) with two modalities was used to assess larval dispersal. The trait data were obtained from the NIVA database (Oug et al., 2012) and various literature sources (see Supplementary Table 4). For ‘Larval type’, where direct observations of deep-water macrofauna are scarce, we used the classification from Josefson (1985): planktotrophs with wide dispersal capabilities and lecithotrophs with either direct development or short-range dispersal with near-bottom currents. The affinities for a specific modality were assigned the following way: 3-exclusive, 2-moderate, 1-low. In case of missing information zero values were assigned. The trait ‘Larval type’ was missing information for about one-third of taxa and was excluded from the analysis of functional structure. For the subsequent analyses, traits were standardised to equal 1 per each trait for one species.

2.4 Data analyses

All statistical analyses were performed in R (version 3.6.1; R Development Core Team, 2019) and Primer 7 (Clarke and Gorley, 2015). Prior to multivariate analyses of species composition, data for abundance and biomass were recalculated to relative proportions by standardising by sample total. Abundance data were subsequently square root transformed and biomass data were fourth root transformed. More powerful transformation (fourth root) was used for biomass data as the magnitude of difference among different species was much higher compared to abundances. Bray-Curtis coefficient (Bray and Curtis, 1957) was used to calculate the similarity matrix based on transformed abundance and biomass. In addition, Sørensen coefficient (Sørensen , 1948) was used to calculate similarity based on presence/absence data. Similarity matrices were visualised using nMDS. One-way factor analysis was performed using PERMANOVA and ANOSIM in conjunction with tests for differences in dispersions PERMDISP (Anderson et al., 2008). Community structure based on species composition has been addressed for most fjords in previous studies (Jordà Molina et al., 2019; Kokarev et al., 2021) and is here only briefly presented.

For the analysis of the functional community composition, square root transformed abundance and fourth root transformed biomass values were multiplied by species affinities across all traits and summarised within stations. The resulting “Stations x Traits” matrix was standardised by each trait and used for Fuzzy Correspondence Analysis (FCA) in the ade4 package (Dray and Dufour, 2007). One-way factor analyses were performed using PERMANOVA and ANOSIM in conjunction with PERMDISP tests for differences in dispersions based on Euclidian distances among the stations in the first two axes of FCA.

Total species number (S) and Shannon index (H’, using log base e) were used to describe species richness and species diversity. We used Functional dispersion (Fdis) as a measure of functional diversity, which was calculated using R package FD (Laliberté and Legendre, 2010). Fdis calculates functional diversity as multivariate dispersion in the traits space, where individual distances of species to the centroid are weighted by their relative abundance. For calculation of Fdis, the species traits matrix was standardised using “prep.fuzzy.var()” in the package ade4. Subsequently, Fdis was calculated in two steps: first, a Gower dissimilarity matrix for species based on six traits (excluding ‘Larval type’) was calculated using R package ade4, which allows for fuzzy coded data. The values in the dissimilarity matrix range from 0 (the same functional guild and high niche overlap) to 1 (no niche overlap). The resulting dissimilarity matrix was used to calculate Fdis using the package FD. We used 1-Fdis/H’ ratio to assess functional redundancy of the communities among different basins: whenever this index decreases, the functional redundancy decreases (van der Linden et al., 2016). To test the differences in species richness, species diversity, functional diversity and functional redundancy among the basins we performed Kruskal-Wallis test with subsequent post-hoc comparisons (with Holm correction) using function “boxplerk()” (Borcard et al., 2018). In addition, we performed linear regression of Fdis on H’, where a strong linear relationship with a slope close to 1 would indicate low functional redundancy (Micheli and Halpern, 2005). Such an approach was used to assess a larger scale pattern in the studied fjords. Before the regression, indexes were normalised (subtracted the mean and divided by standard deviation).

3 Results

3.1 Community structure based on species composition

In total 209 taxa were recorded in the fjord basins. The highest number of taxa was found in Sørfolda (123) whereas the lowest number was found in Mistfjord (15). The differentiation of macrobenthic communities among fjord basins based on species composition was evident from the ordination diagrams (Figure 2). Both tests of PERMANOVA and ANOSIM indicated a significant effect of the factor "basin" (Table 3). PERMDISP was also significant, indicating that the results of the analyses were influenced by the heterogeneity of dispersions. However, although higher dispersions were obvious for Saltfjord and Skjerstadfjord from ordination diagrams, no overlapping among samples from different basins was observed, suggesting that PERMANOVA and ANOSIM results were not due to dispersion effects. There was also a significant difference between fjords with deep and shallow sills (Table 3). Moreover, 39 taxa were recorded only in shallow-silled basins, and 92 only in deep-silled basins. Further details on species composition and dominant species are given in Jordà Molina et al. (2019), Kokarev et al. (2021), and Supplementary tables 2 (recorded species in basins) and 3 (dominant species for each basin).

3.2 Community structure based on trait composition

The first two axes of the FCA analysis based on abundance explained a slightly higher percentage of total variation compared to the analysis based on biomass (54% vs. 42%, Table 4). The separation of different fjord basins was also more evident from the ordination diagram based on abundance (Figure 3A), where the first axis (31%) highlighted differences between shallow-silled basins located on the left (Skjerstadfjord, Mistfjord, Tysfjord inner basin) and deep-silled basins located on the right of the axis (Saltfjord, Sørfolda, Tysfjord deep, Tysfjord middle). Interestingly, Nordfjord grouped with deep-silled basins, but with 120m it has the deepest sill among the shallow-silled fjords (Table 1). The separation according to sill depth was mainly associated with 'Feeding habit' and 'Position in sediment' traits, and to less degree with 'Mobility' and 'Body design'. More common traits in the shallow-silled basins included: mobile (M1), subsurface deposit and symbiont feeding (FH3, FH6), articulate or heart-shaped test body design (BD5, BD7) and deep infaunal position in sediments (PS3) (Figure 3A). The second axis of FCA based on abundance (23%) accentuated differences in 'Body design' between Saltfjord and the rest of deep-silled fjords. The results of FCA based on biomass were similar in terms of the main traits responsible for the variation in the dataset (Table 4). However, the separation of the fjord basins appeared less clear due to the high dispersion of the Saltfjord stations (Figure 3B). PERMANOVA and ANOSIM indicated a significant separation of the basins based on trait composition (Table 5), although results were potentially influenced by heterogeneity of dispersions, same as with species composition.

The differences highlighted by FCA were also evident from abundance-weighted distribution of traits (Figure 4). The fjords are generally inhabited by shallow infaunal discretely mobile burrowers, which are either polychaetes or bivalves (AH4, M2, BD1, BD2; Figure 4). Fjords with deep sills along with Nordfjord have higher proportion of suspension and surface deposit feeders (FH1 and FH2), while shallow-silled fjords have a higher proportion of subsurface deposit feeders (FH6), especially in Skjerstadfjord, where also deeper burrowing infauna (PS3) was observed. Although a different number of species was recorded in each basin (see below), the proportion of species with different larval types was very similar among the fjord basins with lecithotrophic type being considerably more common (Figure 5).

3.3 Diversity and functional redundancy

Apart from their different community structure, the fjord basins were characterised by significantly different levels of species richness (S), species diversity (expressed as H'), functional diversity (expressed as functional dispersion Fdis) and functional redundancy (expressed as 1-Fdis/H' ratio) (Figure 6). Sørfolda, Tysfjord middle basin and Nordfjord had the highest species richness and species diversity. The differences in functional diversity were less pronounced, with only Sørfolda having significantly higher functional diversity among all the fjords. The lowest functional redundancy (high values of 1-Fdis/H') was observed for Mistfjord and Saltfjord, where the lowest number of species was recorded.

Both shallow- and deep-silled fjords showed a similar pattern in their relationship between species diversity and functional diversity (Figure 7). However, at higher levels of species diversity, deep-silled fjords showed generally higher functional diversity. Only a moderate linear relationship was observed, indicating that at some point increase in species diversity does not lead to an increase in functional diversity. Moreover, the linear relationship was weaker for shallow-silled fjords, indicating less dependence of functional diversity on species diversity.

4 Discussion

Previous studies of sub-Arctic silled fjords in Northern Norway have indicated that the macrobenthic communities in fjord basins differ among fjords with basin-specific species composition (Jordà Molina et al., 2019; Kokarev et al., 2021). This is supported by the extended analyses of the data in this study including previously unpublished data on Mistfjord and Nordfjord. The traits analyses have indicated that the fjord basins were different also with regard to biological trait composition. Interestingly, the shallow-silled Nordfjord had clearly different species composition from deep-silled fjords yet showed convergence in trait composition with them. Species composition might be more driven by history of community assembly, while trait composition might reflect more the adaptation of community to the environment (Fukami et al., 2005; McLean et al., 2019). Thus, environmental conditions in Nordfjord might be more similar to deep-silled basins due to relatively deep sill. The functional diversity was roughly similar among most basin communities, though with the highest diversity among deep-silled basins. However, the functional redundancy varied among fjord basins. The variation largely corresponded with the variation in species diversity, indicating that higher numbers of species did not necessarily lead to more functionally diverse communities.

4.1 Community assembly

The most evident difference in community structure was observed between shallow-silled and deep-silled fjords both for species and traits composition. The deep-silled fjords are characterised by good water exchange with surrounding waters, that allow for inflow of warmer and more saline Atlantic waters and, potentially more frequent episodes of advection in and out of the fjords. Advection of nutrients, phytoplankton and zooplankton from adjacent waters plays a vital role in fjord ecosystem, shaping the patterns of productivity and bentho-pelagic coupling, thus playing important role in the carbon flux to the seafloor (Aksnes et al., 1989; Wassmann et al., 1996; Reigstad et al., 2000; Skogen et al., 2009). The differentiation between the two groups of fjord basins was mainly associated with traits of macrofauna 'Feeding habit' and 'Position in sediments', with deep-silled fjords (along with Nordfjord that has the deepest sill of shallow-silled basins) having a higher proportion of surface deposit or suspension feeding and shallow infauna species, while in shallow-silled fjords subsurface deposit feeding and deep burrowing species were predominant in the sediment. Populations of subsurface deposit feeders might feed on more refractory microbially degraded sediment organic matter, and, in general, their populations show less temporal variation in response to episodic inputs of high-quality detritus (Rice and Rhoads, 1989; Josefson et al., 2002; Levinton and Kelaher, 2004). This indicates that with decreasing sill depth the accessibility of freshly deposited or resuspended organic matter for the macrobenthos decreases. Thus, the principal difference of organic matter supply to the seafloor has probably played a role in structuring the composition of macrobenthos. However, the measured sediment variables, such as total organic carbon and total nitrogen as well as their stable isotopic values, did not explain much of the among-fjord variation, but only one shallow-silled fjord was studied (Kokarev et al., 2021). This might be due to the fact that single measurements provide only limited insight into dynamics (e.g. vertical fluxes of organic matter to the seafloor) of an ecosystem as the sediments samples provide information on organic matter integrated over periods of months or years (Burrell, 1988). Most probably when supply of fresh organic matter is limited or more episodic, less resources are available for surface-deposit feeders as well as suspension feeders, such as *Kelliella miliaris*, which is particularly abundant in the deep basin of Tysfjord. Species, associated with sulphur oxidising bacteria, such as *Siboglinum ekmani*, *Thyasira sarsii* and *Parathyasira equalis* (Southward et al., 1981*;* Dando and Spiro, 1993), were relatively more abundant in shallow-silled basins, which might reflect different biogeochemical processes in the sediments resulting in increased sulphide concentrations. The similarities in traits composition among fjords with similar water exchange suggest that they comprise similar environmental settings.

The observed discrepancy between analyses based on species and trait compositions was mainly associated with Nordfjord community. As mentioned previously, species composition might be more influenced by the history of community assembly. The historical processes with respect to fjord communities might reflect their colonization from an offshore pool of species after deglaciation (Smith, 2001). After deglaciation, fjords of Northern Norway were first colonized by Arctic fauna, which was subsequently replaced with boreal fauna after the inflow of relatively warm Norwegian Atlantic Current and the modern assemblages established 7800 years BP (Thomsen and Vorren, 1986). Possibly, both events may have contributed to the present species composition in the basin communities. Many species were recorded only in deep-silled basins, and some were restricted to shallow-silled basins. This might indicate that boreal species, that came with the warm Atlantic waters successfully established their populations in deep-silled basins but had limited colonization success in shallow-silled fjords. The reasons for this may be colder bottom water masses, retained in shallow-silled basins, or a limited supply of larvae/individuals, which is not enough to establish a population. It was previously suggested that a shallow sill might act as a dispersal barrier for fjords in Western Norway (Buhl-Mortensen and Høisæter, 1993). As shallow sills restrict the inflow of Atlantic water into the basin, it might have implications for the dispersal of species with bottom water masses. As previously highlighted by Josefson (1985), deep-water species that are distributed with Atlantic water masses are largely lecithotrophic, as opposed to shelf (< 200m) species. As these species, which mostly have direct or short-pelagic life stage, are distributed with near-bottom currents, they might have limited recruitment success into shallow-silled basins. This is supported by our preliminary unpublished data on population connectivity of the lecithotrophic bivalve *Parathyasira equalis,* which is widely distributed in both shallow- and deep-silled basins. Genotyping by sequencing approach revealed low but significant Fst values between shallow-silled Skjerstadfjord and deep-silled Saltfjord and Sørfolda, but not between Saltfjord and Sørfolda. Thus, a continuous population of *P. equalis* in Atlantic waters is "interrupted" by the presence of a shallow sill.

As mentioned above, shallow-silled basins retain colder water masses, and some species recorded only in shallow-silled basins (e.g. bivalves *Ennucula tenuis, Astarte crenata, Yoldiella lenticula*, scaphopod *Siphonodentalium lobatum,* gastropod *Polynices pallidus*, polychaete *Praxillella gracilis*, seastar *Ctenodiscus crispatus*) are also widely distributed in the high Arctic, indicating that even small temperature difference can affect species composition. Palaeoecological data indicates that *A. crenata, Y. lenticula, E. tenuis, C. crispatus*, and *S. lobatum* inhabited basins before the inflow of Atlantic water (Thomsen and Vorren, 1986). Such species have an upper limit of distribution at 6-7 °C, e.g., 4-6 °C for *C. crispatus* (Renaud et al., 2015), 5.8 °C for *S. lobatum* (Ivanov and Zarubina, 2004), 7 °C for *P. gracilis* (Jirkov, 2001), which corresponds to subtle difference in temperature of bottom water masses between shallow-silled and deep-silled basins (Table 1). A higher proportion of Arctic species has also been recorded in the inner fjords of Svalbard that are less influenced by Atlantic waters (Wlodarska-Kowalczuk et al., 1998). Similarly, deep basins with shallow sills might act as "biogeographical enclaves" for more northern species (Brattegard, 1980). Thus, even a small increase in temperature can potentially lead to significant community shifts in shallow-silled basins (Kordas et al., 2011).

Deep sills as such are not a barrier for dispersal: while shallow sill always corresponds to community change in a fjord system, e.g. Saltfjord and Skjerstadfjord, communities in the deep-silled fjord basins (Saltfjord, Sørfolda Tysfjord deep and

Tysfjord middle basins) have a similar species composition as the adjacent basins beyond the sill (Jordà Molina et al., 2019; Kokarev et al., 2021). Such a pattern indicates high dispersal and resulting in homogenization of communities ("mass effects"; Heino et al., 2015). However, the connectivity among different fjord systems still might be low. For instance, cod egg retention was observed for the fjords in the study area suggesting fjord scale populations of this species (Myksvoll et al., 2011; Myksvoll et al., 2014). Furthermore, genetically different populations of European lobster, a species with a long-living pelagic larva, were found in the closely situated Tysfjord and Folda fjord systems (Jørstad et al., 2004). Retention of larvae was previously suggested to be strong in fjord ecosystems structuring communities within basins (Pearson, 1980). Thus, even in absence of a dispersal barrier, such as a shallow sill, the connectivity among communities in different fjords might be limited. This results in low dispersal, and, consequently, community assembly on a local scale most likely is not influenced by supply of individuals from nearby fjord communities. Deep sub-euphotic basins with good water exchange can be considered physically and chemically stable environments, where carbon fluxes to the seafloor might be the liming factor for benthic populations (Burrell, 1988). The interannual differences in carbon fluxes might largely exceed the differences among closely situated fjords (Reigstad et al., 2000). Therefore, it may be assumed that the inhabitant communities are adapted to some extent to varying organic matter input. Indeed, the position on the first FCA axis suggests very similar dominant functional guilds for Saltfjord, Sørfolda and Tysfjord middle basin. However, in Tysfjord deep basin suspension feeders are more common, which might indicate higher near-bottom flow that gives an advantage to suspension feeders (Snelgrove and Butman, 1994). But based on species composition the pattern of community differentiation on a basin scale is evident even from presence/absence data suggesting that the differences in deep-silled communities are not merely a response to different environments, but rather independently developed communities where colonization history from an offshore pool of species might have contributed as well to the observed differences, as suggested by Smith (2001). The retention of larvae within basins, mentioned earlier, might give an advantage to species that established their populations first. Such priority effects are more likely to happen when local communities are assembled from a large stable pool of species in a way proposed by mainland-island community assembly (Fukami, 2015). The inflow of Atlantic water might connect smaller fjord basins with deeper habitats offshore, which might act as pools of species.

All things considered; our data indicate that community distribution in basins reflects patterns of local connectivity. Furthermore, connectivity to the offshore pool species mediated by Atlantic water inflow has a pronounced effect on community assembly in terms of species composition and structure. Generally, differences in trait composition were less pronounced but still evident on a basin scale. Therefore, trait composition might reflect not only adaptations to the environment, particularly to differences in organic matter inputs to sediment but also differences in resource partitioning of the established populations in accordance with limiting similarity concept (Götzenberger et al., 2012). Combination of stable isotope and fatty acid analyses revealed distinct trophic niches even among species with similar feeding habits in Nordfjord, corroborating that resource partitioning might be an important structuring factor on a basin scale (unpubl. data).

4.2 Diversity and functional redundancy

There were more pronounced differences among fjord basins in species diversity than in functional diversity. In communities, where multiple species perform the same function, the relationship between functional and species diversity can be non-linear, first increasing rapidly at low levels of species diversity and then increasing at declining rates as functional space reaches saturation (Micheli and Halpern, 2005). Although the shape of the relationship appeared to be similar between two groups of fjords, shallow-silled fjords appeared to have higher functional diversity at low species diversity, while deep-silled fjords showed higher functional diversity at higher levels of species diversity. That allows to assume that more niches are available in deep-silled fjords. However, at a certain level of species diversity, further increase does not lead to an increase in functional diversity, indicating that multiple species possess the same traits and, consequently, high functional redundancy at high species diversity.

Functional redundancy is related to the number of species in a basin: Saltfjord and Mistfjord were characterised by the lowest functional redundancy, and also by the lowest number of species. Many biotic and abiotic factors can influence species richness on a small scale (Brown et al., 2016). It may be assumed, that in a very small basin such as Mistfjord, the resources are limited allowing only a few species to coexist. Another reason for lower species richness may be hypoxia that would result in environmental filtering of macrofaunal species that are adapted to low oxygen concentration. Hypoxia is usually defined starting at 2 ml/l (Diaz and Rosenberg, 1995); however, oxygen concentrations in the Mistfjord basin is generally over 3 ml/l, although the lowest value recorded was 1.77 ml/l (Skreslet et al., 2020). However, in Tysfjord inner basins also relatively low oxygen levels were observed, yet species richness was not different from Skjerstadfjord with good water exchange. Therefore, the importance of hypoxia for shallow-silled basins should be further studied. Relatively low diversity in Saltfjord compared to other deep-silled fjords cannot be explained by smaller basin area and might reflect stochasticity during community assembly that resulted in establishment of fewer species and might represent the consequences of small island effects.

Some fjords showed relatively high functional redundancy, which can be considered as insurance for maintaining ecosystem functions after species loss (Micheli and Halpern, 2005). Thus, functional redundancy becomes important when species can become locally extinct, for instance, due to population stochasticity (ecological drift) or different sensitivity to disturbances, or in other words show different levels of response diversity (Elmqvist et al., 2003). However, it is not clear if different functional redundancy would result in different responses to possible environmental changes or anthropogenic impacts. Rapid shifts in community structure were observed in basins of western Norway, where the abundances of only one species, *Polydora sp*., increased significantly in the last decade in response to increasing temperatures, organic matter content in sediments and decrease in dissolved oxygen (Johansen et al., 2018). If similar changes are to happen in northern Norway, homogenization of communities can be expected due to prevalence of few opportunistic species with high dispersal and high competitive potential in areas with organic enrichment. Human-induced homogenization of communities can significantly alter patterns of diversity, and, consequently, ecosystem functioning (Mori et al., 2018).

Overall, the fjords in the study area are characterised by distinct communities and we suggest that this pattern is a result of low connectivity among different basins, presence of shallow sills that act as dispersal barriers and stochasticity during community assembly. However, many aspects of their temporal dynamics, including diversity and abundance requires further investigation. In particular, macrobenthic communities in deep-silled fjords may be more susceptible to interannual change in the flux of organic matter to the seafloor associated with advection of water masses in and out of fjords (Wassmann et al., 1996). Moreover, it is still not clear whether the observed pattern is specific to the deep fjords in the study area, as fjords in other geographical settings can potentially exhibit more environmental filtering of the fauna, which would lead to convergence of communities both in species and traits composition.

References

Aksnes D, Aure J, Kaartvedt S, Magnesen T, Richard J (1989) Significance of advection for the carrying capacities of fjord populations. Mar Ecol Prog Ser 50:263–274.

Anderson M, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-E, Plymouth.

Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: Resilience and ecosystem function on coral reefs. Ecol Lett 6:281–285.

Borcard D, Gillet F, Legendre P (2018) Numerical ecology with R. Springer.

Brattegard T (1980) Why biologists are interested in fjords. In: Freeland HJ, Farmer DM, Levings C (eds) Fjord Oceanography. Plenum Press, New York and London, pp 53–66.

Bray JR, J. T. Curtis (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27:325–349.

Bremner J, Rogers SI, Frid CLJ (2006) Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecol Indic 6:609–622.

Brewin PE, Probert PK, Barker MF (2011) Relative influence of processes structuring fjord deep-water macrofaunal communities across multiple spatial scales. Mar Ecol Prog Ser 425:175–191.

Brown RL, Reilly LAJ, Peet RK (2016). Species richness: Small scale. In eLS, John Wiley & Sons, Ltd (Ed.).

Buhl-Mortensen L, Hoisaeter T (1993) Mollusc fauna along an offshore-fjord gradient. Mar Ecol Prog Ser 97:209–224.

Burrell DC (1988) Carbon flow in fjords. Ocean Mar Biol Annu Rev 26:143–226.

Chase JM (2003) Community assembly: When should history matter? Oecologia 136:489–498.

Chase JM, Myers JA (2011) Disentangling the importance of ecological niches from stochastic processes across scales. Philos Trans R Soc B Biol Sci 366:2351–2363.

Clarke KR, Gorley RN (2015) Getting started with PRIMER v7. PRIMER-E, Plymouth.

Corte GN, Gonçalves-Souza T, Checon HH, Siegle E, Coleman RA, Amaral ACZ (2018) When time affects space: Dispersal ability and extreme weather events determine metacommunity organization in marine sediments. Mar Environ Res 136:139–152.

Dando PR, Spiro B (1993) Varying nutritional dependence of the thyasirid bivalves Thyasira sarsi and T. equalis on chemoautotrophic symbiotic bacteria, demonstrated by isotope ratios of tissue carbon and shell carbonate. Mar Ecol Prog Ser 92:151–158.

Degen R, Aune M, Bluhm BA, Cassidy C, Kędra M, Kraan C, et al. (2018) Trait-based approaches in rapidly changing ecosystems: A roadmap to the future polar oceans. Ecol Indic 91:722–736.

Diaz RJ, Rosenberg R (1995) Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanogr Mar Biol an Annu Rev Vol 33 245–303.

Diaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trend Ecol Evol 16:646-655.

Dray S, Dufour AB (2007) The ade4 package: Implementing the duality diagram for ecologists. J Stat Softw 22:1–20.

Faust JC, Knies J (2019) Organic matter sources in North Atlantic fjord sediments. Geochemistry, Geophys Geosystems 20:2872–2885.

Fukami T (2015) Historical contingency in community sssembly: Integrating niches, species pools, and priority effects. Annu Rev Ecol Evol Syst 46:1–23.

Fukami T, Bezemer TM, Mortimer SR, Van Der Putten WH (2005) Species divergence and trait convergence in experimental plant community assembly. Ecol Lett 8:1283–1290.

Götzenberger L, de Bello F, Bråthen KA, Davison J, Dubuis A, Guisan A, et al. (2012) Ecological assembly rules in plant communities-approaches, patterns and prospects. Biol Rev 87:111–127.

Hart SP, Usinowicz J, Levine JM (2017) The spatial scales of species coexistence. Nat Ecol Evol 1:1066–1073.

Heino J, Melo AS, Siqueira T, Soininen J, Valanko S, Bini LM (2015) Metacommunity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes and prospects. Freshw Biol 60:845–869.

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, et al. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35.

Ivanov D, Zarubina E (2004) Distribution of Scaphopod molluscs in the N Atlantic and Arctic oceans based on materials of russian and Soviet expeditions. Ruthenica 1:89–104.

Jirkov IA (2001) Polychaeta of the Arctic ocean. Janus-K, Moscow.

Johansen PO, Isaksen TE, Bye-Ingebrigtsen E, Haave M, Dahlgren TG, Kvalø SE, et al. (2018) Temporal changes in benthic macrofauna on the west coast of Norway resulting from human activities. Mar Pollut Bull 128:483–495.

Jordà Molina È, Silberberger MJ, Kokarev V, Reiss H (2019) Environmental drivers of benthic community structure in a deep sub-arctic fjord system. Estuar Coast Shelf Sci 225:106239.

Jørstad KE, Paulo A. Prodöhl, Agnalta A-L, Hughes M, Apostolidis AP, Triantafyllidis A, et al. (2004) Sub-arctic populations of European lobster, Homarus gammarus, in northern Norway Knut. Environ Biol Fishes 69:223–231.

Josefson AB (1985) Distribution of diversity and functional groups of marine benthic infauna in the skagerrak (Eastern north sea) - can larval availability affect diversity? Sarsia 70:229–248.

Josefson AB, Forbes TL, Rosenberg R (2002) Fate of phytodetritus in marine sediments: Functional importance of macrofaunal community. Mar Ecol Prog Ser 230:71–85.

Kokarev V, Tachon M, Austad M, McGovern M, Reiss H (2021) Strong macrobenthic community differentiation among sub-Arctic deep fjords on small spatial scales. Estuar Coast Shelf Sci 252:107271.

Kordas RL, Harley CDG, O'Connor MI (2011) Community ecology in a warming world: The influence of temperature on interspecific interactions in marine systems. J Exp Mar Bio Ecol 400:218–226.

Kraft NJB, Adler PB, Godoy O, James EC, Fuller S, Levine JM (2015) Community assembly, coexistence and the environmental filtering metaphor. Funct Ecol 29:592–599.

Laliberte E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305.

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, et al. (2004) The metacommunity concept: A framework for multi-scale community ecology. Ecol Lett 7:601–613.

Levinton J, Kelaher B (2004) Opposing organizing forces of deposit-feeding marine communities. J Exp Mar Bio Ecol 300:65–82.

Lomolino M V. (2000) Ecology' s most general, yet protean pattern : The species-area relationship. J Biogeogr 27:17–26.

McGovern M, Poste AE, Oug E, Renaud PE, Trannum HC (2020) Riverine impacts on benthic biodiversity and functional traits: A comparison of two sub-Arctic fjords. Estuar Coast Shelf Sci 240:106774.

McLean M, Mouillot D, Lindegren M, Villéger S, Engelhard G, Murgier J, et al. (2019) Fish communities diverge in species but converge in traits over three decades of warming. Glob Chang Biol 25:3972–3984.

Micheli F, Halpern BS (2005) Low functional redundancy in coastal marine assemblages. Ecol Lett 8:391–400.

Mori AS, Isbell F, Seidl R (2018) β-Diversity, community assembly, and ecosystem functioning. Trends Ecol Evol 33:549–564.

Mouquet N, Loreau M (2003) Community patterns in source-sink metacommunities. Am Nat 162:544–557.

Myksvoll MS, Jung K, Albretsen J, Sundby S (2014) Norwegian coastal cod subpopulations. 71:957–969.

Myksvoll MS, Sundby S, Ådlandsvik B, Vikebø FB (2011) Retention of coastal cod eggs in a fjord caused by interactions between egg buoyancy and circulation pattern. Mar Coast Fish 3:279–294.

Naeem S (1998) Species redundancy and ecosystem reliability. Conserv Biol 12:39–45.

Orrock JL, Watling JI (2010) Local community size mediates ecological drift and competition in metacommunities. Proc R Soc B Biol Sci 277:2185–2191.

Oug E, Fleddum A, Rygg B, OIsgard F (2012) Biological traits analyses in the study of pollution gradients and ecological functioning of marine soft bottom species assemblages in a fjord ecosystem. J Exp Mar Biol Ecol 432-433:94-105.

Pearson T., Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr Mar Biol An Annu Rev 16:229–331.

Pearson T.H (1980) The macrobenthos of fjords. In: Freeland HJ, Farmer DM, Levings C (eds) Fjord Oceanography. Plenum Press, New York and London, pp 569–602.

R Development Core Team (2019) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Reigstad M, Wassmann P, Ratkova T, Arashkevich E, Pasternak A, Øygarden S (2000) Comparison of the springtime vertical export of biogenic matter in three northern Norwegian fjords. Mar Ecol Prog Ser 201:73–89.

Renaud PE, Sejr MK, Bluhm BA, Sirenko B, Ellingsen IH (2015) The future of Arctic benthos: Expansion, invasion, and biodiversity. Prog Oceanogr 139:244–257.

Rice DL, Rhoads DC (1989) Early Diagenesis of Organic Matter and and the Nutritional Value of Sediment. In: Ecology of Marine Deposit Feeders. pp 114–123.

Scheiner SM, Chiarucci A, Fox GA, Helmus MR, McGlinn DJ, Willig MR (2011) The underpinnings of the relationship of species richness with space and time. Ecol Monogr 81:195–213.

Skogen MD, Eknes M, Asplin LC, Sandvik AD (2009) Modelling the environmental effects of fish farming in a Norwegian fjord. Aquaculture 298:70–75.

Skreslet S, Espinasse M, Olsen K, Espinasse BD (2020) Variable predator–prey relations in zooplankton overwintering in subarctic fjords. Polar Res 39:1–17.

Smith F (2001) Historical regulation of local species richness across a geographic region. Ecology 82:792–801.

Snelgrove PVR, Butman CA (1994) Animal sediment relationships revisited – cause versus effect. Oceanogr Mar Biol 32:111–177.

Sørensen, T. J. (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons Biologiske Skrifter 5:1-34.

Southward AJ, Southward EC, Dando PR, Rau GH, Felbeck H, Flügel H (1981) Bacterial symbionts and low 13C/12C ratios in tissues of Pogonophora indicate unusual nutrition and metabolism. Nature 293:616–619.

Thomsen E, Vorren TO (1986) Macrofaunal palaeoecology and stratigraphy in late quaternary shelf sediments off Northern Norway. Palaeogeogr Palaeoclimatol Palaeoecol 56:103–150.

Van der Linden P, Marchini A, Dolbeth M, Patricio J, Verissimo H, Marques JC (2016) The performance of trait-based indices in an estuarine environment. Ecol Ind 61:378-389.

Walker B, Kinzig A, Langridge J (1999) Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. Ecosystems 2:95–113.

Wassmann P, Svendsen H, Keck A, Reigstad M (1996) Selected aspects of the physical oceanography and particle fluxes in fjords of northern Norway. J Mar Syst 8:53–71.

Weiher E, Freund D, Bunton T, Stefanski A, Lee T, Bentivenga S (2011) Advances, challenges and a developing synthesis of ecological community assembly theory. Philos Trans R Soc B Biol Sci 366:2403–2413.

Wlodarska-Kowalczuk M, Pearson TH (2004) Soft-bottom macrobenthic faunal associations and factors affecting species distributions in an Arctic glacial fjord (Kongsfjord, Spitsbergen). Polar Biol 27:155–167.

Włodarska-Kowalczuk M, Renaud PE, Węsławski JM, Cochrane SKJ, Denisenko SG (2012) Species diversity, functional complexity and rarity in Arctic fjordic versus open shelf benthic systems. Mar Ecol Prog Ser 463:73–87.

Włodarska-Kowalczuk M, Węsawski JM, Kotwicki L (1998) Spitsbergen glacial bays macrobenthos - A comparative study. Polar Biol 20:66–73.

Tables

Table 1. Summary for locations studied in this study. *In brackets the number of stations located outside the main basin. **Nordfjord is separated from adjacent Saltfjord by another 180 m deep basin with a 90 m sill. T – temperature, S – salinity, O_2 – oxygen saturation.

Site	Year of sampling	Maximum depth (m)	Depth at the entrance sill (m)	Bottom water properties			Number of samples	Number of stations*
				T (°C)	S	O_2 (%)		
Saltfjord and adjacent basin	2013	380	220	7.3	35.3	77.3-79.6	22	11 (3)
Sørfolda and adjacent basin	2015	560	260	7.0	35.3	67.7-74.2	26	13 (2)
Skjerstadfjord	2013	540	26	4.9	33.8	71-73.4	22	11
Nordfjord	2019	390	120**	6.2	34.3	90-91.4	5	5
Mistfjord	2017	294	34	5.9	34.3	75.5-88.7	4	4
Tysfjord deep and adjacent basin	2017	725	280	7.5	35.2	77-96.7	16	16 (2)
Tysfjord middle and adjacent basin	2017	375	300	7.5	35.2	75.7-78.7	11	11 (3)
Tysfjord innermost basin	2017	455	60	6.5	34.6	43.4-56.4	5	5

Table 2. Traits used in this study and related modalities.

Trait	Code	Modalities
Adult life habit	AH1	Non-tube sessile
	AH2	Permanent tube
	AH3	Semi-permanent tube
	AH4	Burrower
	AH5	Surface crawler
	AH6	Swimmer
Mobility	M1	Mobile
	M2	Discretely mobile
	M3	Sessile
Body design	BD1	Bivalved
	BD2	Vermiform, segmented
	BD3	Vermiform, unsegmented
	BD4	Radial
	BD5	Articulate
	BD6	Turbinate
	BD7	Heart-shaped test
Feeding habit	FH1	Suspension
	FH2	Surface deposit
	FH3	Dissolved matter/symbionts
	FH4	Carnivore/omnivore
	FH5	Parasite/commensal
	FH6	Subsurface deposit
Larval type	LT1	Planktotroph
	LT2	Lecithotroph
Normal adult size	NS1	Minute (<0.5 cm)
	NS2	Small (0.5-1 cm)
	NS3	Medium (1-3 cm)
	NS4	Large (>3 cm)
Position in sediments	PS1	Epifauna
	PS2	Infauna shallow
	PS3	Infauna deep (>5 cm)

Table 3.One-way factor analysis based on species composition.

	Basin					
	PERMANOVA		ANOSIM		PERMDISP	
	Pseudo-F	p-value	R	p-value	F	p-value
Abundance	27.108	0.001	0.936	0.001	6.6897	0.001
Biomass	18.788	0.001	0.836	0.001	13.03	0.001
Presence/absence	21.508	0.001	0.84	0.001	9.4107	0.001
	Sill depth					
	PERMANOVA		ANOSIM		PERMDISP	
	Pseudo-F	p-value	R	p-value	F	p-value
Abundance	29.335	0.001	0.648	0.001	0.4695	0.556
Biomass	24.352	0.001	0.678	0.001	0.31327	0.637
Presence/absence	26.566	0.001	0.593	0.001	1.4859	0.288

Table 4. Correlation ratios and total inertia of first two axes of FCA. Traits correlated most with the axes are in bold.

	Abundance		Biomass	
	Axis 1	Axis 2	Axis 1	Axis 2
Adult living habit	0.038498	0.019485	0.03846	0.035989
Mobility	**0.05105**	0.016959	0.021225	0.002487
Body design	**0.054347**	**0.132378**	**0.086273**	**0.098835**
Feeding habit	**0.08062**	0.0488	**0.065096**	0.014683
Normal adult size	0.035118	0.025971	0.02533	0.005711
Position in sediments	**0.094681**	0.026416	**0.061072**	0.025513
Total inertia	0.31	0.23	0.26	0.16

Table 5. One-way factor analysis based on trait composition.

	Basin					
	PERMANOVA		ANOSIM		PERMDISP	
	Pseudo-F	p-value	R	p-value	F	p-value
Abundance	91.037	0.001	0.801	0.001	4.4861	0.003
Biomass	30.871	0.001	0.55	0.001	5.3935	0.001
	Sill depth					
	PERMANOVA		ANOSIM		PERMDISP	
	Pseudo-F	p-value	R	p-value	F	p-value
Abundance	50.072	0.001	0.392	0.001	6.2616	0.036
Biomass	48.391	0.001	0.504	0.001	3.796	0.063

Figure legends

Figure 1. Map of the study area showing geomorphology of the study area and locations of the basins studied. Two basins in an inner branch of the Tysfjord system (Hellmofjord) are here referred to as Tysfjord middle basin and Tysfjord innermost basin in accordance with the previous study (Jordà Molina et al., 2019).

Figure 2. Results of nMDS based on species composition: A, based on abundance data; B, based on biomass data; C, based on presence/absence data. Squares indicate deep-silled basins, circles indicate shallow-silled basins. Note: no biomass data are available for Nordfjord.

Figure 3. Results of FCA: A, based on abundance; B, based on biomass. For the modality codes see Table 2. Note: no biomass data are available for Nordfjord.

Figure 4. The average abundance-weighted trait profile for studied fjord basins. Deep silled fjords (Saltfjord, Sørfolda, Tysfjord deep, Tysfjord middle) are on the left, shallow silled fjords on the right (Skjerstadfjord, Nordfjord, Mistfjord, Tysfjord inner). For the modality codes see Table 2.

Figure 5. The proportion of species with different larval types recorded in different basins.

Figure 6. Box plots and results of Kruskal-Wallis tests with post-hoc comparison for number of species (S), Shannon diversity index H'(loge), functional dispersion (Fdis) and functional redundancy (Fdis/H' ratio). Deep silled fjords (Saltfjord, Sørfolda, Tysfjord deep, Tysfjord middle) are on the left, shallow silled fjords on the right (Skjerstadfjord, Nordfjord, Mistfjord, Tysfjord inner). Stars indicate significance level ($p<0.001$). Groups with the same letters are not significantly different.

Figure 7. Relationship between species diversity (H', x-axis)') and functional diversity (Fdis, y-axis) for deep-silled and shallow silled fjords.

Figure 1

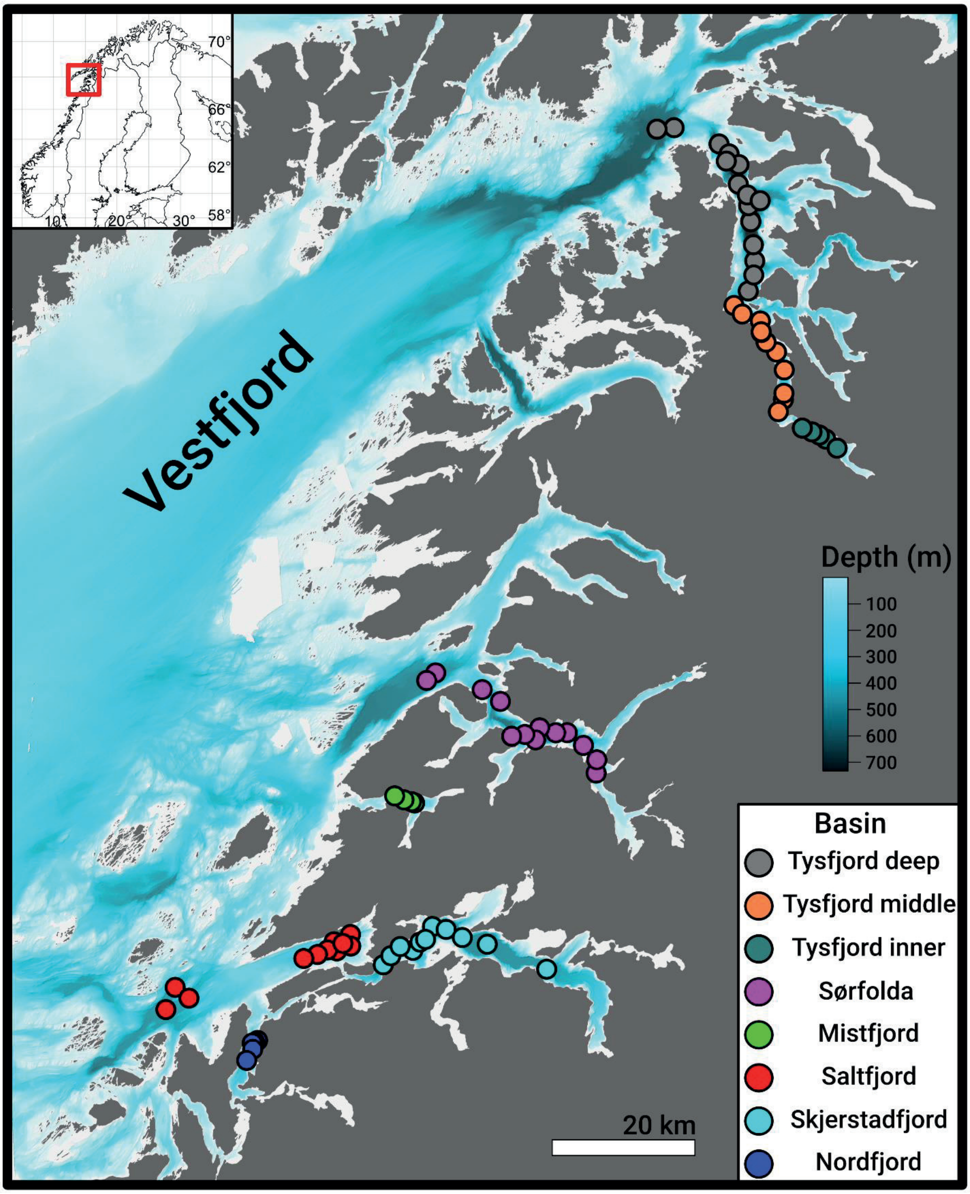

70°
66°
62°
58°
10°
20°
30°
Vestfjord
Depth (m)
100
200
300
400
500
600
700
Basin
Tysfjord deep
Tysfjord middle
Tysfjord inner
Sørfolda
Mistfjord
Saltfjord
Skjerstadfjord
Nordfjord
20 km

Figure 2

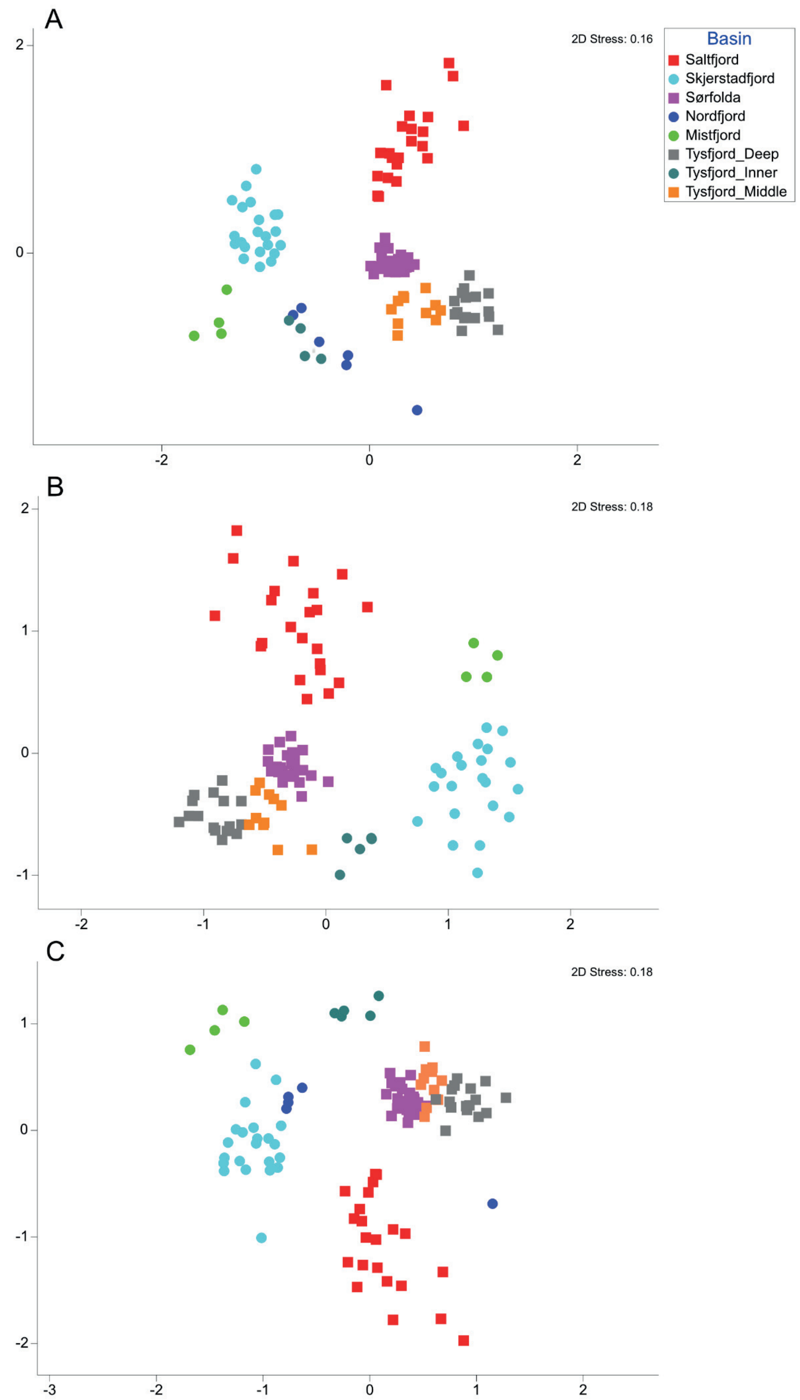

A
2D Stress: 0.16
Basin
Saltfjord
Skjerstadfjord
Sørfolda
Nordfjord
Mistfjord
Tysfjord_Deep
Tysfjord_Inner
Tysfjord_Middle
2
0
-2
0
2
B
2D Stress: 0.18
2
1
0
-1
-2
-1
0
1
2
C
2D Stress: 0.18
1
0
-1
-2
-3
-2
-1
0
1
2

Figure 3

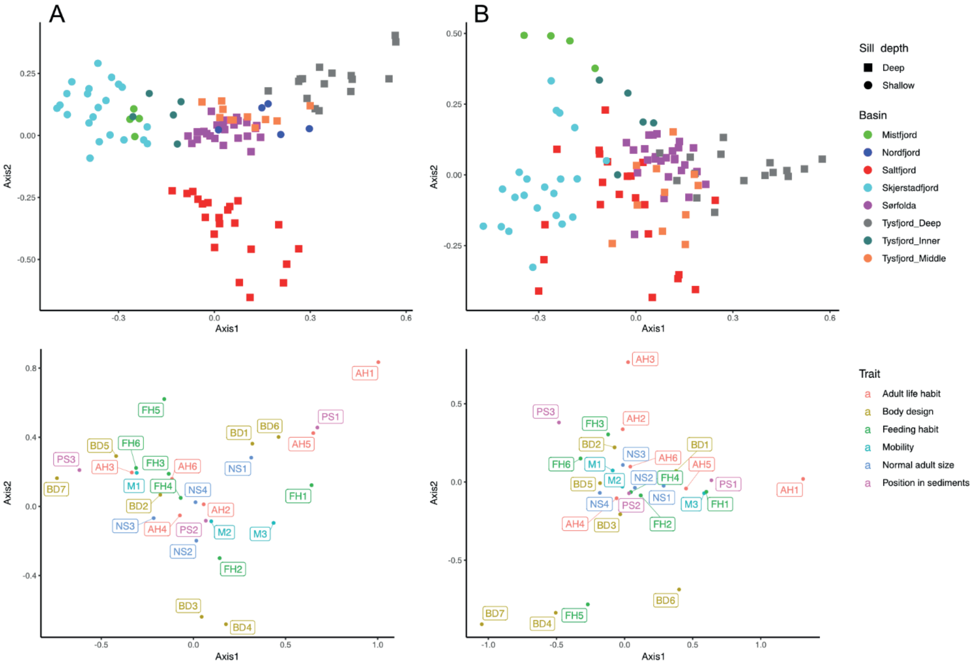

A
B
Axis1
Axis2
Sill depth
Deep
Shallow
Basin
Mistfjord
Nordfjord
Saltfjord
Skjerstadfjord
Sørfolda
Tysfjord_Deep
Tysfjord_Inner
Tysfjord_Middle
Trait
Adult life habit
Body design
Feeding habit
Mobility
Normal adult size
Position in sediments
AH1
AH2
AH3
AH4
AH5
AH6
BD1
BD2
BD3
BD4
BD5
BD6
BD7
FH1
FH2
FH3
FH4
FH5
FH6
M1
M2
M3
NS1
NS2
NS3
NS4
PS1
PS2
PS3

Figure 4

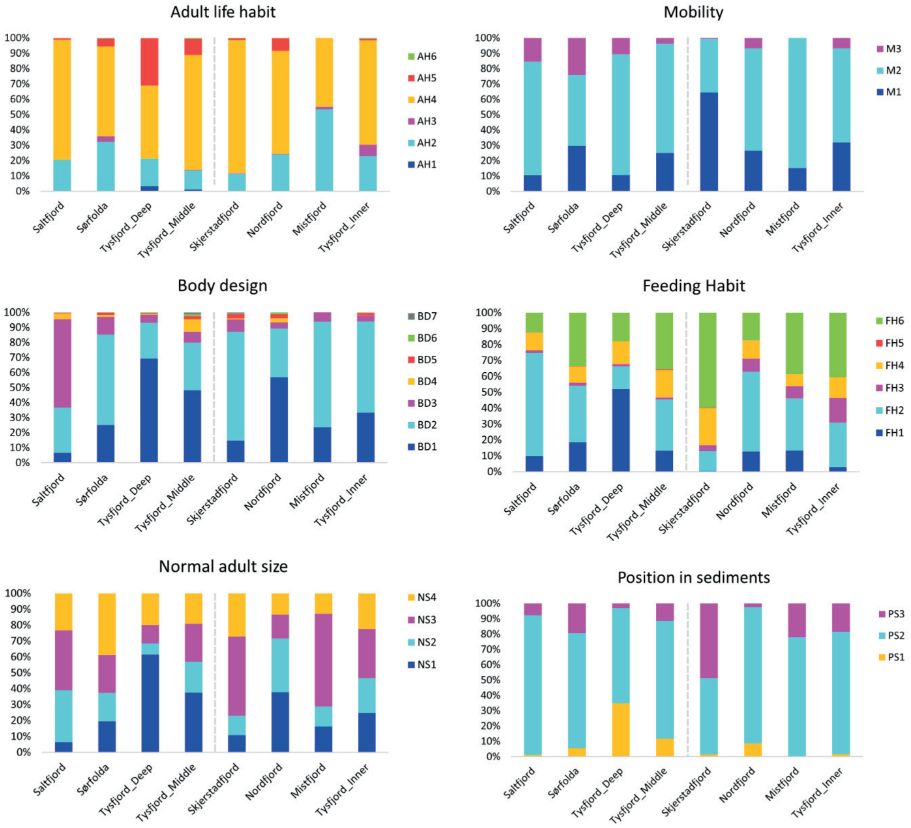

Adult life habit
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
AH6
AH5
AH4
AH3
AH2
AH1
Mobility
M3
M2
M1
Body design
BD7
BD6
BD5
BD4
BD3
BD2
BD1
Feeding Habit
FH6
FH5
FH4
FH3
FH2
FH1
Normal adult size
NS4
NS3
NS2
NS1
Position in sediments
PS3
PS2
PS1
Saltfjord
Sørfolda
Tysfjord_Deep
Tysfjord_Middle
Skjerstadfjord
Nordfjord
Mistfjord
Tysfjord_Inner

Figure 5

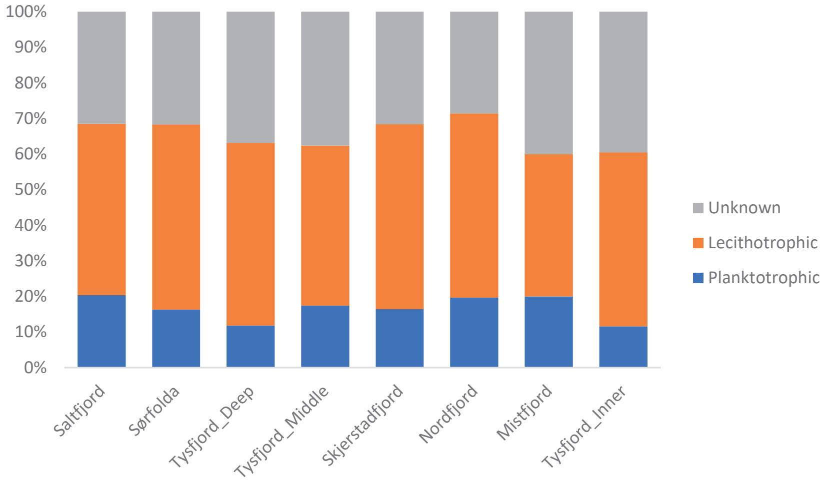
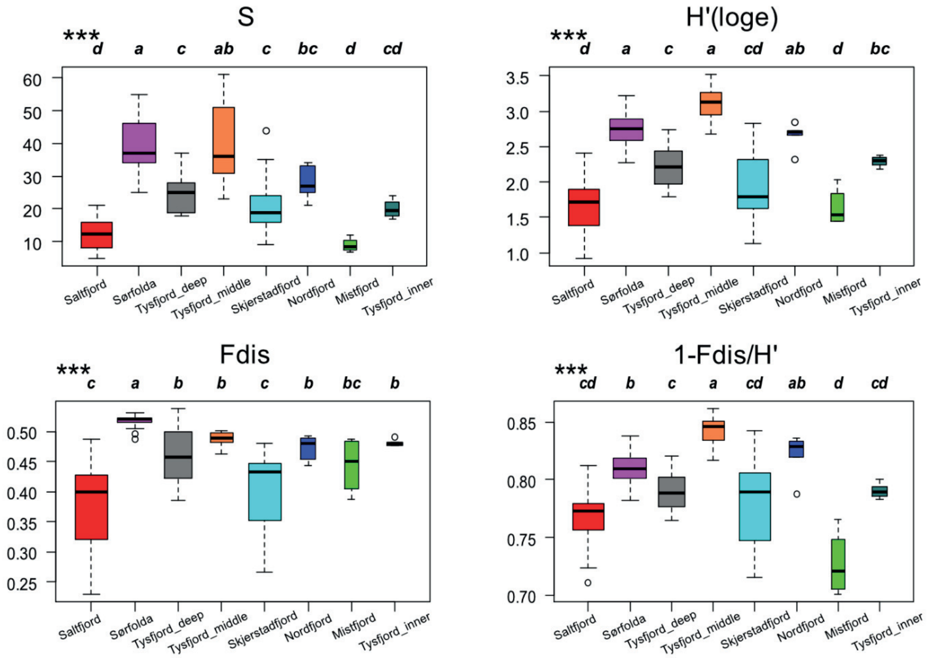
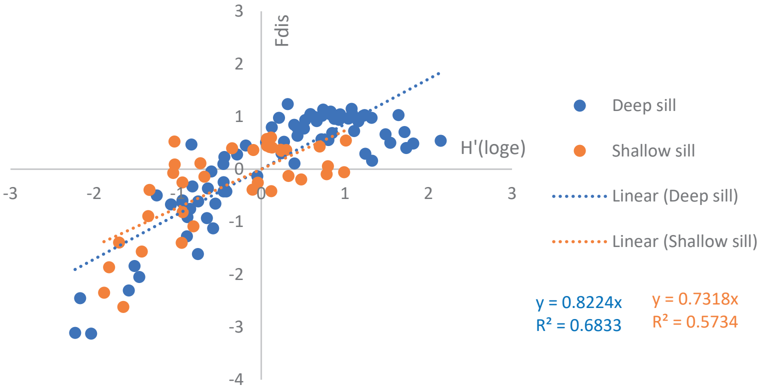

100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Saltfjord
Sørfolda
Tysfjord_Deep
Tysfjord_Middle
Skjerstadfjord
Nordfjord
Mistfjord
Tysfjord_Inner
Unknown
Lecithotrophic
Planktotrophic

Figure 6


S
***
d a c ab c bc d cd
60
50
40
30
20
10
H'(loge)
***
d a c a cd ab d bc
3.5
3.0
2.5
2.0
1.5
1.0
Fdis
***
c a b b c b bc b
0.50
0.45
0.40
0.35
0.30
0.25
1-Fdis/H'
***
cd b c a cd ab d cd
0.85
0.80
0.75
0.70
Saltfjord
Sørfolda
Tysfjord_deep
Tysfjord_middle
Skjerstadfjord
Nordfjord
Mistfjord
Tysfjord_inner

731 **Figure 7**



732

733

Supplementary table 1. Station coordinates.

Date	Fjord/Basin	Station	Latitude (°N)	Longitude (°E)	Depth (m)
30 April 2013	Saltfjord	S4	67.271	14.588	373
30 April 2013	Saltfjord	S5	67.259	14.595	373
30 April 2013	Saltfjord	S6	67.261	14.565	372
30 April 2013	Saltfjord	S7	67.256	14.531	371
30 April 2013	Saltfjord	S8	67.252	14.485	367
08 May 2013	Skjerstadfjord	K6	67.282	14.915	510
08 May 2013	Skjerstadfjord	K7	67.277	14.959	509
08 May 2013	Skjerstadfjord	K8	67.265	15.010	511
08 May 2013	Skjerstadfjord	K9	67.254	15.090	503
08 May 2013	Skjerstadfjord	K10	67.216	15.278	475
10 May 2013	Saltfjord	S1	67.279	14.644	369
10 May 2013	Saltfjord	S2	67.264	14.642	369
10 May 2013	Saltfjord	S3	67.268	14.617	374
21 May 2013	Skjerstadfjord	K3	67.253	14.845	516
21 May 2013	Skjerstadfjord	K4	67.263	14.870	512
21 May 2013	Skjerstadfjord	K5	67.266	14.889	514
11 June 2013	Skjerstadfjord	K0	67.237	14.744	544
11 June 2013	Skjerstadfjord	K1	67.248	14.771	514
11 June 2013	Skjerstadfjord	K2	67.259	14.804	510
13 June 2013	Saltfjord	S10	67.197	14.022	475
13 June 2013	Saltfjord	S11	67.225	14.057	462
13 June 2013	Saltfjord	S12	67.210	14.100	455
18 May 2015	Sørfolda	F4	67.566	15.199	488
18 May 2015	Sørfolda	F3	67.583	15.142	361
18 May 2015	Sørfolda	F2	67.609	14.992	505
18 May 2015	Sørfolda	F1	67.600	14.960	516
19 May 2015	Sørfolda	F14	67.464	15.496	349
19 May 2015	Sørfolda	F13	67.481	15.502	359
19 May 2015	Sørfolda	F12	67.501	15.462	403
19 May 2015	Sørfolda	F11	67.519	15.412	551
19 May 2015	Sørfolda	F10	67.520	15.374	557
19 May 2015	Sørfolda	F9	67.528	15.322	551
19 May 2015	Sørfolda	F8	67.513	15.305	558
19 May 2015	Sørfolda	F7	67.521	15.271	566
20 May 2015	Sørfolda	F6	67.520	15.227	558
22-26 May 2017	Tysfjord Deep	1	68.262	16.105	630
22-26 May 2017	Tysfjord Deep	2	68.248	16.136	620
22-26 May 2017	Tysfjord Deep	3	68.233	16.166	630
22-26 May 2017	Tysfjord Deep	4	68.239	16.124	580
22-26 May 2017	Tysfjord Deep	15	68.069	16.155	486

Date	Fjord/Basin	Station	Latitude (°N)	Longitude (°E)	Depth (m)
22-26 May 2017	Tysfjord Deep	16	68.107	16.187	703
22-26 May 2017	Tysfjord Deep	17	68.128	16.188	708
22-26 May 2017	Tysfjord Deep	18	68.159	16.187	710
22-26 May 2017	Tysfjord Deep	19	68.158	16.187	713
22-26 May 2017	Tysfjord Deep	20	68.179	16.185	715
22-26 May 2017	Tysfjord Deep	21	68.208	16.157	716
22-26 May 2017	Tysfjord Deep	22	68.193	16.184	719
22-26 May 2017	Tysfjord Deep	23	68.184	16.226	714
22-26 May 2017	Tysfjord Deep	24	68.089	16.179	575
22-26 May 2017	Tysfjord Deep	34	68.288	15.957	548
22-26 May 2017	Tysfjord Deep	36	68.288	15.898	596
22-26 May 2017	Tysfjord Inner	5	67.869	16.366	450
22-26 May 2017	Tysfjord Inner	6	67.875	16.346	455
22-26 May 2017	Tysfjord Inner	7	67.880	16.322	452
22-26 May 2017	Tysfjord Inner	32	67.856	16.401	354
22-26 May 2017	Tysfjord Inner	33	67.886	16.291	438
22-26 May 2017	Tysfjord Middle	8	67.925	16.237	333
22-26 May 2017	Tysfjord Middle	9	67.933	16.241	346
22-26 May 2017	Tysfjord Middle	10	67.963	16.250	360
22-26 May 2017	Tysfjord Middle	11	67.987	16.230	367
22-26 May 2017	Tysfjord Middle	12	68.001	16.198	374
22-26 May 2017	Tysfjord Middle	13	68.014	16.185	350
22-26 May 2017	Tysfjord Middle	14	68.029	16.186	334
22-26 May 2017	Tysfjord Middle	25	68.052	16.102	325
22-26 May 2017	Tysfjord Middle	26	68.040	16.127	325

Date	Fjord/Basin	Station	Latitude (°N)	Longitude (°E)	Depth (m)
22-26 May 2017	Tysfjord Middle	27	68.015	16.185	375
22-26 May 2017	Tysfjord Middle	28	67.910	16.216	278
13 June 2017	Mistfjord	M1	67.443	14.888	280
13 June 2017	Mistfjord	M2	67.445	14.878	294
13 June 2017	Mistfjord	M3	67.448	14.854	294
13 June 2017	Mistfjord	M4	67.454	14.824	293
10 July 2019	Nordfjord	V1	67.150	14.315	393
10 July 2019	Nordfjord	V2	67.148	14.305	390
10 July 2019	Nordfjord	V3	67.147	14.297	379
10 July 2019	Nordfjord	V4	67.139	14.297	390
10 July 2019	Nordfjord	V5	67.125	14.275	381

Supplementary table 2. Species recorded in each basin.

	Deep-silled basins				Shallow silled basins			
	Saltfjord	Sørfolda	Tysfjord Deep	Tysfjord Middle	Skjerstadfjord	Nordfjord	Mistfjord	Tysfjord Inner
Abra nitida	+	+	+	+	+	+		
Abyssoninoe sp.		+	+	+			+	+
Actinaraea indet.	+							
Aglaophamus pulcher	+	+		+				
Alvania testae			+					
Amaeana trilobata				+				+
Ampelisca cf. amblyops		+						
Ampharete gr. lindstoemi		+			+			+
Ampharete octocirrata				+				
Ampharetidae indet.				+			+	
Amphicteis gunneri				+	+			
Amphictene auricoma		+		+		+		
Amphilepis norvegica	+	+	+	+	+	+		+
Amythasides macroglossus		+	+	+		+		+
Anatoma crispata				+				
Anobothrus gracilis						+		
Antalis entalis		+	+	+				
Aphelochaeta sp.	+	+	+	+	+	+		+
Aphrodita aculeata		+	+	+				
Aphroditidae indet.		+				+		
Apodida indet.		+	+					
Aricidea catherinae		+						
Arrhinopsis longicornis		+		+				
Arrhis phyllonyx					+			
Astarte crenata					+			
Augeneria sp.		+	+	+	+			+
Bathyarca pectunculoides	+	+		+				

	Deep-silled basins				Shallow silled basins			
	Saltfjord	Sørfolda	Tysfjord Deep	Tysfjord Middle	Skjerstadfjord	Nordfjord	Mistfjord	Tysfjord Inner
Bivalvia indet.						+		
Bradabyssa villosa		+		+	+			
Brisaster fragilis		+		+	+			
Brissopsis lyrifera	+							
Bruzelia typica				+				
Bylgides groenlandicus		+				+		
Calocaris macandreae		+	+					
Campylaspis costata		+						
Capitella capitata					+			
Caudofoveata indet.	+	+				+		
Ceratocephale loveni		+		+	+	+	+	+
Ceriantharia					+			
Chaetoderma nitidulum	+	+	+	+	+	+		
Chaetozone setosa agg.					+	+		
Chirimia biceps	+	+			+			
Chone sp.				+	+			
Clymenura borealis		+	+	+	+	+	+	+
Cossura sp.					+			
Ctenodiscus crispatus					+	+		
Cumacea indet.		+						
Cuspidaria indet.		+			+			
Cuspidaria lamellosa		+	+	+				
Cuspidaria obesa			+					
Cuspidaria rostrata		+	+	+		+		
Dacrydium ockelmanni				+				
Delectopecten vitreus		+	+	+				
Diastylis cornuta	+	+		+				
Diastylis lucifera		+	+	+				
Diastylis rathkei					+			

	Deep-silled basins				Shallow silled basins			
	Saltfjord	Sørfolda	Tysfjord Deep	Tysfjord Middle	Skjerstadfjord	Nordfjord	Mistfjord	Tysfjord Inner
Diplocirrus glaucus	+	+		+		+		+
Dipolydora coeca					+			
Drilonereis brattstroemi			+	+	+	+		
Eclysippe vanelli		+	+	+				+
Edwardsiidae gen. sp. B					+			
Ennucula corticata		+		+				
Ennucula tenuis					+	+		
Entalina tetragona		+	+	+				
Eriopisa elongata	+	+	+	+	+			+
Eteone flava					+			
Eteone longa					+			
Euchone arenae	+	+		+				
Euchone incolor		+						
Euchone pseudolimnicola				+				
Euclymene lindrothi			+	+				+
Euclymeninae indet.		+	+					
Eucranta villosa		+						+
Eudorella emarginata			+		+	+		
Eudorella indet.		+						
Eulalia tjalfiensis		+		+	+			
Eulimidae		+	+	+	+			
Eunice dubitata	+							
Euspira montagui				+				
Euspira pallida					+	+		
Exogone verugera		+			+			+
Falcidens crossotus	+	+		+	+	+		
Flabelligeridae indet.	+	+						
Galathowenia oculata					+			
Gastropoda indet.		+						

	Deep-silled basins				Shallow silled basins			
	Saltfjord	Sørfolda	Tysfjord Deep	Tysfjord Middle	Skjerstadfjord	Nordfjord	Mistfjord	Tysfjord Inner
Genaxinus eumyarius		+	+	+				
Glycera lapidum		+	+	+				+
Goniada maculata				+				+
Harpinia crenulata			+	+				
Harpinia propinqua					+	+		
Heteranomia squamula			+					
Heteromastus filiformis	+	+	+	+	+	+	+	+
Idas lamellosus								+
Kefersteinia cirrata		+						
Kelliella miliaris		+	+	+		+		
Labidoplax buskii		+		+	+			
Lanassa venusta		+						
Laona quadrata			+	+		+		+
Laonice sarsi		+	+	+				
Leuconidae indet.			+					
Levinsenia flava/gracilis spp.	+	+	+	+	+			+
Limatula gwyni		+						
Limnactinia laevis	+							
Limopsis tenella			+					
Lumbriclymene cylindricauda				+				
Lumbriclymene minor		+						
Lumbrineris near cingulata	+	+	+	+		+		+
Lysianassidae gen. sp.	+		+	+				
Makrokylindrus sp.		+						
Maldane sarsi					+		+	
Malletia obtusa	+	+	+	+				
Melinna cristata	+	+			+	+		
Mendicula ferruginosa		+	+	+				
Mendicula pygmaea								+

	Deep-silled basins				Shallow silled basins			
	Saltfjord	Sørfolda	Tysfjord Deep	Tysfjord Middle	Skjerstadfjord	Nordfjord	Mistfjord	Tysfjord Inner
Microclymene acirrata	+	+			+	+	+	+
Microclymene tricirrata	+	+		+	+			+
Myriochele olgae					+	+		
Myrioglobula islandica		+		+				
Myriotrochus vitreus			+	+	+			
Nemertea	+	+	+	+	+	+		
Neoleanira tetragona	+	+			+			
Nephasoma sp.	+	+	+	+	+		+	+
Nephtys hystricis		+	+	+				
Nephtys paradoxa	+	+	+			+		
Nereimyra punctata			+					
Nicomache lumbricalis					+			
Nothria conchylega		+						
Notomastus latericeus			+	+	+			
Notoproctus oculatus		+	+	+	+			
Nucula tumidula	+	+	+	+	+	+		+
Oligochaeta							+	
Onchnesoma squamatum	+	+	+	+				
Onchnesoma steenstrupii	+	+	+	+	+	+		
Ophelina abranchiata		+						
Ophelina minima					+			
Ophelina norvegica	+	+	+					
Ophiocten gracilis		+						
Ophiopholis aculeata					+			
Ophiura albida				+				
Ophiura sarsii		+		+		+		
Ophiura sp. juv.				+				
Ophiuroidea indet.						+		
Owenia gr. fusiformis					+			

	Deep-silled basins				Shallow silled basins			
	Saltfjord	Sørfolda	Tysfjord Deep	Tysfjord Middle	Skjerstadfjord	Nordfjord	Mistfjord	Tysfjord Inner
Paradiopatra fiordica		+	+	+				
Paradiopatra quadricuspis	+	+	+	+				
Paradoneis eliasoni		+						+
Paraedwardsia arenaria		+	+	+	+			
Paraedwardsia sarsii		+			+			
Paramphinome jeffreysii	+	+		+	+			+
Paraonides nordica			+	+				
Paraphoxus oculatus					+	+		
Parathyasira dunbari			+	+	+	+		
Parathyasira equalis	+	+	+	+	+	+	+	+
Parexogone longicirris				+				+
Parvicardium minimum				+				
Pectinaria belgica	+	+		+		+		
Phascolion strombus		+						
Philinidae indet.	+							
Pholoe indet.		+						
Pholoe longa					+			
Pholoe pallida	+							
Phylo norvegicus	+	+	+	+	+	+	+	+
Pista bansei	+	+		+				
Polycirrus latidens		+						
Polycirrus medusa		+		+	+			
Polyphysia crassa					+			
Praxillella gracilis					+	+	+	
Praxillura longissima		+		+				
Prionospio cirrifera		+		+	+	+	+	+
Prionospio dubia	+	+						
Protodorvillea atlantica		+	+	+				
Pseudamussium peslutrae		+	+	+				

	Deep-silled basins				Shallow silled basins			
	Saltfjord	Sørfolda	Tysfjord Deep	Tysfjord Middle	Skjerstadfjord	Nordfjord	Mistfjord	Tysfjord Inner
Psilaster andromeda	+	+						
Psolus phantapus			+					
Retusa umbilicata			+	+				
Rhachotropis macropus		+						
Rhodine loveni	+	+		+				
Sabellidae gen. sp. A		+						
Scalibregma inflatum		+			+			+
Scaphander punctostriatus	+	+	+					
Scolelepis korsuni				+				
Scoloplos/Leitoscoloplos indet.					+			
Scutopus ventrolineatus	+	+	+	+	+	+	+	+
Siboglinum ekmani		+	+	+		+		+
Siphonodentalium lobatum					+	+		
Sipunculus norvegicus		+		+				
Sosane bathyalis		+						
Spatangus raschi				+				+
Spiochaetopterus typicus	+	+	+	+	+	+		
Spiophanes kroyeri	+	+		+		+	+	+
Synchelidium intermedium			+					
Tanaidacea indet. (male)		+						
Taranis moerchii			+	+				
Tellimya tenella	+			+				
Terebellidae indet.								+
Terebellides stroemii agg.	+	+	+	+	+	+		+
Therochaeta flabellata				+				
Thyasira obsoleta		+	+	+		+		+
Thyasira sarsii					+	+		
Thyasiridae indet.	+	+			+	+		
Trichobranchidae gen. sp. A								+

	Deep-silled basins				Shallow silled basins			
	Saltfjord	Sørfolda	Tysfjord Deep	Tysfjord Middle	Skjerstadfjord	Nordfjord	Mistfjord	Tysfjord Inner
Trichobranchus roseus				+				
Tropidomya abbreviata		+	+	+		+		
Typhlotanais aequiremis		+	+					
Westwoodilla caecula		+		+				
Yoldiella lenticula						+		
Yoldiella lucida	+	+	+	+	+	+		
Yoldiella nana		+		+	+	+		
Yoldiella philippiana								+

Supplementary table 3. Dominant species in each basin.

	Deep-silled basins			
	Saltfjord	Sørfolda	Tysfjord Deep	Tysfjord Middle
Abundance (% of total abundance)	Onchnesoma steenstrupii (50.00)	Spiochaetopterus typicus (23.63)	Kelliella miliaris (45.33)	Kelliella miliaris (10.07)
	Spiochaetopterus typicus (15.26)	Heteromastus filiformis (16.20)	Genaxinus eumyarius (6.69)	Heteromastus filiformis (7.92)
	Parathyasira equalis (4.87)	Parathyasira equalis (4.80)	Mendicula ferruginosa (6.18)	Mendicula ferruginosa (7.67)
	Falcidens crossotus (3.80)	Kelliella miliaris (4.67)	Paradiopatra fiordica (6.01)	Thyasira obsoleta (6.65)
	Heteromastus filiformis (3.80)	Thyasira obsoleta (4.66)	Spiochaetopterus typicus (6.01)	Abra nitida (6.03)
Biomass (% of total biomass)	Brissopsis lyrifera (81.17)	Brisaster fragilis (20.87)	Limopsis tenella (16.13)	Brisaster fragilis (60.20)
	Psilaster andromeda (2.82)	Sipunculus norvegicus (19.05)	Kelliella miliaris (13.70)	Spatangus raschi (11.26)
	Onchnesoma steenstrupii (2.50)	Terebellides stroemii agg. (7.79)	Scaphander punctostriatus (12.50)	Sipunculus norvegicus (4.91)
	Nemertea (1.68)	Ophiura sarsii (7.33)	Delectopecten vitreus (10.45)	Abra nitida (3.03)
	Parathyasira equalis (1.59)	Parathyasira equalis (6.13)	Parathysira dunbari (6.00)	Ophiura albida (2.40)

	Shallow-silled basins			
	Skjerstadfjord	Nordfjord	Mistfjord	Tysfjord Inner
Abundance (% of total abundance)	Heteromastus filiformis (40.23)	Parathyasira equalis (13.23)	Spiophanes kroyeri (38.20)	Parathyasira equalis (26.56)
	Parathyasira equalis (11.19)	Yoldiella nana (12.06)	Parathyasira equalis (23.60)	Heteromastus filiformis (13.54)
	Paramphinome jeffreysii (8.96)	Myriochele olgae (11.89)	Heteromastus filiformis (7.30)	Terebellides stroemii agg. (10.07)
	Ceratocephale loveni (7.58)	Abra nitida (11.72)	Ceratocephale loveni (5.62)	Lumbrineris near cingulata (7.47)
	Galathowenia oculata (5.21)	Kelliella miliaris (10.55)	Maldane sarsi (5.62)	Prionospio cirrifera (7.47)
Biomass (% of total biomass)	Brisaster fragilis (42.48)	no data	Parathyasira equalis (47.01)	Parathyasira equalis (45.75)
	Ctenodiscus crispatus (25.78)		Praxillella gracilis (17.07)	Terebellides stroemii agg. (16.86)
	Polyphysia crassa (10.82)		Phylo norvegicus (11.24)	Nucula tumidula (5.85)
	Astarte crenata (5.21)		Spiophanes kroyeri (10.87)	Heteromastus filiformis (5.13)
	Ceratocephale loveni (2.16)		Ceratocephale loveni (8.12)	Spatangus raschi (4.56)

Supplementary table 4. Species traits.

	Adult life habit						Mobility			Body design							Feeding habit						Larval type		Normal adult size				Position in sediments		
	AH1	AH2	AH3	AH4	AH5	AH6	M1	M2	M3	BD1	BD2	BD3	BD4	BD5	BD6	BD7	FH1	FH2	FH3	FH4	FH5	FH6	LT1	LT2	NS1	NS2	NS3	NS4	PS1	PS2	PS3
Abra nitida	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	2	1	0	0	3	0
Abyssoninoe sp.	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	2	2	0	3	0
Actinaraea indet.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aglaophamus pulcher	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	1	2	0	3	0
Alvania testae	0	0	0	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0
Amaeana trilobata	0	0	1	2	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	2	1	0	3	0
Ampelisca cf. amblyops	0	0	3	0	0	0	0	3	0	0	0	0	0	3	0	0	2	1	0	0	0	0	0	3	0	0	3	0	0	3	0
Ampharete gr. lindstoemi	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	2	1	0	0	3	0
Ampharete octocirrata	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	2	1	0	0	3	0
Ampharetidae indet.	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	3	0
Amphicteis gunneri	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	2	1	3	0	0
Amphictene auricoma	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	2	1	0	2	2
Amphilepis norvegica	0	0	0	3	0	0	0	3	0	0	0	0	3	0	0	0	2	2	0	0	0	0	0	3	2	1	0	0	0	3	0
Amythasides macroglossus	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	2	1	0	0	3	0
Anatoma crispata	0	0	0	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0
Anobothrus gracilis	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	2	2	0	3	0

	Adult life habit						Mobility			Body design							Feeding habit						Larval type		Normal adult size				Position in sediments		
	AH1	AH2	AH3	AH4	AH5	AH6	M1	M2	M3	BD1	BD2	BD3	BD4	BD5	BD6	BD7	FH1	FH2	FH3	FH4	FH5	FH6	LT1	LT2	NS1	NS2	NS3	NS4	PS1	PS2	PS3
Antalis entalis	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	3	0	3	0
Aphelochaeta sp.	0	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	0	2	0	0	0	2	0	3	0	0	2	2	0	3	0
Aphrodita aculeata	0	0	0	2	1	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	1	2	1	2	0
Aphroditidae indet.	0	0	0	2	1	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	1	2	0
Apodida indet.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aricidea catherinae	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	1	0	0	0	2	0	3	1	2	0	0	0	2	2
Arrhinopsis longicornis	0	0	0	1	1	1	3	0	0	0	0	0	0	3	0	0	0	2	0	2	0	0	0	3	3	0	0	0	2	2	0
Arrhis phyllonyx	0	0	0	1	1	1	3	0	0	0	0	0	0	3	0	0	0	2	0	2	0	0	0	3	0	3	0	0	2	2	0
Astarte crenata	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	3	0	0	3	0
Augeneria sp.	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	2	2	0	3	0
Bathyarca pectunculoides	3	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	0	3	3	0	0	0	3	0	0
Bivalvia indet.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bradabyssa villosa	0	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	2	1	0	3	0
Brisaster fragilis	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	3	0	2	0	0	0	2	0	3	0	0	0	3	0	3	0
Brissopsis lyrifera	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	3	0	2	0	0	0	2	3	0	0	0	0	3	0	3	0
Bruzelia typica	0	0	0	0	2	2	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	3	2	1	0	0	3	0	0
Bylgides groenlandicus	0	0	0	0	2	2	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	2	2	3	0	0
Calocaris macandreae	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0	0	0	0	2	0	2	0	3	0	0	0	3	0	2	2
Campylaspis costata	0	0	0	2	0	1	0	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	2	1	0	0	1	2	0

	Adult life habit						Mobility			Body design							Feeding habit						Larval type		Normal adult size				Position in sediments		
	AH1	AH2	AH3	AH4	AH5	AH6	M1	M2	M3	BD1	BD2	BD3	BD4	BD5	BD6	BD7	FH1	FH2	FH3	FH4	FH5	FH6	LT1	LT2	NS1	NS2	NS3	NS4	PS1	PS2	PS3
Capitella capitata	0	0	1	2	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	3	0	1	2	1	0	3	0
Caudofoveata indet.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratocephale loveni	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	3	0	0	3	0
Ceriantharia	0	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3	0	3	0
Chaetoderma nitidulum	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	0	2	2	0	3	0
Chaetozone setosa agg.	0	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	3	0	0	3	0
Chirimia biceps	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	0	3	0	0	3
Chone sp.	0	3	0	0	0	0	0	0	3	0	3	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3	0
Clymenura borealis	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	1	2	0	0	3
Cossura sp.	0	0	0	0	0	3	0	0	0	2	2	0	0	3	0	0	0	0	0	0	0	3	0	0	0	2	2	0	0	3	0
Ctenodiscus crispatus	0	0	0	3	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	0	3	0	3	0	0	0	3	0	3	0
Cumacea indet.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cuspidaria indet.	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0
Cuspidaria lamellosa	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	3	0	0	0	3	3	0	0	0	0	3	0
Cuspidaria obesa	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	3	0	0	0	3	0	2	1	0	0	3	0
Cuspidaria rostrata	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	3	0	0	3	0
Dacrydium ockelmanni	3	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	0
Delectopecten vi treus	3	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0	3	0	0
Diastylis cornuta	0	0	0	2	0	1	0	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0	3	0	1	2	0
Diastylis lucifera	0	0	0	2	0	1	0	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	1	2	0	0	1	2	0

	Adult life habit						Mobility			Body design							Feeding habit						Larval type		Normal adult size				Position in sediments		
	AH1	AH2	AH3	AH4	AH5	AH6	M1	M2	M3	BD1	BD2	BD3	BD4	BD5	BD6	BD7	FH1	FH2	FH3	FH4	FH5	FH6	LT1	LT2	NS1	NS2	NS3	NS4	PS1	PS2	PS3
Diastylis rathkei	0	0	0	2	0	1	0	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0	3	0	1	2	0
Diplocirrus glaucus	0	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	3	0	0	3	0
Dipolydora coeca	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	1	2	0	0	0	0	3	0	0	0	3	0	0	3	0
Drilonereis brattstroemi	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3	0	3	0
Eclysippe vanelli	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	2	1	0	0	3	0
Edwardsiidae gen. sp. B	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0
Ennucula corticata	0	0	0	3	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	3	3	0	0	0	0	3	0
Ennucula tenuis	0	0	0	3	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	3	0	2	1	0	0	3	0
Entalina tetragona	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	0	3	0	0	3	0
Eriopisa elongata	0	0	0	1	1	1	3	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	3	0	0	2	2	0
Eteone flava	0	0	0	2	1	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	2	2	1	2	0
Eteone longa	0	0	0	2	1	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	2	2	1	2	0
Euchone arenae	0	3	0	0	0	0	0	0	3	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	0
Euchone incolor	0	3	0	0	0	0	0	0	3	0	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	1	2	0	0	3	0
Euchone pseudolimnicola	0	3	0	0	0	0	0	0	3	0	3	0	0	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	0
Euclymene lindr othi	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	3
Euclymeninae indet.	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	3
Eucranta villosa	0	0	0	0	2	2	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	3	0	3	0	0
Eudorella emarginata	0	0	0	2	0	1	0	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	2	1	0	1	2	0
Eudorella indet.	0	0	0	2	0	1	0	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	2	1	0	1	2	0

	Adult life habit						Mobility			Body design							Feeding habit						Larval type		Normal adult size				Position in sediments		
	AH1	AH2	AH3	AH4	AH5	AH6	M1	M2	M3	BD1	BD2	BD3	BD4	BD5	BD6	BD7	FH1	FH2	FH3	FH4	FH5	FH6	LT1	LT2	NS1	NS2	NS3	NS4	PS1	PS2	PS3
Eulalia tjalfiensis	0	0	0	2	1	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	2	2	1	2	0
Eulimidae	3	0	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	2	2	0	0	0	0	0
Eunice dubitata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euspira montagui	0	0	0	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	3	0	0	3	0	3	0	0
Euspira pallida	0	0	0	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	3	0	0	3	0	3	0	0
Exogone verugera	0	0	0	2	2	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	0	3	0	0	2	2	0
Falcidens crossotus	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	2	2	0	0	3	0
Flabelligeridae indet.	0	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	3	0
Galathowenia oculata	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	3	0	0	3	0
Gastropoda indet.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Genaxinus eumyarius	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	0	0	3	0	3	3	0	0	0	0	3	0
Glycera lapidum	0	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	1	2	0	3	0
Goniada maculata	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	1	2	0	3	0
Harpinia crenulata	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	3	3	0	0	0	0	3	0
Harpinia propinqua	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	3	3	0	0	0	0	3	0
Heteranomia squamula	3	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0	3	0	0
Heteromastus filiformis	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	3	0	0	0	2	2	0	0	3
Idas lamellosus	3	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	3	0	0

	Adult life habit						Mobility			Body design							Feeding habit						Larval type		Normal adult size				Position in sediments		
	AH1	AH2	AH3	AH4	AH5	AH6	M1	M2	M3	BD1	BD2	BD3	BD4	BD5	BD6	BD7	FH1	FH2	FH3	FH4	FH5	FH6	LT1	LT2	NS1	NS2	NS3	NS4	PS1	PS2	PS3
Kefersteinia cirrata	0	0	0	2	1	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	3	0	1	2	0	0	0	3	0
Kelliella miliaris	0	0	0	1	2	0	0	3	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	3	0	0	0	2	1	0
Labidoplax buskii	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0	3	0	0	3	0	0	3	0
Lanassa venusta	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	2	2	0	3	0
Laona quadrata	0	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	0	3	0
Laonice sarsi	0	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	1	2	0	3	0
Leuconidae indet.	0	0	0	2	0	1	0	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	3	0	0	0	1	2	0
Levinsenia flava/gracilis spp.	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	1	0	0	0	2	0	3	0	0	3	0	0	2	2
Limatula gwyni	3	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0	3	0	0
Limnactinia laevis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limopsis tenella	3	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	3	0	3	0	0
Lumbriclymene cylindricauda	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	3
Lumbriclymene minor	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	3
Lumbrineris near cingulata	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	2	2	0	3	0
Lysianassidae gen. sp.	0	0	0	0	2	2	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	3	0	0
Makrokylindrus sp.	0	0	0	2	0	1	0	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0	3	0	1	2	0
Maldane sarsi	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	2	2	0	0	3
Malletia obtusa	0	0	0	3	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	3	0
Melinna cristata	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	1	2	0	3	0

	Adult life habit						Mobility			Body design							Feeding habit						Larval type		Normal adult size				Position in sediments		
	AH1	AH2	AH3	AH4	AH5	AH6	M1	M2	M3	BD1	BD2	BD3	BD4	BD5	BD6	BD7	FH1	FH2	FH3	FH4	FH5	FH6	LT1	LT2	NS1	NS2	NS3	NS4	PS1	PS2	PS3
Mendicula ferruginosa	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	0	0	3	0	3	3	0	0	0	0	3	0
Mendicula pygmaea	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	0	0	3	0	3	3	0	0	0	0	3	0
Microclymene acirrata	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	3
Microclymene tricirrata	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	3
Myriochele olgae	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	3	0	0	3	0	0	0	3	0
Myrioglobula islandica	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	3	0	0	3	0	0	0	3	0
Myriotrochus vitreus	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	3	0
Nemertea	0	0	0	2	2	0	3	0	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	2	2	2	2	2	0
Neoleanira tetragona	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	1	2	0	3	0
Nephasoma sp.	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0	0	0	0	0	0	2	1	0	0	3	0
Nephtys hystricis	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	1	2	0	3	0
Nephtys paradoxa	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	1	2	0	3	0
Nereimyra punctata	0	0	0	2	1	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	3	0	1	2	0
Nicomache lumbricalis	0	3	0	0	0	0	0	0	3	0	3	0	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	3	0	0
Nothria conchylega	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	3	3	0	0
Notomastus latericeus	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	0	3	0	0	3

	Adult life habit						Mobility			Body design							Feeding habit						Larval type		Normal adult size				Position in sediments		
	AH1	AH2	AH3	AH4	AH5	AH6	M1	M2	M3	BD1	BD2	BD3	BD4	BD5	BD6	BD7	FH1	FH2	FH3	FH4	FH5	FH6	LT1	LT2	NS1	NS2	NS3	NS4	PS1	PS2	PS3
Notoproctus oculatus	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	2	2	0	0	3
Nucula tumidula	0	0	0	3	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	3	0	3	0	0	0	3	0
Oligochaeta	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	3	3	0	0	0	0	3	0
Onchnesoma squamatum	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0	0	0	0	3	0	2	2	0	0	3	0
Onchnesoma steenstrupii steenstrupii	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0	0	0	0	3	0	2	2	0	0	3	0
Ophelina abranchiata	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	3	0	3	0	0	0	3	0
Ophelina minima	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	3	0
Ophelina norvegica	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	2	1	0	2	2
Ophiocten gracilis	0	0	0	0	3	0	3	0	0	0	0	0	3	0	0	0	0	2	0	2	0	0	3	0	0	0	3	0	3	0	0
Ophiopholis aculeata	0	0	0	0	3	0	0	3	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0	0	3	0	3	0	0
Ophiura albida	0	0	0	2	1	0	0	3	0	0	0	0	3	0	0	0	0	2	0	2	0	0	3	0	0	0	3	0	1	2	0
Ophiura sarsii	0	0	0	0	3	0	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	3	0	0	0	2	2	3	0	0
Ophiura sp. juv.	0	0	0	2	1	0	0	3	0	0	0	0	3	0	0	0	0	2	0	2	0	0	3	0	0	0	0	0	1	2	0
Ophiuroidea indet.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Owenia gr. fusiformis	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	2	2	0	0	0	0	3	0	0	1	2	0	0	3	0
Paradiopatra fiordica	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	3	0	3	0
Paradiopatra quadricuspis	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	0	3	0	3	0

	Adult life habit						Mobility			Body design							Feeding habit						Larval type		Normal adult size				Position in sediments		
	AH1	AH2	AH3	AH4	AH5	AH6	M1	M2	M3	BD1	BD2	BD3	BD4	BD5	BD6	BD7	FH1	FH2	FH3	FH4	FH5	FH6	LT1	LT2	NS1	NS2	NS3	NS4	PS1	PS2	PS3
Paradoneis eliasoni	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	1	0	0	0	2	0	3	0	3	0	0	0	2	2
Paraedwardsia arenaria	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	2	1	0	3	0
Paraedwardsia sarsii	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	2	1	0	3	0
Paramphinome jeffreysii	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	2	0	1	3	0	0	1	2	0	0	2	1
Paraonides nordica	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	1	0	0	0	2	0	3	0	3	0	0	0	2	2
Paraphoxus oculatus	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	3	3	0	0	0	0	3	0
Parathyasira dunbari	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	0	0	3	0	3	2	1	0	0	0	3	0
Parathyasira equalis	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	0	0	1	0	0	2	0	3	2	1	0	0	0	3	0
Parexogone longicirris	0	0	0	2	2	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	2	2	0
Parvicardium minimum	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	2	1	0	0	3	0
Pectinaria belgica	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	3	3	0	0	0	1	2	0	2	2
Phascolion strombus	0	0	3	0	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0	3	0	0	2	1	0	3	0
Philinidae indet.	0	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	0	3	0
Pholoe indet.	0	0	0	2	1	0	3	0	0	2	2	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	1	2	0
Pholoe longa	0	0	0	2	1	0	3	0	0	2	2	0	0	0	0	0	0	0	0	3	0	0	0	0	0	2	3	0	1	2	0
Pholoe pallida	0	0	0	2	1	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	3	0	2	1	0	1	2	0
Phylo norvegicus	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	0	3	0	2	2
Pista bansei	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0	3	0

	Adult life habit						Mobility			Body design							Feeding habit						Larval type		Normal adult size				Position in sediments		
	AH1	AH2	AH3	AH4	AH5	AH6	M1	M2	M3	BD1	BD2	BD3	BD4	BD5	BD6	BD7	FH1	FH2	FH3	FH4	FH5	FH6	LT1	LT2	NS1	NS2	NS3	NS4	PS1	PS2	PS3
Polycirrus latidens	0	0	1	2	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	3	0	3	0
Polycirrus medusa	0	0	1	2	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	3	0	0	0	0	0	0	0	3	0	3	0
Polyphysia crassa	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	3
Praxillella gracilis	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	1	2	0	0	3
Praxillura longissima	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	0	3	0	0	3
Prionospio cirrifera	0	0	3	0	0	0	0	3	0	0	3	0	0	0	0	0	1	2	0	0	0	0	3	0	0	1	2	0	0	3	0
Prionospio dubia	0	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	1	2	0	0	0	0	3	0	0	0	2	1	0	3	0
Protodorvillea atlantica	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	3	0
Pseudamussium peslutrae	0	0	0	1	2	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	3	0	0
Psilaster andromeda	0	0	0	3	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	3	0	3	0	3	0	0	0	3	0	3	0
Psolus phantapus	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	3	0
Retusa umbilicata	0	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	0	3	0
Rhachotropis macropus	0	0	0	0	2	2	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	3	0	0	3	0	3	0	0
Rhodine loveni	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	0	3	0	0	3
Sabellidae gen. sp. A	0	3	0	0	0	0	0	0	3	0	3	0	0	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Scalibregma inflatum	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	2	2	0	0	3

	Adult life habit						Mobility			Body design							Feeding habit						Larval type		Normal adult size				Position in sediments		
	AH1	AH2	AH3	AH4	AH5	AH6	M1	M2	M3	BD1	BD2	BD3	BD4	BD5	BD6	BD7	FH1	FH2	FH3	FH4	FH5	FH6	LT1	LT2	NS1	NS2	NS3	NS4	PS1	PS2	PS3
Scaphander punctostriatus	0	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	2	1	0	3	0
Scolelepis korsuni	0	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	1	2	0	0	0	0	3	0	0	0	3	0	0	3	0
Scoloplos/Leitoscoloplos indet.	0	0	0	3	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	3	0	0	2	2
Scutopus ventrolineatus	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	3	0	1	2	0	0	3	0
Siboglinum ekmani	0	3	0	0	0	0	0	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0
Siphonodentalium lobatum	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	3	0
Sipunculus norvegicus	0	0	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0	3	0
Sosane bathyalis	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	0	0	3	0
Spatangus raschi	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	3	0	3	0
Spiochaetopterus typicus	0	3	0	0	0	0	0	0	3	0	3	0	0	0	0	0	2	2	0	0	0	0	3	0	0	0	0	3	0	3	0
Spiophanes kroyeri	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	1	2	0	0	0	0	3	0	0	0	3	0	0	3	0
Synchelidium intermedium	0	0	0	1	1	1	3	0	0	0	0	0	0	3	0	0	0	2	0	2	0	0	0	3	3	0	0	0	3	0	0
Tanaidacea indet. (male)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Taranis moerchii	0	0	0	0	3	0	3	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	3	0	0
Tellimya tenella	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	0	3	0	3	0	2	1	0	0	0	3	0
Terebellidae indet.	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	3	0
Terebellides stroemii agg.	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	1	2	0	3	0

	Adult life habit						Mobility			Body design							Feeding habit						Larval type		Normal adult size				Position in sediments		
	AH1	AH2	AH3	AH4	AH5	AH6	M1	M2	M3	BD1	BD2	BD3	BD4	BD5	BD6	BD7	FH1	FH2	FH3	FH4	FH5	FH6	LT1	LT2	NS1	NS2	NS3	NS4	PS1	PS2	PS3
Therochaeta flabellata	0	0	0	3	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	3	0
Thyasira obsoleta	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	0	0	3	0	3	3	0	0	0	0	3	0
Thyasira sarsii	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	0	0	2	0	0	2	0	3	0	2	2	0	0	2	1
Thyasiridae indet.	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	0	0	3	0	3	2	1	0	0	0	3	0
Trichobranchidae gen. sp. A	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	2	1	0	3	0
Trichobranchus roseus	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	3	0
Tropidomya abbreviata	0	0	0	3	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	3	0
Typhlotanais aequiremis	0	3	0	0	0	0	0	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	3	0	0	0	0	3	0
Westwoodilla caecula	0	0	0	1	1	1	3	0	0	0	0	0	0	3	0	0	0	2	0	2	0	0	0	3	0	3	0	0	3	0	0
Yoldiella lenticula	0	0	0	3	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	3	0	3	0	0	0	3	0
Yoldiella lucida	0	0	0	3	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	3	0	3	0	0	0	3	0
Yoldiella nana	0	0	0	3	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	3	3	0	0	0	0	3	0
Yoldiella philippiana	0	0	0	3	0	0	3	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	3	3	0	0	0	0	3	0

Paper IV

Combining stable isotope and fatty acid analyses to assess trophic niches of macrofauna in an anthropogenically influenced deep fjord basin

Valentin Kokarev*, Sylvie Bolla, Henning Reiss

Faculty of Biosciences and Aquaculture, Nord University, 8049 Bodø, Norway

*corresponding author: valentin.kokarev@nord.no

Abstract

The link between biodiversity and ecosystem functioning is mediated by the functions that species perform in a community. The ecological role of a species largely depends on its trophic niche. However, little is known about trophic niches of benthic fauna and whether resource partitioning occurs at the interspecific level. In the present study, we investigated trophic niches of macrobenthic invertebrates in a deep (380 m) sub-Arctic fjord. We hypothesized that possible food resource partitioning among species with similar feeding habits can be influenced by the input of qualitatively different organic from an Atlantic salmon fish farm located in the fjord. Combination of stable isotope and fatty acid analyses revealed that biomass-dominant species were characterized by a distinct trophic niche, but the effects of fish farm waste sedimentation could not be traced in our study. Results of our study indicate that food resource partitioning might be more important for macrobenthic communities located in isolated habitats with weaker bentho-pelagic coupling.

1 Introduction

A widely accepted assumption in community ecology postulates, that two species can co-exist in a given locality if they differ in some aspect of their ecological niche ("limiting similarity"), which can be achieved through resource partitioning (Schoener, 1974; Abrams, 1983). Thus, the trophic niche of a species would define which food resources it utilises, and, to some extent, which interspecific competition interactions it would be involved in. In marine benthic food webs, macrobenthic primary consumers, which feed directly on suspended and sediment particulate organic matter, are the most species-rich group (Sokołowski et al., 2012). However, little is known about the mechanisms of coexistence of ecologically similar macrobenthic consumers. Macrobenthic feeding habits are diverse, including microphages (suspension, surface deposit, and subsurface deposit feeders) and macrophages (carnivores, herbivores, and omnivores) (Jumars et al., 2015). Competition can be expected the highest among species with the same feeding habit, yet often studies find little or no evidence for food resource partitioning among ecologically similar macrobenthic species (e.g. Godbold et al., 2006; Karlson et al. 2015; Oxtoby et al., 2016), although feeding selectivity was also documented (e.g. Hudson et al., 2003; Richoux et al., 2014). Deposit feeders, common for depositional environments such as deep basins, may differ in their vertical position within sediments (Josefson, 1981; Dauwe et al., 1998), which might also correspond with their different trophic strategies and partitioning of food resources. Partitioning of food resources might be more important for small and isolated habitats such as basins with restricted water exchange where effects of dispersal from nearby communities on coexistence of species are limited (Leibold et al., 2004; Hart et al., 2017). Macrobenthic communities of sub-Arctic fjords differ in their structure approximately on a basin scale (Jordà Molina et al., 2019; Kokarev et al., 2021), which might result in different resource partitioning within macrobenthic consumers, and differences in organic matter remineralization among basins (Witte et al., 2003; Sweetman and Witte, 2008). Thus, understanding the trophic niches of macrobenthos might help to also better understand the processes shaping its community structure and functioning.

Trophic niches can be assessed using indirect methods such as stable isotope and fatty acid analyses as these methods provide long-term dietary information (Kelly and Scheibling, 2012). Stable isotopic signatures of carbon and nitrogen, $\delta^{15}N$ and $\delta^{13}C$, are routinely used in trophic ecology due to the predictable behaviour in food webs: $\delta^{15}N$ and $\delta^{13}C$ are enriched by 2.5-5‰ and approximately 1‰ at each trophic level, respectively (Bearhop et al., 2004). Stable isotopes provide easily obtainable and comparable information about trophic niches but information about food sources is limited, particularly if they are not known or have similar isotopic signatures. Fatty acids can provide more qualitative information on diets and are widely used as markers to study trophic relationships, particularly between primary producers, such as microalgae, and primary consumers, although with some limitations as the majority of fatty acid markers cannot be assigned to a single source (Dalsgaard et al., 2003; Kelly and Scheibling, 2012). For instance, polyunsaturated fatty acids, such as 20:5n-3 and 22:6n-3, that for a long time have been considered specific markers of diatoms and dinoflagellates, can be also synthetised by marine bacteria (Jøstensen and Landfald, 1997; Nichols, 2003). Both methods can be i.a. used to track terrestrial organic matter in transitional environments such as estuaries, as terrestrial inputs to marine ecosystem are characterised by lighter δ^{13}C, as well as presence of 18:2n-6 and 18:3n-3 polyunsaturated fatty acids, which are not very common in marine environment (Dalsgaard et al., 2003; Dunton et al., 2012).

Numerous fish farms located in the fjords along the Norwegian coast can potentially act as additional carbon sources to the basins. The particulate organic matter sedimentation in the vicinity of a fish farm can be several times higher than in the reference conditions during production (Kutti et al., 2007a). Unconsumed fish feed and faecal pellets are dispersed mainly near a fish farm location (<500m) (Bannister et al., 2016), but changes in sediment biogeochemistry, such as an increase in organic matter content, can be expected up to 1 km from a fish farm (Yakushev et al., 2020). While considerable excess of organic matter triggers shifts in community structure in the direct vicinity of a fish farm (e.g. Kutti et al., 2007b), little is known how smaller amounts of fish farm waste that can be dispersed further can affect benthic communities. Benthic consumers may switch their diet to fish farm waste, which is confirmed by elevated levels of 18:2n-6 and 18:3n-3 in their fatty acid composition (Olsen et al., 2012; White et al., 2017; Woodcock et al., 2019). These fatty acids can be used as markers of aquaculture waste as terrestrial crops are a major component of fish food (White et al., 2019). Qualitatively different food sources from fish farm waste can affect resource partitioning among macrobenthic invertebrates and, consequently, community structure in areas with a significant impact of fish farm production. Fjords are estuarine environments, however, the contribution of terrestrial inputs to their organic matter pools differs greatly, particularly, sub-Arctic fjords in the Vestfjord region have the lowest values of terrestrial organic matter fraction in their surface sediments in the North Atlantic (Faust and Knies, 2019). Consequently, low levels of fatty acids characteristic of terrestrial vegetation, such as

18:2n-6 and 18:3n-3, not associated with the fish farm input, can be expected, which can facilitate the detection of fish farm footprints on the benthic community.

In the present study, we investigated the trophic niches of macrofauna and sediment organic matter in a deep (380 m) sub-Arctic fjord basin at different distances from a fish farm using a combination of stable isotope and fatty acid analyses. Particularly, we aimed to answer the following questions: 1) what are the trophic niches of the most common macrofaunal species in the basin and to what extent they overlap and 2) do their trophic niches differ in the direct vicinity of the fish farm? Such data would contribute to the understanding of macrobenthic community organization in the deep fjord basins.

2. Material and methods

2.1 Study area

Nordfjord, a small fjord in the Vestjord region (67.12° N, 14.28° E), is about 7.5 km long and 2.5 km wide, with a maximum depth of 390 m and a 120 m deep sill (Figure 1). During the sampling in July, the bottom water masses had a salinity of 34.3-34.4 and a temperature of 6.1-6.2° C with oxygen saturation of over 90% (CTD measurements). Similar to other fjords with relatively shallow sills in the study area, the bottom water masses indicated that more saline and dense Atlantic water masses do not or do rarely enter the fjord, suggesting restricted water exchange (Jordà Molina et al., 2019; Skreslet et al., 2020; Kokarev et al., 2021). There are several salmon farm localities in the fjord, but we focused our sampling campaign on the largest one in the fjord, with total fish biomass of 2711 tonnes and feed consumption of 2900 tonnes. The fish was removed from the farm on the 10th of June 2019, a month before the sampling campaign for this study took place.

2.2 Sampling and collection of the fauna and sediments

The sampling campaign took place in the period 08.07.2019-10.07.2019. The sampling campaign focused on the deep basin (> 350 m), where the bottom topography is relatively homogeneous. The closest station located at 500 m from the fish farm (V3) and the furthest location at 2.2 km from the fish farm (V5 Ref). Sampling closer to the farm was not possible because of the position of anchor lines and fjord morphology. On each station four Van Veen grab samples (0.1 m^2) were taken. From one of the grabs at each station, where the sediment surface was visually undisturbed, three syringes from different spots were taken for the sediment analyses. The sediment from each of syringes was cut in three intervals 0-2 cm, 2-5 cm and 5-10 cm, pooled for each station and frozen at -24°C. The sediment from the grabs was sieved on 1 mm mesh sieve and subsequently invertebrates were sorted alive from the remaining fraction. Animals were identified to species level and frozen in liquid nitrogen (fatty acids and stable isotopes analyses) or frozen at -24 °C (stable isotopes). Due to low abundance and limited processing time, three replicates from the same station were pooled during sample sorting and individuals were pooled in order to obtain enough biomass for the analyses in case of smaller species. For the larger specimens of *Ctenosdicus crispatus* and *Ophioscolex glacialis* only arms were used for the analyses. For the large individual of *Thyasira sarsii* one gill and the foot were used for the separate stable isotope analyses and the remaining viscera, gill and mantle were used for fatty acids analysis. For the rest of the bivalves, shells were removed upon collection and all the soft tissues were used for the analyses. From the fourth grab replicate, which was sorted separately, animals were taken for trophic analyses and the remaining animals were fixed in 4% buffered formaldehyde and subsequently counted to obtain quantitative data on species composition per sample.

2.3 Stable isotope analysis

Prior to analysis, the samples of sediments and invertebrates were freeze-dried. Freeze-dried samples were sent to Iso-Analytical (UK), where they were processed using Elemental Analysis - Isotope Ratio Mass Spectrometry (EA-IRMS). Samples that contained inorganic carbon were acidified to remove inorganic carbon, but acidification can alter $\delta^{15}N$ (Silberberger et al., 2021). Therefore, the sediments and echinoderm taxa were processed twice, raw (for nitrogen analysis) and acid-washed with 1M hydrochloric acid (for carbon analysis), all the other samples were processed untreated. The layers 2-5cm and 5-10 cm were analyzed only for stations V3 and V5. Stable isotope ratios are expressed in the conventional delta notation ($\delta^{13}C$ / $\delta^{15}N$) relative to VPDB (Vienna PeeDee Belemnite standard) and atmospheric nitrogen. 20% of the samples were analysed twice for quality check.

2.4 Fatty acid analysis

After snap freezing in liquid nitrogen, invertebrate samples for fatty acid analysis were freeze-dried and stored at -80°C under nitrogen until further processing. The total lipids were extracted using Bligh and Dyer method modified for small samples (Bligh and Dyer, 1959). The total lipid content was estimated by weighing an aliquot of lipid samples and expressed relative to dry weight. The chloroform phase was then dried under nitrogen at 40 °C. The lipids were saponified with 0.5M NaOH in methanol under N_2 at 100°C for 15 min. After cooling fatty acid methyl esters were obtained through methylation using 12% BF_3 solution in methanol under N_2 at 100°C for 5 min, the tubes were cooled again and the FAMEs were extracted with 1 ml hexane for 1 min at 100°C. The hexane phase containing methyl esters was washed with 3 ml saturated NaCl solution, transferred to glass vials, dried under nitrogen, and sent to The Station Biologique de Roscoff (France) for GC-MS analysis The obtained chromatograms were processed with Chrombox Q (www.chrombox.org). The identification of fatty acid methyl esters was based on the retention time of standard mixture containing 37 compounds as well as mass spectrum data compared to the reference database (www.chrombox.org). The similarity of species fatty acid profiles was assessed using Bray-Curtis similarity index based on square-root transformed percentage composition (Legeżyńska et al., 2014). Fatty acids were clustered together using index of association: a similarity index, that is calculated as a Bray-Curtis index based on variable abundances standardized across samples with values ranging from 0 (perfect “negative” association) to 100 (perfect “positive” association”) (Clarke et al., 2014).

3. Results and discussion

3.1 Trophic niches of the macrofauna

Overall, 20 taxa were sampled for stable isotope analysis, most of the taxa studied belong to deposit feeders, with a few being carnivore species (Table 1). While many taxa showed overlap in their isotopic niche (Figure 2), fatty acid profiles were highly species-specific (over 80% similarity) (Figure 3).

The results of stable isotope analysis revealed that most of the benthic taxa studied were more enriched in carbon and nitrogen than sediment organic matter, except the ophiuroid *Amphilepis norvegica*, bivalves *Ennucula tenuis,* and *Thyasira sarsii* (Figure 2). $\delta^{13}C$ of sediment organic matter was close to the marine end-member defined for the region ($\delta^{13}C$ = -19.3‰; Faust and Knies, 2019), indicating that most of the organic matter in sediments is of phytoplankton origin. Marine polyunsaturated fatty acids 20:5n-3 and 22:6n-3, typical markers for diatoms and dinoflagellates, respectively (Dalsgaard et al., 2003), were present in all taxa present (Figure 4), but higher percentages are reported for 20:5n-3. This reflects the phytoplankton composition in the area, where diatoms are present from May to August, while dinoflagellates are found occasionally in smaller numbers (Skreslet et al., 2000). Another common polyunsaturated fatty acid was 20:4n-6, particularly abundant in the echinoderm *Ctenodiscus crispatus*, the sipunculid *Golfingia margaritacea,* and the polychaete *Phylo norvegicus,* all of which can be considered as subsurface deposit feeders. Although 20:4n-6 is often used as a marker for macroalgal consumption, in other habitats, where macroalgal vegetation is absent, e.g. deep sea, it is believed to be of sediment origin, where it might be synthesized by bacteria and protists, particularly by foraminifera, and therefore is characteristic of subsurface deposit feeders (Howell et al., 2003; Legeżyńska et al., 2014; Kharlamenko et al., 2018). Iso and anteiso fatty acids, commonly used as bacterial markers of heterotrophic bacteria in marine food webs (Dalsgaard et al., 2003) were present in all taxa, except *Thyasira sarsii*. Bacterial fatty acids, together with common polyunsaturated fatty acids suggest that bacterially reworked marine organic matter is the primary source for the macrobenthic community in the fjord basin. However, the relative proportion of these fatty acids differed among the taxa studied even with the same feeding habit.

Surface deposit feeding bivalves, *Nucula tumidula* and *Abra nitida,* differed both in their stable isotopic niche and fatty acid composition. *Abra nitida* had the lowest trophic level of all the deposit feeding taxa (excluding *Ennucula tenuis*), while fatty acid composition was characterised by the highest abundance of 20:5n-3 fatty acid and low proportion of bacterial fatty acids, indicating that this species prefers less degraded organic matter of phytoplankton origin. *Nucula tumidula* had a high niche overlap with the polychaete *Melinna cristata,* but the latter showed a wider isotopic niche. The fatty acid analysis revealed that *N. tumidula* had a higher proportion of 20:4n-6, while *M. cristata* was characterised by the presence of 16:1n-10, 7 Me fatty acid. The latter fatty acid is considered to be of bacterial origin (Imbs et al., 2007) and might indicate a preference towards feeding on detritus associated with different bacterial groups. The three surface deposit feeders were all characterised by the presence of 4,8,12-Me 13:0 fatty acid, which is a degradation product of phytol, the ester-linked side-chain of chlorophyll-a (Rontani and Valkman, 2003). The surface deposit feeding polychaetes *Chaetozone setosa* and *Terebellides stroemii,* had stable isotope values in the range of *M. cristata,* but occurred much rarer at the stations*.* Compared to *M. cristata*, *T. stroemii* had a higher concentration of 20:5n-3 and lower concentrations of 22:6n-3 as well as n-6 polyunsaturated fatty acids, indicating more selective feeding on diatom-derived phytodetritus. Among the surface deposit feeding taxa, the bivalve *Ennucula tenuis* had the lowest δ^{15}N values, almost the same as sediment organic matter. Generally, *E. tenuis* has a shallower distribution compared to the bathyal *N. tumidula* (Josefson, 1985), so the only individual that was recovered during our sampling campaign might be a migrant from shallower depths, where the bentho-pelagic coupling is stronger, which could explain the lower δ^{15}N as a result of feeding on fresher phytoplankton material.

Among the subsurface deposit feeders, the polychaete families Maldanidae (*Clymenura borealis* and *Praxillella gracilis*) and Pectinaridae (*Amphictene auricoma* and *Pectinaria belgica)* also showed differentiation in their trophic niches indicated by both stable isotope and fatty acid analysis. Specifically, the maldanid polychaetes showed a high proportion of 12:0 fatty acid along with higher abundance of 16:1n-7 and 18:1n-7, which are characteristic of facultative anaerobic bacteria (Parkes and Taylor, 1983), while higher concentrations of iso and anteiso fatty acids were found in pectinarids. This, again, can indicate the species' affinities to different detritus patches and microbial communities within the sediment or feeding at different sediment depths. Compared to other subsurface deposit feeding polychaetes, *Phylo norvegicus* had high amounts of n-3 (20:5n-3 and 22:5n-3) and n-6 (20:4n-6 and 22:4n6) polyunsaturated fatty acids, as well as lower amounts of iso and anteiso fatty acids. The high amount of polyunsaturated fatty acids is similar to a related species of the same family, *Scoloplos armiger*, in Kongsfjord, Svalbard (Legeżyńska et al., 2014). *Phylo norvegicus* can borrow quite deep in the sediment (Josefson, 1981), which together with a quite narrow isotopic niche and high values of δ^{15}N, suggests more selective feeding behaviour, possibly ingesting meiobenthic prey, compared to pectinarid and maldanid polychaetes.

The polychaete *Aphelochaeta sp.* had an isotopic niche between *M. cristata* and pectinarid polychaetes, which is consistent with its feeding habit as it is both surface and subsurface deposit feeder. However, compared to other polychaete species, it had an unusual fatty acid profile with a high contribution of non-methylene interrupted fatty acids, particularly 22:2. These fatty acids are not of phytoplankton or bacterial origin but rather synthetised by marine invertebrates, although the importance of non-methylene interrupted fatty acids is not completely understood (Barnathan, 2009). The high content of non-methylene interrupted fatty acids was also characteristic for the sipunculid *Golfingia margaritacea*, which is consistent with previous data on this species (Kharlamenko et al., 2018). Kharlamenko et al. (2018) classified *G. margaritacea* as a subsurface deposit feeder but found that its fatty acid composition is more similar to other surface deposit feeders in their study. In our study, $\delta^{15}N$ of this species indicated subsurface deposit feeding as it was similar to maldanid polychaetes.

The echinoderm *Ctenodiscus crispatus* had a very distinct isotopic niche as well as fatty acid profile. It non-selectively ingests mud and various prey items were identified in its stomach content, including nematodes and foraminifera (Shick et al., 1981; Gale et al., 2013). During field sampling, we also observed individuals of *C. crispatus* with stomachs filled with mud. In general, the fatty acid composition of this species was similar to previously described compositions (Sargent et al., 1983; Bell and Sargent, 1985; Kharlamenko et al., 2013). Also, the isotopic profile with enriched $\delta^{15}N$ and $\delta^{13}C$ values was similar to findings along the Norwegian coast, the Sea of Japan, and eastern Canada (Nilsen et al., 2008; Gale et al., 2013; Kharlamenko et al., 2013; Silberberger et al., 2018). The major polyunsaturated fatty acid in this species is 20:4n-6, which origin remains unknown, but might be linked to the benthic microbial food web (Kharlamenko et al., 2013). We found two isoprenoid fatty acids previously not reported for *C. crispatus*, phytanic and pristanic, which are products of phytol degradation (Rontani and Valkman, 2003). Unlike the other phytol degradation product 4,8,12-Me 13:0, which was observed in several other taxa, these two compounds were not observed in any other taxon suggesting that *C. crispatus* has a metabolic pathway to utilise phytol in sediments converting it to phytanic, and, consequently, to pristanic acid (Rontani and Valkman, 2003). This highlights the wide trophic niche of this species, which might utilise very different food sources from sediments.

Species recognized as carnivore in the study included polychaetes *Neoleanira tetargona*, *Lumbrineris near cingulata, Drilonereis brattsroemi* and the echinoderm *Ophioscolex glacialis*. These species showed very different stable isotopic signatures, suggesting different prey animals for these species. Moreover, two individuals of *N. tetragona* differed greatly in their isotopic signatures, differing greatly in $\delta^{15}N$, indicating that this species might have a more omnivorous feeding strategy, possibly relying in part on surface deposit feeding or ingestion of phytodetritus.

The bivalve *Thyasira sarsii* was the species that differed most from the other species in the basin, both in the stable isotopic signature as well as fatty acid composition. The values of the stable carbon isotopes in the gill and the foot are consistent with measurements performed on *T. sarsii* collected in deep Skagerrak and suggest high dependence on the sulphur-oxidizing bacteria in the gills (Schmaljohann et al., 1990; Dando and Spiro, 1993). The high abundance of 16:1n-7 and 18:1n-7 fatty acids as well as absence of branched iso and anteiso fatty acids is similar to *T. flexuosa* (Fullarton et al., 1995) and highly contrasts with the fatty acid composition of other macrofaunal taxa that rely on sediment organic matter. The difference in isotopic signature between foot and gill tissue suggests that symbiotic bacteria are the main source of carbon for *T. sarsii,* which is different from symbiotic *T. cf. gouldi*, which relies in part on deposit feeding (Zanzerl et al., 2019). Interestingly, in Malnesfjord, northern Norway, a *Thyasira sp.*, with a similar isotopic signature was suggested as possible prey for carnivore polychaete Nephtys sp., which had also a very depleted $\delta^{13}C$ (Silberberger et al., 2018). This indicates that carbon of chemosynthetic origin can be occasionally transferred to higher trophic levels, although it was not observed in our study. Another species, an ophiuroid *Amphilepis norvegica,* was also more depleted in $\delta^{13}C$ than organic matter of sediments, indicating that it is not the only source of carbon for the species. Most probably this species, originally described as Amphiura and phylogenetically related to Amphiuridae (Hunter et al., 2016), is also able to suspension feed similar to some species of *Amphiura* ophiuroids (Ockelmann and Muus, 1978), as pelagic carbon might have lower values of $\delta^{13}C$ compared to sediment organic matter (Nilsen et al., 2008; Sokołowski et al., 2014).

3.2 Effects of fish farming

Overall, the sediment characteristics showed variation in a narrow range among the stations (Figure 5). A small increase in TOC was observed at stations closer to the fish farm compared to the reference station, especially on the stations V2 and V3, which was accompanied by slightly more depleted values of δ^{13}C and δ^{15}N. The difference among sediment layers in sediment characteristics was much more pronounced for the station closest to the fish farm (V3) compared to the reference station (V5). However, the observed values (up to 2.08 %) are in the range of the TOC values recorded in other fjords in the region (Faust and Knies, 2019; Kokarev et al., 2021). In a study from a deep fjord (Uggdalsfjord) in western Norway high sedimentation rates and shift in macrobenthic community structure was observed only within 250 meters of the fish farm, while TOC and TON in the sediment were not elevated (Kutti et al., 2007a; Kutti et al., 2007b). Our closest station was located approximately 500 meters from the fish farm. Therefore, it is not clear, if the elevated TOC in our study is a consequence of sedimentation from the fish farm or natural variation. Two fatty acids, 18:2n-6 and 18:3n-3, are commonly associated with consumption of feed farm waste in benthic invertebrates (White et al., 2019). 18:2n-6 was common for many species in the basin (Figure 4) independent of their distance to the farm. The concentration of 18:2n-6 fatty acid showed an increase near the fish farm only for *Aphelochaeta sp.* but was insignificant in this species from other locations (Figure 6). We did not observe 18:3n-3 in our samples at all, and no particular relationship was observed between δ^{13}C values of the most common surface deposit feeding fauna and distance from the fish farm (Figure 6). This suggests that 18:2n-6 in our study might come from an alternative source, most probably microalgae (White et al., 2019). Therefore, sedimentation from the fish farm could not be traced as a source for macrobenthic consumers in our study.

4 Conclusion

Although some macrobenthic species studied show trophic niche overlap indicated by stable isotope and fatty acid analyses, the most common species (with a higher number of samples) have distinct trophic niches, which indicates that niche partitioning processes are important for the coexistence of species in habitats such as deep fjord basins, particularly with restricted water exchange. Restricted water exchange with surrounding waters limits dispersal of individuals from neighbouring communities increasing the role of competition. Moreover, as suggested by our data, the community relies on bacterially reworked organic matter of phytoplankton origin, which makes the basin a more food-limited environment for macrobenthos compared to shallower habitats, where the bentho-pelagic coupling is stronger and more fresh organic matter of phytoplankton reaches the seafloor. Indeed, evidence of resource partitioning was documented for bathyal holothurians in the Northeast Atlantic (Hudson et al., 2003). In other studies, no evidence of food partitioning was observed among co-occurring echinoderm species in a shallow fjord (Godbold et al., 2009), but also in a deep area of the Antarctic shelf with high food supply from overlying waters (Wigham et al., 2008). No food partitioning was observed for three deposit feeding bivalves on the Bering sea shelf (Oxtoby et al., 2016) and among native species of deposit feeders in the Baltic sea (Karlson et al., 2015). In our study, small-scale heterogeneity in the distribution of detritus patches and associated bacteria/meiofauna on and within the sediment possibly might create small-scale heterogeneity that sustains the diversity of niches available for macrofauna. However, we did not observe the effects of fish farm waste on the basin community, but aquaculture impact might be basin specific and dependent on fjord geomorphology and hydrology. In this study, we mainly focused on biomass-dominant species, which are easier to collect for stable isotope and, particularly, fatty acid analyses, as sufficient biomasses are required. Some of the smaller common species in the basin (bivalves *Kelliella miliaris*, *Parathyasira equalis, Yoldiella nana* and the polychaete *Myriochele olgae*) were not collected for such analyses, and their trophic niches remain unknown and require further investigation.

References

Abrams P (1983) The Theory of Limiting Similarity. Annu Rev Ecol Syst 14:359–376.

Bannister RJ, Johnsen IA, Hansen PK, Kutti T, Asplin L (2016) Near- and far-field dispersal modelling of organic waste from Atlantic salmon aquaculture in fjord systems. ICES J Mar Sci 73:2408–2419.

Barnathan G (2009) Non-methylene-interrupted fatty acids from marine invertebrates: Occurrence, characterization and biological properties. Biochimie 91:671–678.

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: A novel approach using stable isotope analysis. J Anim Ecol 73:1007–1012.

Bell M V., Sargent JR (1985) Fatty acid analyses of phosphoglycerides from tissues of the clam Chlamys islandica (Muller) and the starfish Ctenodiscus crispatus (Retzius) from Balsfjorden, Northern Norway. J Exp Mar Bio Ecol 87:31–40.

Bligh, E.G. and Dyer WJ (1959) A rapid method of total lipid extraction and purification. Can J Biochem Physiol 37:911-917.

Clarke, K. R., Gorley, R. N., Somerfield, P. J., & Warwick, R. M. (2014). Change in marine communities: an approach to statistical analysis and interpretation. Primer-E Ltd, Plymouth.

Dalsgaard J, John MS, Kattner G, Müller-Navarra D, Hagen W (2003) Fatty acid trophic markers in pelagic marine environment. Adv Mar Biol 46:225–352.

Dando PR, Spiro B (1993) Varying nutritional dependence of the thyasirid bivalves Thyasira sarsi and T. equalis on chemoautotrophic symbiotic bacteria, demonstrated by isotope ratios of tissue carbon and shell carbonate. Mar Ecol Prog Ser 92:151–158.

Dauwe B, Herman PMJ, Heip CHR (1998) Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. Mar Ecol Prog Ser 173:67–83.

Dunton KH, Schonberg S V., Cooper LW (2012) Food web structure of the Alaskan nearshore shelf and estuarine lagoons of the Beaufort Sea. Estuaries and Coasts 35:416–435.

Faust JC, Knies J (2019) Organic matter Sources in North Atlantic fjord sediments. Geochemistry, Geophys Geosystems 20:2872–2885.

Fullarton JG., Dando PR., Sargent JR., Southwards AJ., & Southward EC (1995) Fatty acids of hydrothermal vent Ridgeia Piscesae and inshore bivalves containing symbiotic bacteria. J Mar Biol Assoc United Kingdom 75:455–468.

Gale KSP, Hamel JF, Mercier A (2013) Trophic ecology of deep-sea Asteroidea (Echinodermata) from eastern Canada. Deep Res Part I Oceanogr Res Pap 80:25–36.

Godbold JA, Rosenberg R, Solan M (2009) Species-specific traits rather than resource partitioning mediate diversity effects on resource use. PLoS One 4: e7423.

Hart SP, Usinowicz J, Levine JM (2017) The spatial scales of species coexistence. Nat Ecol Evol 1:1066–1073.

Howell KL, Pond DW, Billett DSM, Tyler PA (2003) Feeding ecology of deep-sea seastars (Echinodermata: Asteroidea): A fatty-acid biomarker approach. Mar Ecol Prog Ser 255:193–206.

Hudson IR, Wigham BD, Billett DSM, Tyler PA (2003) Seasonality and selectivity in the feeding ecology and reproductive biology of deep-sea bathyal holothurians. Prog Oceanogr 59:381–407.

Hunter RL, Brown LM, Alexander Hill C, Kroeger ZA, Rose SE (2016) Additional insights into phylogenetic relationships of the Class Ophiuroidea (Echinodermata) from rRNA gene sequences. J Zool Syst Evol Res 54:269–275.

Imbs AB, Latyshev NA, Zhukova N V., Dautova TN (2007) Comparison of fatty acid compositions of azooxanthellate Dendronephthya and zooxanthellate soft coral species. Comp Biochem Physiol - B Biochem Mol Biol 148:314–321.

Jordà Molina È, Silberberger MJ, Kokarev V, Reiss H (2019) Environmental drivers of benthic community structure in a deep sub-arctic fjord system. Estuar Coast Shelf Sci 225:106239.

Josefson AB (1981) Persistence and structure of two deep macrobenthic communities in the Skagerrak (west coast of Sweden). J Exp Mar Bio Ecol 50:63–97.

Josefson AB (1985) Distribution of diversity and functional groups of marine benthic infauna in the skagerrak (Eastern north sea) - can larval availability affect diversity? Sarsia 70:229–248.

Jøstensen JP, Landfald B (1997) High prevalence of polyunsaturated-fatty-acid producing bacteria in arctic invertebrates. FEMS Microbiol Lett 151:95–101.

Jumars PA, Dorgan KM, Lindsay SM (2015) Diet of worms emended: An update of polychaete feeding guilds. Ann Rev Mar Sci 7:497–520.

Karlson AML, Gorokhova E, Elmgren R (2015) Do deposit-feeders compete? Isotopic niche analysis of an invasion in a species-poor system. Sci Rep 5:1–8.

Kelly JR, Scheibling RE (2012) Fatty acids as dietary tracers in benthic food webs. Mar Ecol Prog Ser 446:1–22.

Kharlamenko VI, Brandt A, Kiyashko SI, Laura W (2013) Trophic relationship of benthic invertebrate fauna from the continental slope of the Sea of Japan. Deep Res Part II Top Stud Oceanogr 87:34–42.

Kharlamenko VI, Maiorova AS, Ermolenko E V. (2018) Fatty acid composition as an indicator of the trophic position of abyssal megabenthic deposit feeders in the Kuril Basin of the Sea of Okhotsk. Deep Res Part II Top Stud Oceanogr 154:374–382.

Kokarev V, Tachon M, Austad M, Mcgovern M, Reiss H (2021) Strong macrobenthic community differentiation among sub-Arctic deep fjords on small spatial scales. Estuar Coast Shelf Sci 252:107271.

Kutti T, Ervik A, Hansen PK (2007a) Effects of organic effluents from a salmon farm on a fjord system. I. Vertical export and dispersal processes. Aquaculture 262:367–381.

Kutti T, Hansen PK, Ervik A, Høisæter T, Johannessen P (2007b) Effects of organic effluents from a salmon farm on a fjord system. II. Temporal and spatial patterns in infauna community composition. Aquaculture 262:355–366.

Legeżyńska J, Kędra M, Walkusz W (2014) Identifying trophic relationships within the high Arctic benthic community: How much can fatty acids tell? Mar Biol 161:821–836.

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, et al. (2004) The metacommunity concept: A framework for multi-scale community ecology. Ecol Lett 7:601–613.

Nichols DS (2003) Prokaryotes and the input of polyunsaturated fatty acids to the marine food web. FEMS Microbiol Lett 219:1–7.

Nilsen M, Pedersen T, Nilssen EM, Fredriksen S (2008) Trophic studies in a high-latitude fjord ecosystem - A comparison of stable isotope analyses (δ13C and δ15N) and trophic-level estimates from a mass-balance model. Can J Fish Aquat Sci 65:2791–2806.

Ockelmann KW, Muus K (1978) The biology, ecology and behaviour of the bivalve Mysella bidentata (Montagu). Ophelia 17:1–93.

Olsen SA, Ervik A, Grahl-Nielsen O (2012) Tracing fish farm waste in the northern shrimp Pandalus borealis (Krøyer, 1838) using lipid biomarkers. Aquac Environ Interact 2:133–144.

Oxtoby LE, Budge SM, Iken K, O'Brien DM, Wooller MJ (2016) Feeding ecologies of key bivalve and polychaete species in the Bering Sea as elucidated by fatty acid and compound-specific stable isotope analyses. Mar Ecol Prog Ser 557:161–175.

Parkes RJ, Taylor J (1983) The relationship between fatty acid distributions and bacterial respiratory types in contemporary marine sediments. Estuar Coast Shelf Sci 16:173-174.

Richoux NB, Vermeulen I, Froneman PW (2014) Fatty acid profiles reveal temporal and spatial differentiation in diets within and among syntopic rocky shore suspension-feeders. Mar Ecol Prog Ser 495:143–160.

Rontani J-F, Volkman JK (2003) Phytol degradation products as biogeochemical tracers in aquatic environments. Org Geochem 34:1–35.

Sargent J. R., Falk-Petersen I-B, Calder AG (1983) Fatty acid compositions of neutral glycerides from the ovaries of the asteroids Ctenodiscus crispatus, Asterias lincki and Pteraster militaris from Balsfjorden, northern Norway. Mar Biol 72:257–264.

Schmaljohann R, Faber E, Whiticar M, Dando P (1990) Co-existence of methane- and sulphur-based endosymbioses between bacteria and invertebrates at a site in the Skagerrak. Mar Ecol Prog Ser 61:119–124.

Schoener TW (1974) Resource Partitioning in Ecological Communities. Science 185:27–39.

Shick J, Edwards K, Dearborn J (1981) Physiological ecology of the deposit-feeding sea star Ctenodiscus crispatus: Ciliated surfaces and animal-sediment interactions. Mar Ecol Prog Ser 5:165–184.

Silberberger MJ, Koziorowska-Makuch K, Kuliński K, Kędra M (2021) Stable isotope mixing models are biased by the choice of sample preservation and pre-treatment: Implications for studies of aquatic food webs. Front Mar Sci 7:1–18.

Silberberger MJ, Renaud PE, Kröncke I, Reiss H (2018) Food-web structure in four locations along the European shelf indicates spatial differences in ecosystem functioning. 5:1–15.

Skreslet S, Espinasse M, Olsen K, Espinasse BD (2020) Variable predator–prey relations in zooplankton overwintering in subarctic fjords. Polar Res 39:1–17.

Skreslet S, Olsen K, Mohus Å, Tande KS (2000) Stage-specific habitats of Calanus finmarchicus and Calanus helgolandicus in a stratified northern Norwegian fjord. ICES J Mar Sci 57:1656–1663.

Sokołowski A, Szczepańska A, Richard P, Kędra M, Wołowicz M, Węsławski JM (2014) Trophic structure of the macrobenthic community of Hornsund, Spitsbergen, based on the determination of stable carbon and nitrogen isotopic signatures. Polar Biol 37:1247–1260.

Sokołowski A, Wołowicz M, Asmus H, Asmus R, Carlier A, Gasiunaité Z, et al. (2012) Is benthic food web structure related to d.iversity of marine macrobenthic communities? Estuar Coast Shelf Sci 108:76–86

Sweetman AK, Witte U (2008) Macrofaunal response to phytodetritus in a bathyal Norwegian fjord. Deep Res Part I Oceanogr Res Pap 55:1503–1514.

Warner G (1982) Food and feeding mechanisms: Ophiuroidea. In: Jangoux M, Lawrence JM. (Eds) Echinoderm Nutrition. A.A.Balkema, Rotterdam, Netherlands pp.161-181.

White CA, Bannister RJ, Dworjanyn SA, Husa V, Nichols PD, Kutti T, et al. (2017) Consumption of aquaculture waste affects the fatty acid metabolism of a benthic invertebrate. Sci Total Environ 586:1170–1181.

White CA, Woodcock SH, Bannister RJ, Nichols PD (2019) Terrestrial fatty acids as tracers of finfish aquaculture waste in the marine environment. Rev Aquac 11:133–148.

Wigham BD, Galley EA, Smith CR, Tyler PA (2008) Inter-annual variability and potential for selectivity in the diets of deep-water Antarctic echinoderms. Deep Res Part II Top Stud Oceanogr 55:2478–2490.

Wikander PB (1980) Biometry and behaviour in Abra nitida (Müller) and A. longicallus (Scacchi) (Bivalvia, Tellinacea). Sarsia 65:255–268.

Witte U, Aberle N, Sand M, Wenzhöfer F (2003) Rapid response of a deep-sea benthic community to POM enrichment: An in situ experimental study. Mar Ecol Prog Ser 251:27–36.

Woodcock SH, Meier S, Keeley NB, Bannister RJ (2019) Fate and longevity of terrestrial fatty acids from caged fin-fish aquaculture in dynamic coastal marine systems. Ecol Indic 103:43–54.

Yakushev E V., Wallhead P, Renaud PE, Ilinskaya A, Protsenko E, Yakubov S, et al. (2020) Understanding the biogeochemical impacts of fish farms using a benthic-pelagic model. Water (Switzerland) 12:2384.

Zanzerl H, Salvo F, Jones SW, Dufour SC (2019) Feeding strategies in symbiotic and asymbiotic thyasirid bivalves. J Sea Res 145:16–23.

Tables

Table 1. Taxa sampled and number of samples (N) for stable isotope analysis. SDF – surface deposit feeders, SSDF – subsurface deposit feeders, C—carnivore, SY—symbiont bacteria.*Reference for feeding habit. For polychaetes feeding habit was assigned according to Jumars et al., 2015.

Higher taxon	Family	Species	Feeding habit	N	δ^{13}C (‰)	SD	δ^{15}N (‰)	SD	Reference*
Bivalvia	Semelidae	Abra nitida	SDF	8	-18.88	0.29	7.76	0.29	Wikander, 1980
Bivalvia	Nuculidae	Ennucula tenuis	SDF	1	-19.26	NA	5.76	NA	Oxtoby et al., 2016
Bivalvia	Nuculidae	Nucula tumidula	SDF	5	-19.68	0.15	8.79	0.32	
				1 (gill)	-38.50	NA	-8.89	NA	
Bivalvia	Thyasiridae	Thyasira sarsii	SSDF/ SY	1 (foot)	-35.93	NA	-4.14	NA	Dando and Spiro, 1993
Echinodermata	Amphilepididae	Amphilepis norvegica	No data	1	-22.11	NA	11.33	NA	
Echinodermata	Ctenodiscidae	Ctenodiscus crispatus	SSDF	10	-16.62	1.08	13.10	0.67	Shick et al., 1981; Gale et al., 2013
Echinodermata	Ophioscolecidae	Ophioscolex glacialis	C	3	-20.13	0.48	11.31	0.34	Warner, 1982
Polychaeta	Ampharetidae	Melinna cristata	SDF	9	-20.13	0.33	9.60	0.69	
Polychaeta	Cirratulidae	Aphelochaeta sp.	SDF/SSDF	5	-19.93	0.27	10.51	0.52	
Polychaeta	Cirratulidae	Chaetozone setosa agg.	SDF	1	-20.69	NA	8.99	NA	
					-19.93	NA	12.87	NA	
Polychaeta	Lumbrineridae	Lumbrineris near cingulata	C	2	-21.01	NA	12.18	NA	
Polychaeta	Maldanidae	Clymenura borealis	SSDF	1	-17.94	NA	11.17	NA	
					-18.91	NA	11.60	NA	
Polychaeta	Maldanidae	Praxillella gracilis	SSDF	2	-19.05	NA	11.77	NA	
Polychaeta	Oenonidae	Drilonereis brattstroemi	C	1	-18.48	NA	13.17	NA	
Polychaeta	Orbiniidae	Phylo norvegicus	SSDF	4	-19.77	0.08	12.34	0.14	

Polychaeta	Pectinariidae	Amphictene auricoma	SSDF	1	-19.79	NA	10.89	NA	
Polychaeta	Pectinariidae	Pectinaria belgica	SSDF	3	-20.10	0.64	10.82	0.48	
					-18.48	NA	11.18	NA	
Polychaeta	Sigalionidae	Neoleanira tetragona	C	2	-19.20	NA	9.40	NA	
Polychaeta	Trichobranchidae	Terebellides stroemii agg.	SDF	1	-20.10	NA	8.85	NA	
Sipuncula	Golfingiidae	Golfingia maragritacea	SSDF	1	-18.13	NA	11.27	NA	Kharlamenko et al., 2018

Figure legends

Figure 1. Map of the study area. Blues circles indicate grab sampling locations and CTD measurements, green square indicates a fish farm, a dashed line – 350 meters isobath

Figure 2. Biplot of stable isotope data. Species with three or more measurements are represented as mean and 95% confidence interval (error bars). *T. sarsii* was identified as an outlier and not shown on the plot

Figure 3. UPGMA clustering of species Bray-Curtis similarities based on square-root transformed percent fatty acid composition.

Figure 4. Shade plot of square root transformed percent fatty acid composition. Scale is square root transformed percent contribution of a fatty acid to the total fatty acid composition. Fatty acids clustered using UPGMA algorithm based on index of association.

Figure 5. Characteristics of the sediment samples: total organic carbon (TOC), carbon stable isotope ratio ($\delta^{13}C$), total nitrogen content (TN), nitrogen stable isotope ratio ($\delta^{15}N$). Note: stations V2 and V4 have the same distance to the fish farm. Only closest (V3) and reference station (V5) were analysed for different sediment layers. In case of the same value for different sediment layers, only lower value is shown.

Figure 6. Relationship between distance from the fish farm and A) content of 18:2n-6 fatty acid in the most common surface deposit feeders, B)stable isotope ratio of most common surface-deposit feeders.

Figure 1

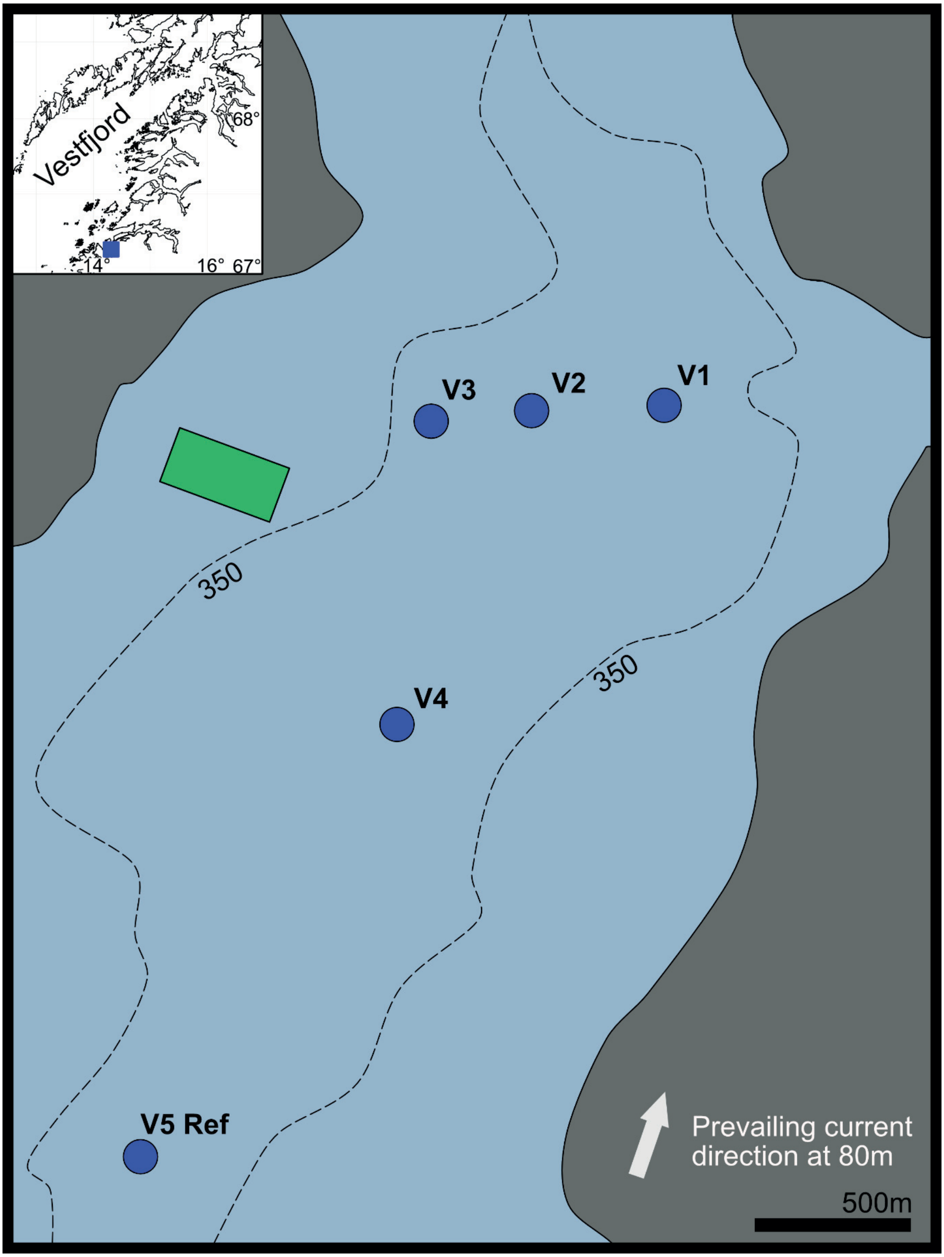

Vestfjord
68°
14°
16°
67°
V3
V2
V1
350
V4
350
V5 Ref
Prevailing current direction at 80m
500m

Figure 2

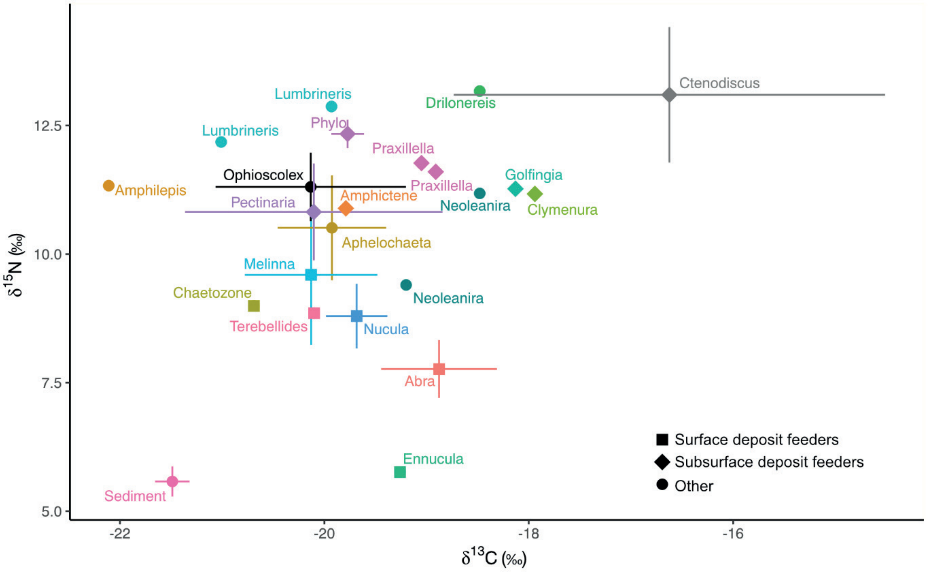
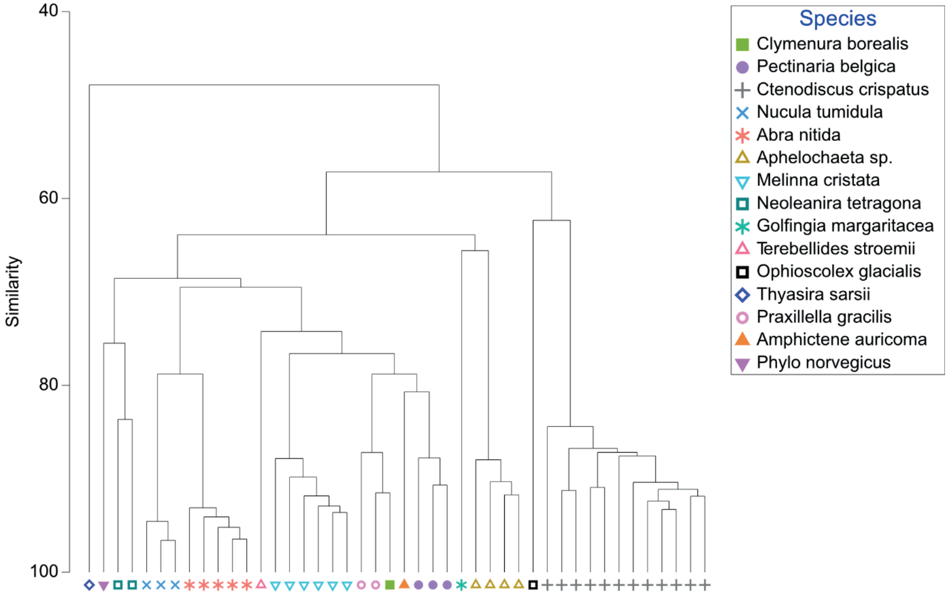

Ctenodiscus
Drilonereis
Lumbrineris
Lumbrineris
Phylo
Praxillella
Praxillella
Ophioscolex
Amphilepis
Amphictene
Pectinaria
Neoleanira
Golfingia
Clymenura
Aphelochaeta
Melinna
Neoleanira
Chaetozone
Terebellides
Nucula
Abra
Ennucula
Sediment
■ Surface deposit feeders
◆ Subsurface deposit feeders
● Other
12.5
10.0
7.5
5.0
-22
-20
-18
-16
$\delta^{15}N$ (‰)
$\delta^{13}C$ (‰)

Figure 3



40
60
80
100
Similarity
Species
Clymenura borealis
Pectinaria belgica
Ctenodiscus crispatus
Nucula tumidula
Abra nitida
Aphelochaeta sp.
Melinna cristata
Neoleanira tetragona
Golfingia margaritacea
Terebellides stroemii
Ophioscolex glacialis
Thyasira sarsii
Praxillella gracilis
Amphictene auricoma
Phylo norvegicus

Figure 4

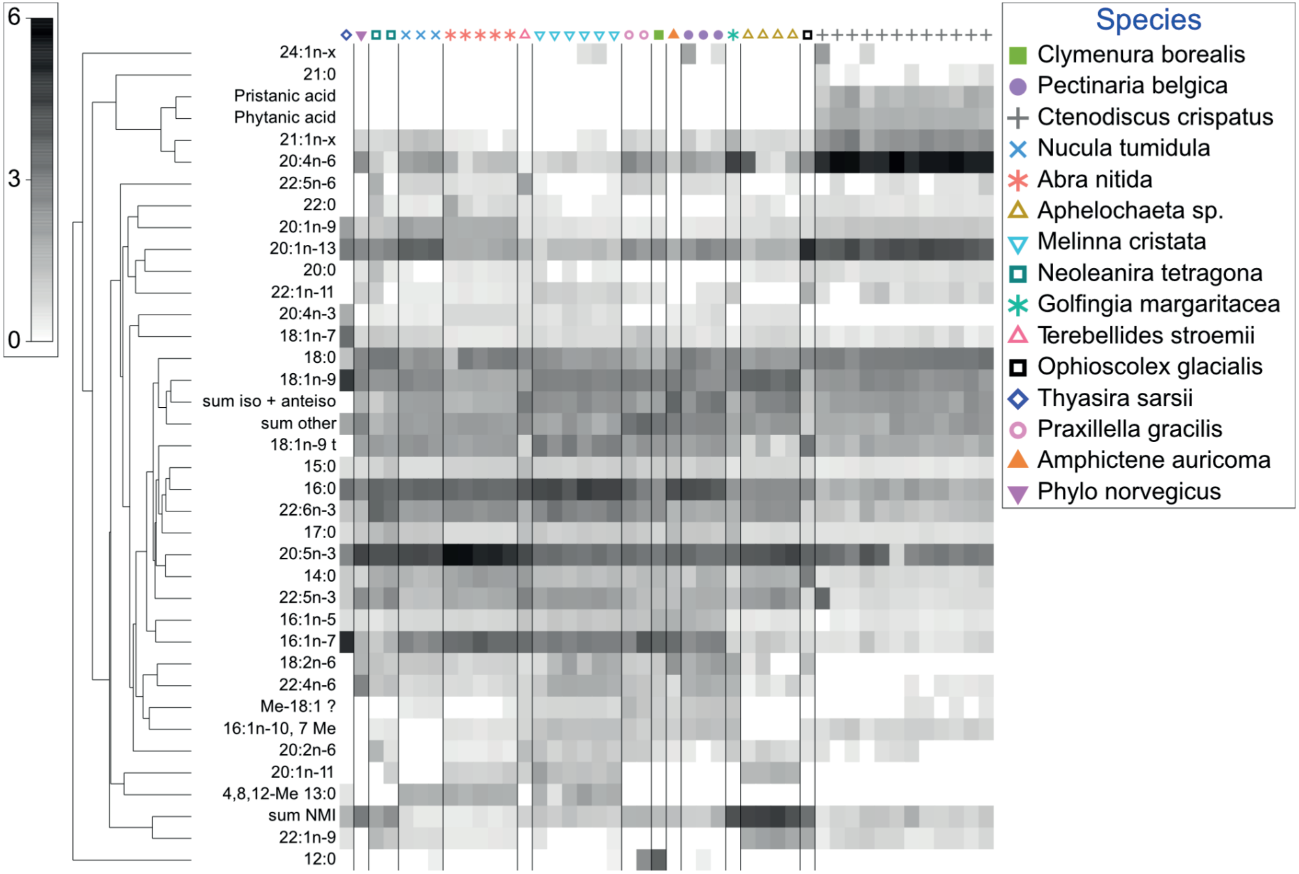

6
3
0
24:1n-x
21:0
Pristanic acid
Phytanic acid
21:1n-x
20:4n-6
22:5n-6
22:0
20:1n-9
20:1n-13
20:0
22:1n-11
20:4n-3
18:1n-7
18:0
18:1n-9
sum iso + anteiso
sum other
18:1n-9 t
15:0
16:0
22:6n-3
17:0
20:5n-3
14:0
22:5n-3
16:1n-5
16:1n-7
18:2n-6
22:4n-6
Me-18:1 ?
16:1n-10, 7 Me
20:2n-6
20:1n-11
4,8,12-Me 13:0
sum NMI
22:1n-9
12:0
Species
Clymenura borealis
Pectinaria belgica
Ctenodiscus crispatus
Nucula tumidula
Abra nitida
Aphelochaeta sp.
Melinna cristata
Neoleanira tetragona
Golfingia margaritacea
Terebellides stroemii
Ophioscolex glacialis
Thyasira sarsii
Praxillella gracilis
Amphictene auricoma
Phylo norvegicus

Figure 5

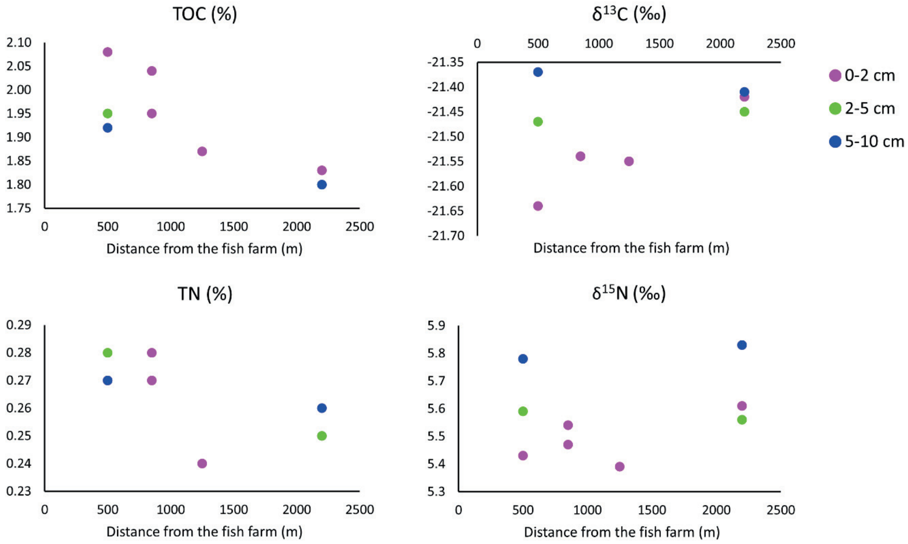
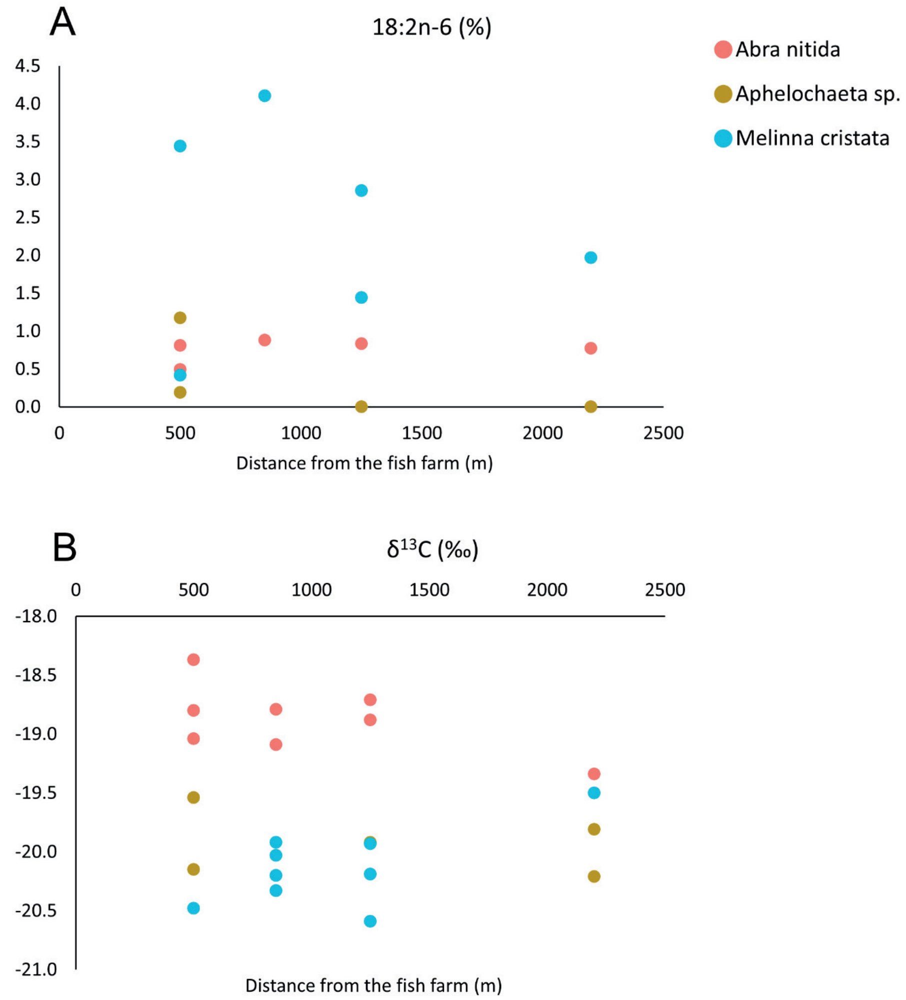

TOC (%)
2.10
2.05
2.00
1.95
1.90
1.85
1.80
1.75
0
500
1000
1500
2000
2500
Distance from the fish farm (m)
δ13C (‰)
0
500
1000
1500
2000
2500
-21.35
-21.40
-21.45
-21.50
-21.55
-21.60
-21.65
-21.70
Distance from the fish farm (m)
● 0-2 cm
● 2-5 cm
● 5-10 cm
TN (%)
0.29
0.28
0.27
0.26
0.25
0.24
0.23
0
500
1000
1500
2000
2500
Distance from the fish farm (m)
δ15N (‰)
5.9
5.8
5.7
5.6
5.5
5.4
5.3
0
500
1000
1500
2000
2500
Distance from the fish farm (m)

Figure 6


A
18:2n-6 (%)
● Abra nitida
● Aphelochaeta sp.
● Melinna cristata
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
500
1000
1500
2000
2500
Distance from the fish farm (m)
B
δ13C (‰)
0
500
1000
1500
2000
2500
-18.0
-18.5
-19.0
-19.5
-20.0
-20.5
-21.0
Distance from the fish farm (m)

List of previously published theses for PhD in Aquaculture / PhD in Aquatic Biosciences, Nord University

No. 1 (2011)
PhD in Aquaculture
Chris André Johnsen
Flesh quality and growth of farmed Atlantic salmon (*Salmo salar* L.) in relation to feed, feeding, smolt type and season
ISBN: 978-82-93165-00-2

No. 2 (2012)
PhD in Aquaculture
Jareeporn Ruangsri
Characterization of antimicrobial peptides in Atlantic cod
ISBN: 978-82-93165-01-9

No. 3 (2012)
PhD in Aquaculture
Muhammad Naveed Yousaf
Characterization of the cardiac pacemaker and pathological responses to cardiac diseases in Atlantic salmon (*Salmo salar* L.)
ISBN: 978-82-93165-02-6

No. 4 (2012)
PhD in Aquaculture
Carlos Frederico Ceccon Lanes
Comparative Studies on the quality of eggs and larvae from broodstocks of farmed and wild Atlantic cod
ISBN: 978-82-93165-03-3

No. 5 (2012)
PhD in Aquaculture
Arvind Sundaram
Understanding the specificity of the innate immune response in teleosts: Characterisation and differential expression of teleost-specific Toll-like receptors and microRNAs
ISBN: 978-82-93165-04-0

No. 6 (2012)
PhD in Aquaculture
Teshome Tilahun Bizuayehu
Characterization of microRNA during early ontogeny and sexual development of Atlantic halibut (*Hippoglossus hippoglossus* L.)
ISBN: 978-82-93165-05-7

No. 7 (2013)
PhD in Aquaculture
Binoy Rajan
Proteomic characterization of Atlantic cod skin mucosa – Emphasis on innate immunity and lectins
ISBN: 978-82-93165-06-04

No. 8 (2013)
PhD in Aquaculture
Anusha Krishanthi Shyamali Dhanasiri
Transport related stress in zebrafish: physiological responses and bioremediation
ISBN: 978-82-93165-07-1

No. 9 (2013)
PhD in Aquaculture
Martin Haugmo Iversen
Stress and its impact on animal welfare during commercial production of Atlantic salmon (*Salmo salar* L.)
ISBN: 978-82-93165-08-8

No. 10 (2013)
PhD in Aquatic Biosciences
Alexander Jüterbock
Climate change impact on the seaweed *Fucus serratus*, a key foundational species on North Atlantic rocky shores
ISBN: 978-82-93165-09-5

No. 11 (2014)
PhD in Aquatic Biosciences
Amod Kulkarni
Responses in the gut of black tiger shrimp *Penaeus monodon* to oral vaccine candidates against white spot disease
ISBN: 978-82-93165-10-1

No. 12 (2014)
PhD in Aquatic Biosciences
Carlo C. Lazado
Molecular basis of daily rhythmicity in fast skeletal muscle of Atlantic cod *(Gadus morhua)*
ISBN: 978-82-93165-11-8

No. 13 (2014)
PhD in Aquaculture
Joanna Babiak
Induced masculinization of Atlantic halibut (*Hippoglossus hippoglossus* L.): towards the goal of all-female production
ISBN: 978-82-93165-12-5

No. 14 (2015)
PhD in Aquaculture
Cecilia Campos Vargas
Production of triploid Atlantic cod: A comparative study of muscle growth dynamics and gut morphology
ISBN: 978-82-93165-13-2

No. 15 (2015)
PhD in Aquatic Biosciences
Irina Smolina
Calanus in the North Atlantic: species identification, stress response, and population genetic structure
ISBN: 978-82-93165-14-9

No. 16 (2016)
PhD in Aquatic Biosciences
Lokesh Jeppinamogeru
Microbiota of Atlantic salmon (*Salmo salar L.*), during their early and adult life
ISBN: 978-82-93165-15-6

No. 17 (2017)
PhD in Aquatic Biosciences
Christopher Edward Presslauer
Comparative and functional analysis of microRNAs during zebrafish gonadal development
ISBN: 978-82-93165-16-3

No. 18 (2017)
PhD in Aquatic Biosciences
Marc Jürgen Silberberger
Spatial scales of benthic ecosystems in the sub-Arctic Lofoten-Vesterålen region
ISBN: 978-82-93165-17-0

No. 19 (2017)
PhD in Aquatic Biosciences
Marvin Choquet
Combining ecological and molecular approaches to redefine the baseline knowledge of the genus Calanus in the North Atlantic and the Arctic Oceans
ISBN: 978-82-93165-18-7

No. 20 (2017)
PhD in Aquatic Biosciences
Torvald B. Egeland
Reproduction in Arctic charr – timing and the need for speed
ISBN: 978-82-93165-19-4

No. 21 (2017)
PhD in Aquatic Biosciences
Marina Espinasse
Interannual variability in key zooplankton species in the North-East Atlantic: an analysis based on abundance and phenology
ISBN: 978-82-93165-20-0

No. 22 (2018)
PhD in Aquatic Biosciences
Kanchana Bandara
Diel and seasonal vertical migrations of high-latitude zooplankton: knowledge gaps and a high-resolution bridge
ISBN: 978-82-93165-21-7

No. 23 (2018)
PhD in Aquatic Biosciences
Deepti Manjari Patel
Characterization of skin immune and stress factors of lumpfish, *Cyclopterus lumpus*
ISBN: 978-82-93165-21-7

No. 24 (2018)
PhD in Aquatic Biosciences
Prabhugouda Siriyappagouder
The intestinal mycobiota of zebrafish – community profiling and exploration of the impact of yeast exposure early in life
ISBN: 978-82-93165-23-1

No. 25 (2018)
PhD in Aquatic Biosciences
Tor Erik Jørgensen
Molecular and evolutionary characterization of the Atlantic cod mitochondrial genome
ISBN: 978-82-93165-24-8

No. 26 (2018)
PhD in Aquatic Biosciences
Yangyang Gong
Microalgae as feed ingredients for Atlantic salmon
ISBN: 978-82-93165-25-5

No. 27 (2018)
PhD in Aquatic Biosciences
Ove Nicolaisen
Approaches to optimize marine larvae production
ISBN: 978-82-93165-26-2

No. 28 (2019)
PhD in Aquatic Biosciences
Qirui Zhang
The effect of embryonic incubation temperature on the immune response of larval and adult zebrafish (*Danio rerio*)
ISBN: 978-82-93165-27-9

No. 29 (2019)
PhD in Aquatic Biosciences
Andrea Bozman
The structuring effects of light on the deep-water scyphozoan *Periphylla periphylla*
ISBN: 978-82-93165-28-6

No. 30 (2019)
PhD in Aquatic Biosciences
Helene Rønquist Knutsen
Growth and development of juvenile spotted wolffish (*Anarhichas minor*) fed microalgae incorporated diets
ISBN: 978-82-93165-29-3

No. 31 (2019)
PhD in Aquatic Biosciences
Shruti Gupta
Feed additives elicit changes in the structure of the intestinal bacterial community of Atlantic salmon
ISBN: 978-82-93165-30-9

No. 32 (2019)
PhD in Aquatic Biosciences
Peter Simon Claus Schulze
Phototrophic microalgal cultivation in cold and light-limited environments
ISBN: 978-82-93165-31-6

No. 33 (2019)
PhD in Aquatic Biosciences
Maja Karoline Viddal Hatlebakk
New insights into Calanus glacialis and C. finmarchicus distribution, life histories and physiology in high-latitude seas
ISBN: 978-82-93165-32-3

No. 34 (2019)
PhD in Aquatic Biosciences
Arseny Dubin
Exploration of an anglerfish genome
ISBN: 978-82-93165-33-0

No. 35 (2020)
PhD in Aquatic Biosciences
Florence Chandima Perera Willora Arachchilage
The potential of plant ingredients in diets of juvenile lumpfish (*Cyclopterus lumpus*)
ISBN: 978-82-93165-35-4

No. 36 (2020)
PhD in Aquatic Biosciences
Ioannis Konstantinidis
DNA hydroxymethylation and improved growth of Nile tilapia (*Oreochromis niloticus*) during domestication
ISBN: 978-82-93165-36-1

No. 37 (2021)
PhD in Aquatic Biosciences
Youngjin Park
Transcriptomic and cellular studies on the intestine of Atlantic salmon
Discovering intestinal macrophages using omic tools
ISBN: 978-82-93165-34-7

No. 38 (2021)
PhD in Aquatic Biosciences
Purushothaman Kathiresan
Proteomics of early embryonic development of zebrafish (Danio rerio)
ISBN: 978-82-93165-37-8

Fjords are marine inlets characteristic for the entire Norwegian coast. They are not only important habitats for diverse populations of marine species, but also locations for industrial settlement. Globally fjords play an important role in carbon cycling and sequestration through burial of organic matter in the sediments, where remineralisation of organic matter is facilitated by benthic fauna. The biodiversity of benthos remains understudied as well as many other ecological components in fjord ecosystems, which limits our understanding of ecological processes and their vulnerability to changes associated with ocean warming and direct human impacts. The aim of the present thesis is to investigate taxonomic and functional composition of macrobenthic communities in eight deep sub-Arctic fjord basins (>290 m) in the Vestfjord region. Two groups of basins could be distinguished in the study area based on macrobenthic community structure, which corresponded to different bottom water masses, with further differentiation on a basin scale. It is suggested that low connectivity among basins and fjord systems, and particularly the presence of dispersal barriers such as shallow sills, results in independent community assembly and, consequently, among-basin macrobenthos variation. This finding indicates that ecological processes in closely situated fjords are only weakly interconnected.

NORD
University

ISBN: 978-82-93165-38-5
Trykk: Trykkeriet, Nord universitet
www.nord.no