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

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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

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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.

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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

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.

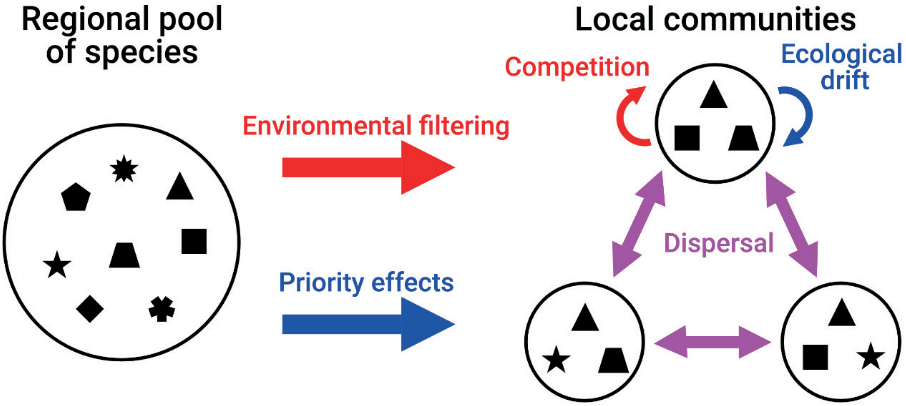

Figure 1. Conceptual scheme of community assembly processes. Red arrows indicate deterministic processes, blue ones indicate stochastic processes.

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).

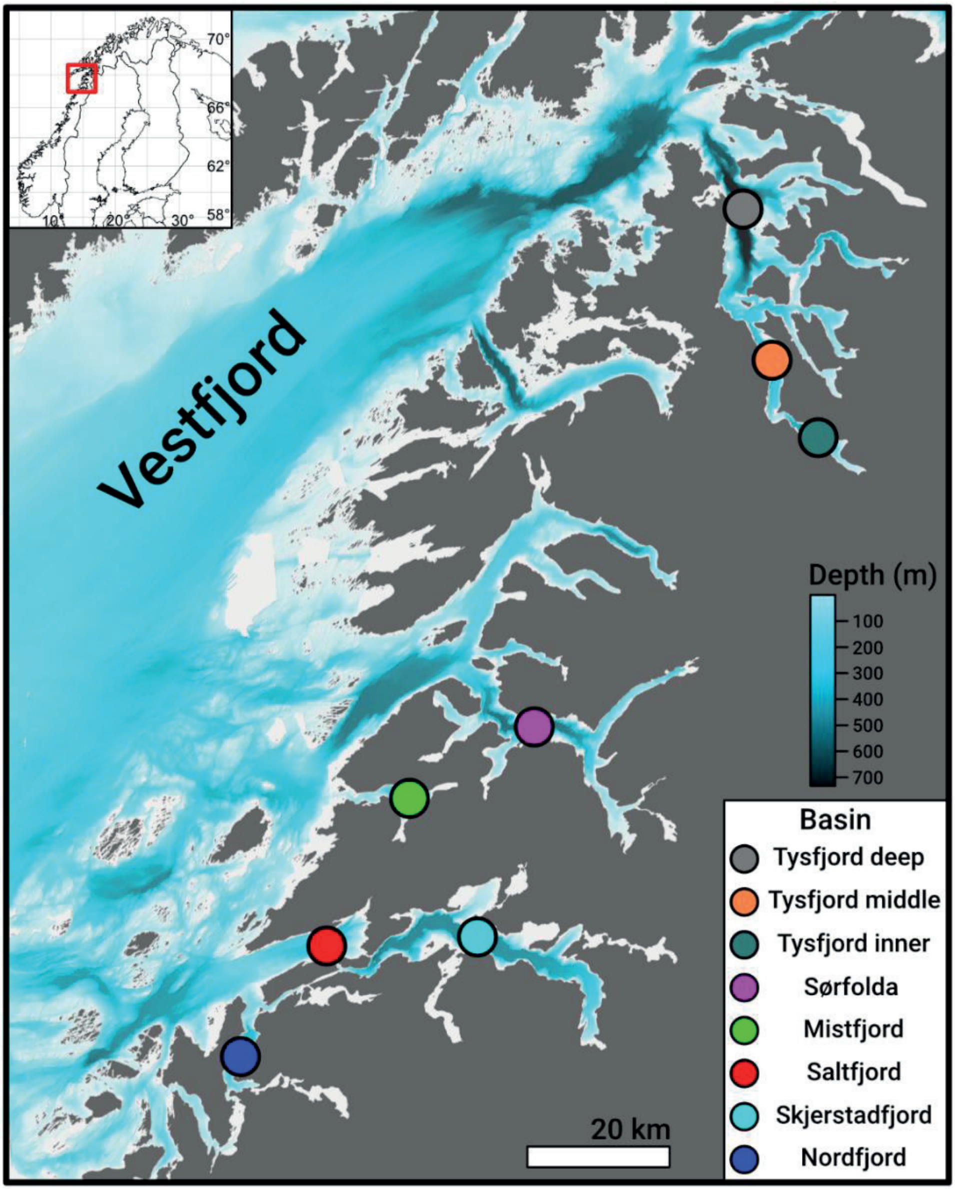

Figure 2. Map of the study area, showing locations of the sampled basins

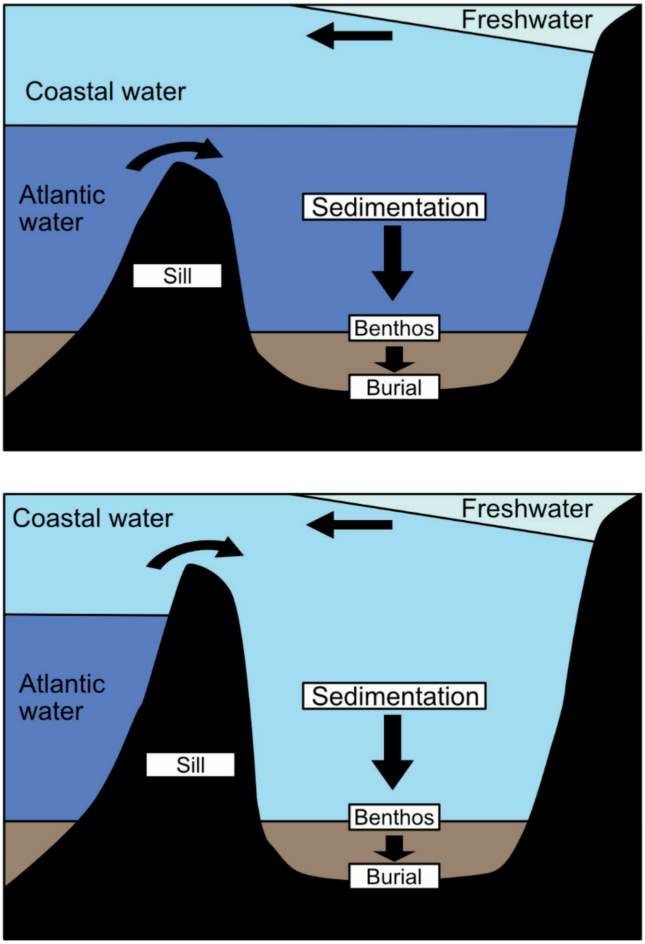

Figure 3. A scheme representing the difference between deep-silled (top) and shallowed-silled fjords (bottom) in water exchange: shallow sill hampers inflow of Atlantic water into the basin and resulting bottom water masses are colder and less saline.

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.

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Paper I

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

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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

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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

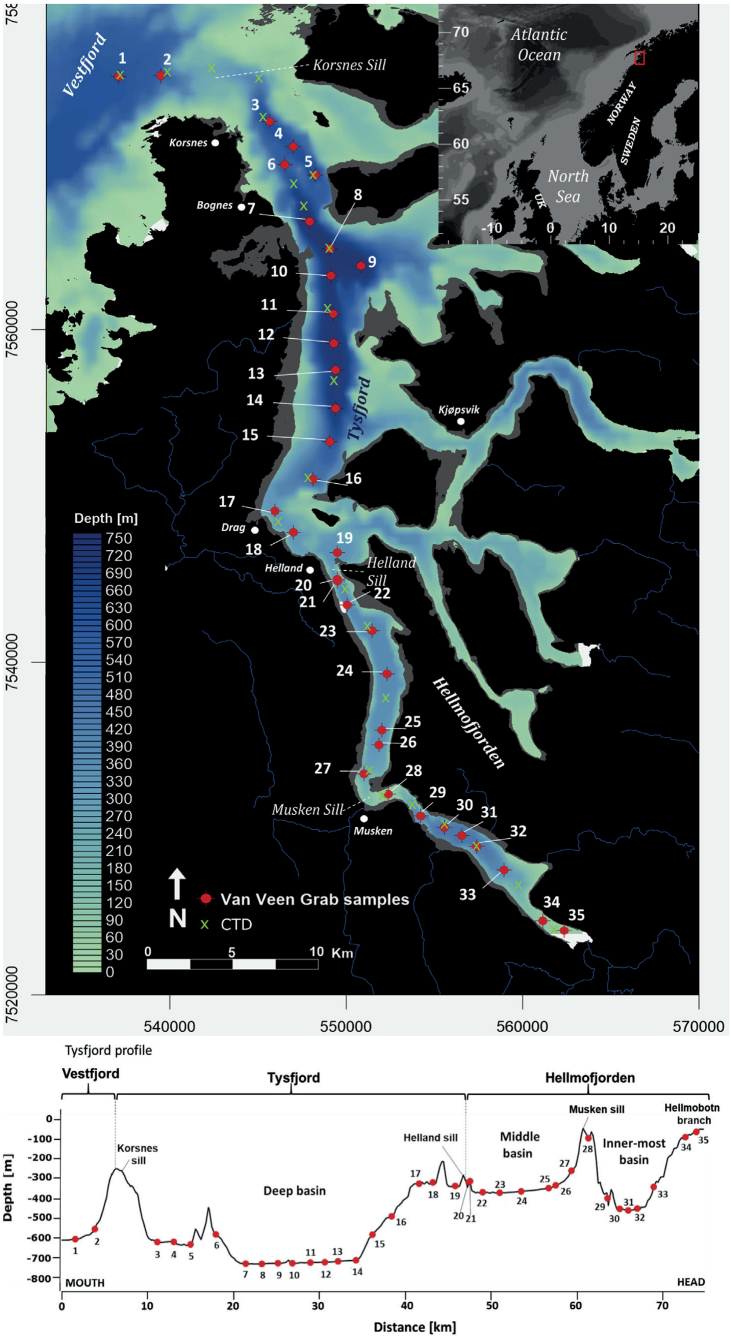


Fig. 1. Study region. *top*: Map of Tysfjord, benthos stations indicated in red, CTD stations indicated in green; *bottom*: depth profile of the sampled transect, benthos stations indicated in red. Main basins and sills are labeled. *Note*: The depicted depth profile follows the benthos stations through 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).

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]**

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).

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

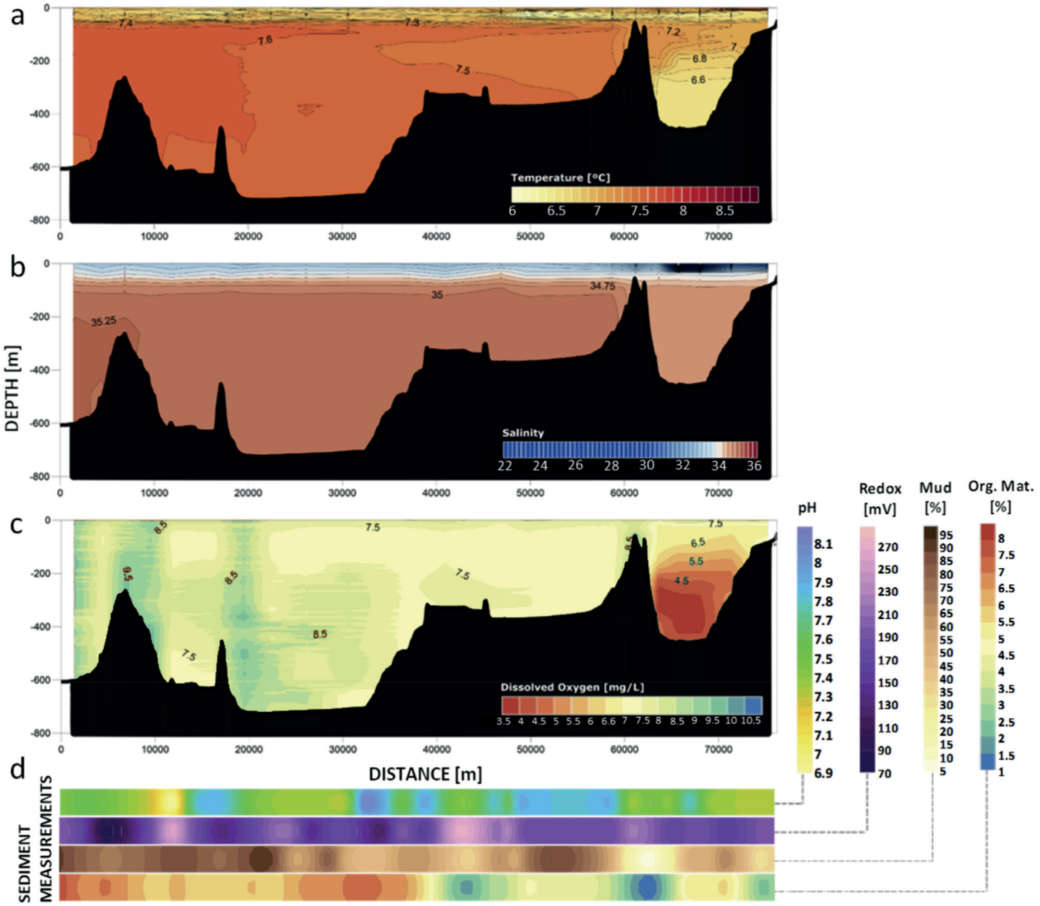


Fig. 2. Results of the CTD casts along the fjord transect showing (a) Temperature [°C], (b) Salinity and (c) Dissolved Oxygen [mg/l], and (d) the results for the sediment parameters showing from top to bottom pH, Redox potential [mV], Mud content [%], and Organic Matter content [%].

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

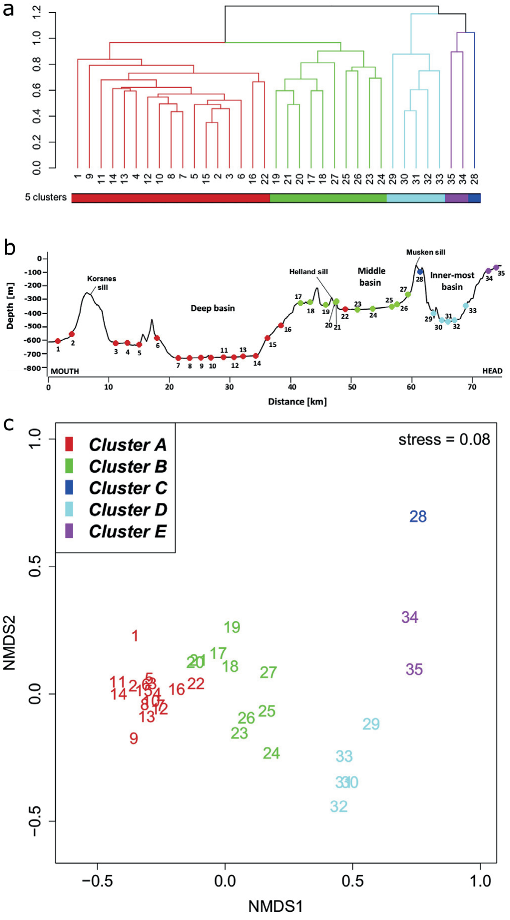


Fig. 3. Structure of the Hellinger transformed abundance data. (a) Dendrogram of the UPGMA clustering, (b) cluster affiliation of each sample along the fjord transect, and (c) plot of the nMDS ordination are shown. The identified sample clusters are indicated by different colors. (For interpretation 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

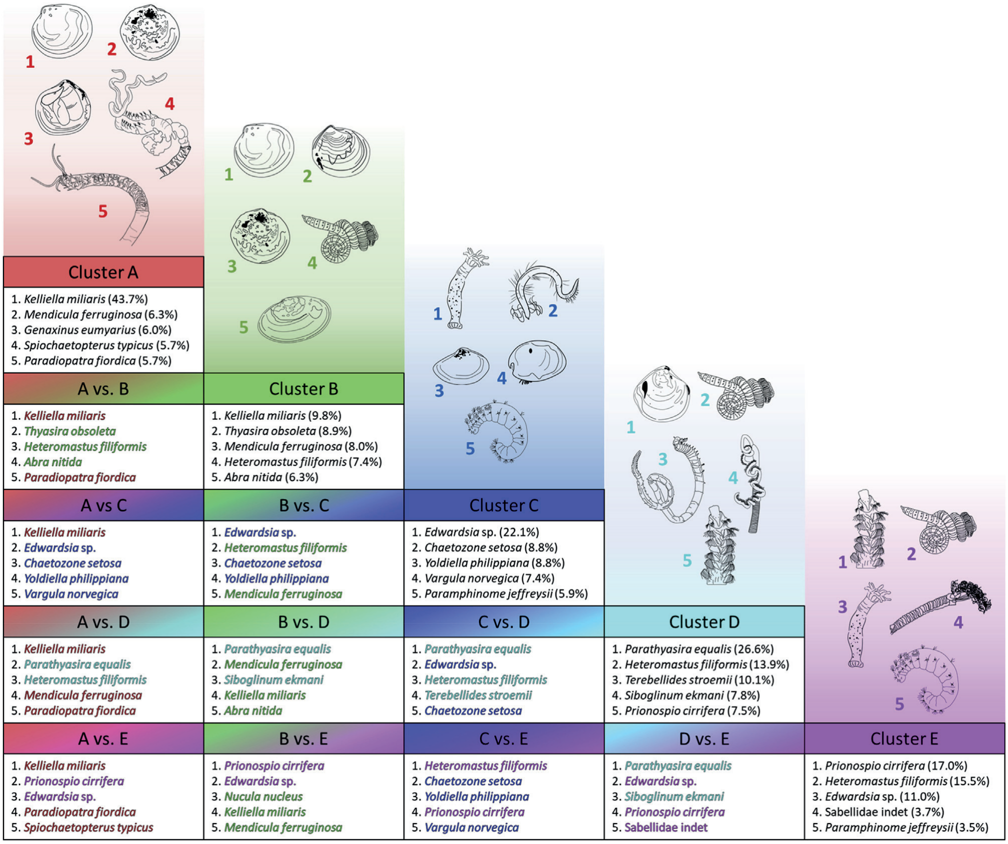
Although we report total infaunal abundances throughout the Tysfjord system that seem to vary unrelated to the sampled depth gradient (Table 2), a separation in deep (depth $>$ 400 m; cluster A and D) and shallow (depth $<$ 400 m; cluster B) basin community clusters became apparent regarding the applied 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%)

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

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%)

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***

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%)

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***

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%)

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**

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%)

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.)

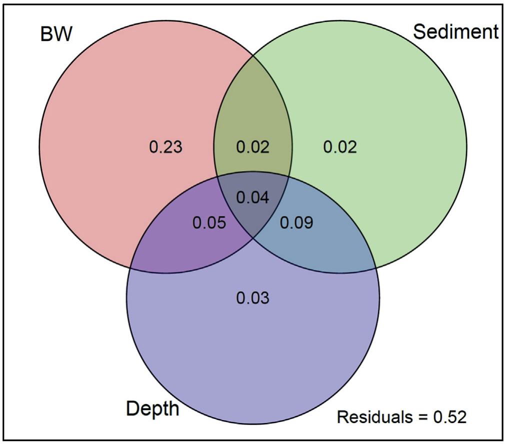


Fig. 5. Venn diagram showing the results of the variation partitioning. The explained fraction of the total variation in the Hellinger transformed abundance data is given for all three sets of environmental variables and all combinations of them. Bottom water properties (BW) includes the variables salinity, 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

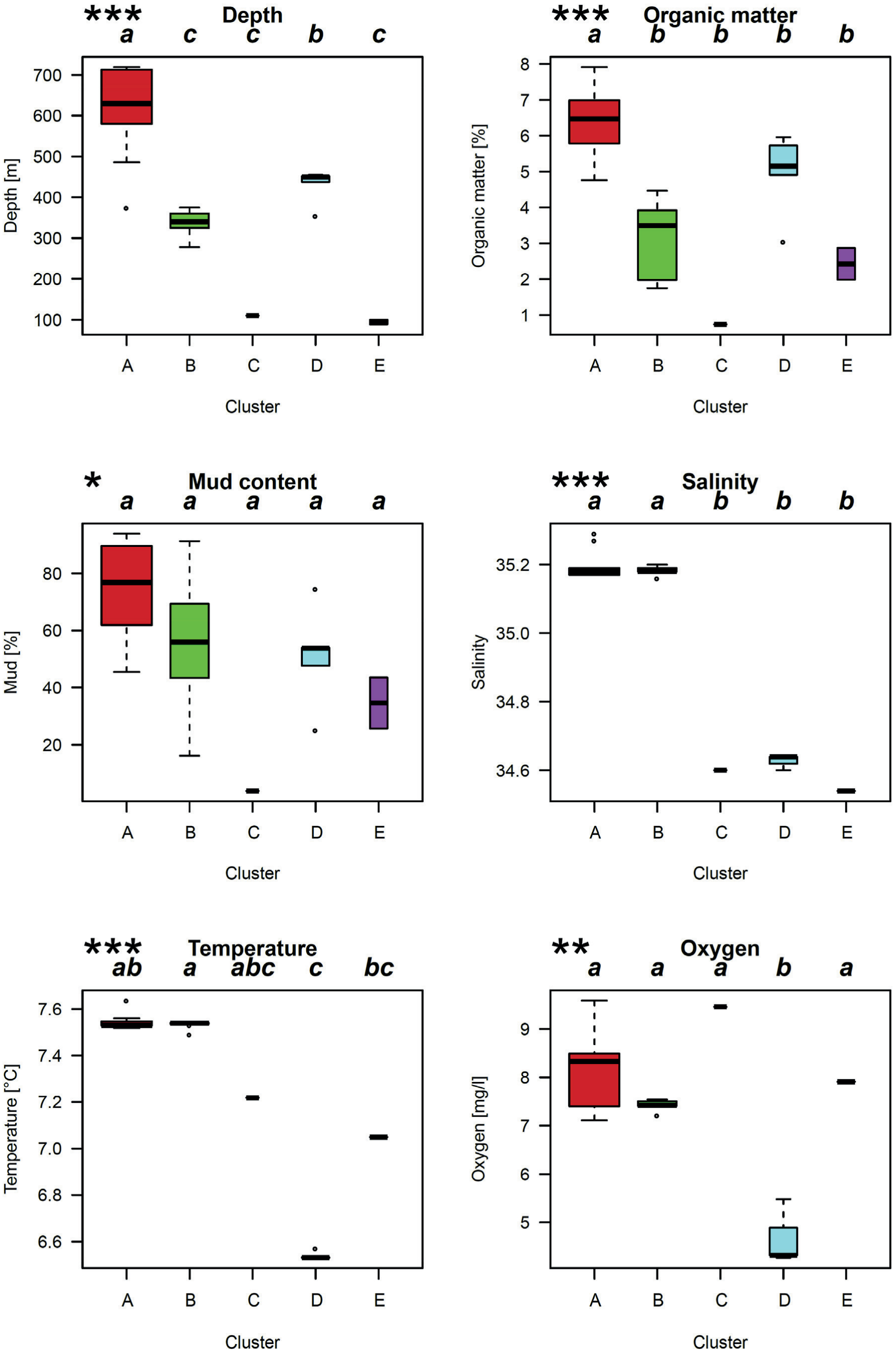


Fig. 6. Box plots for all environmental variables selected by the forward selection procedure. Stars indicate the significance of the differences among groups for each environmental variable, according to Kruskal–Wallis test. Letters indicate results of the post-hoc comparison. Groups with the same letter 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.

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Appendix A. Supplementary data

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

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

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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

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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

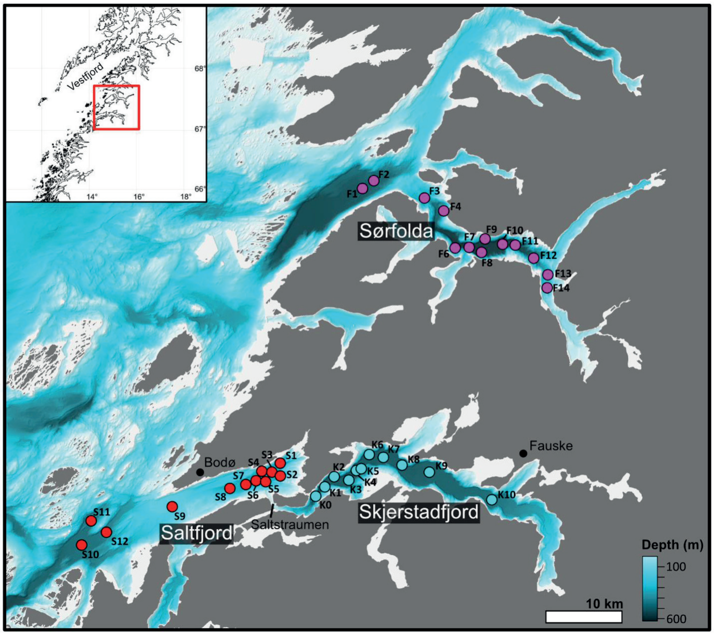

Fig. 1. Map of the study area. Stations denoted the following: S – Saltfjord transect (red), K – Skjerstadfjord transect (blue), F – Sørfolda transect (purple). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

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

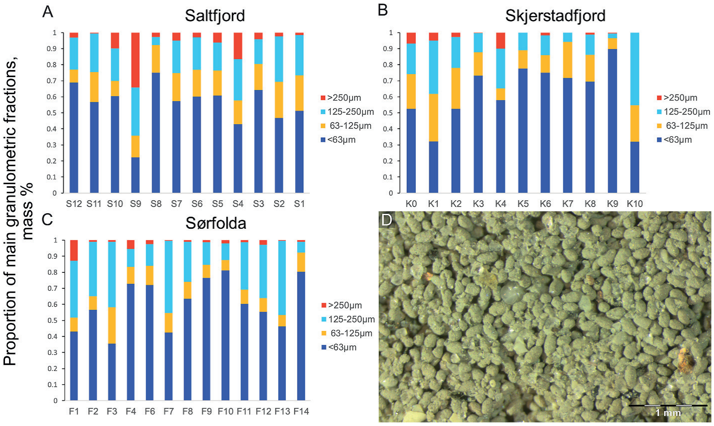

Fig. 2. Results of granulometry for three fjords: A Saltfjord, B Skjerstadfjord, C Sørfolda. For each station, the contribution of the three main fractions are shown: >250 μm, 125–250 μm, 63–125 μm and <63 μm. D: a macrophotograph of the 125 μm fraction from station F3, showing the high abundance of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

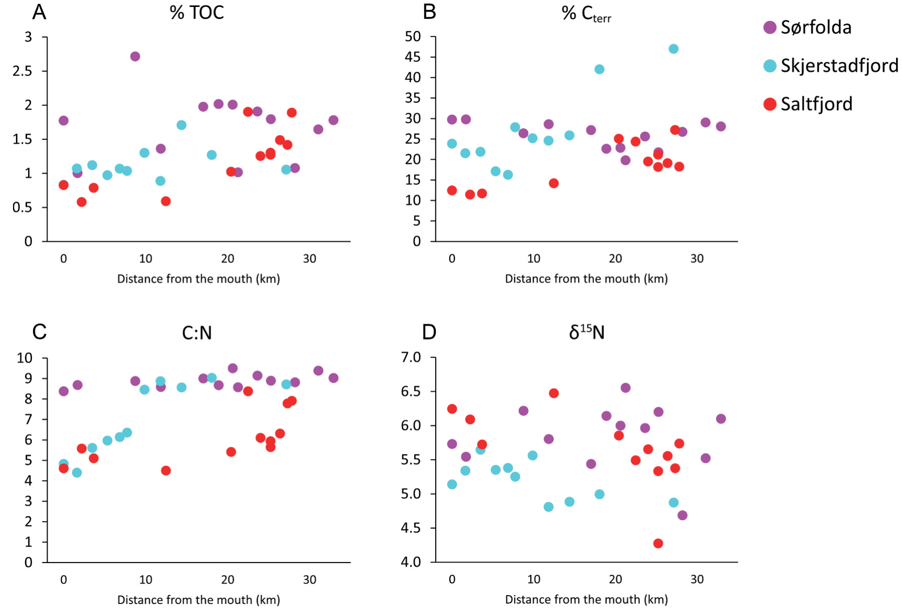

Fig. 3. Characteristics of organic matter in surface sediments: A, % of total organic carbon (% TOC); B, % of terrigenous organic matter (% C_{terr}); C, C:N ratio and D, $\delta^{15}N$ (‰).

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).

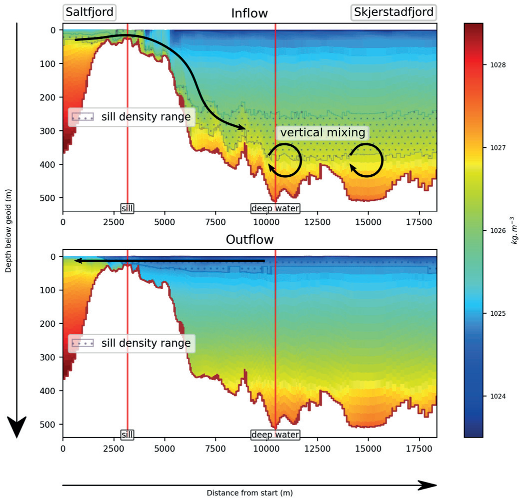

Fig. 4. Seawater density along Saltstraumen, modelled for the 1st June 2013 during both the rising tide (top) and the falling tide (bottom). The shaded area highlights the depth of the water masses which have a density that falls within the density range of the water flowing over the sill.

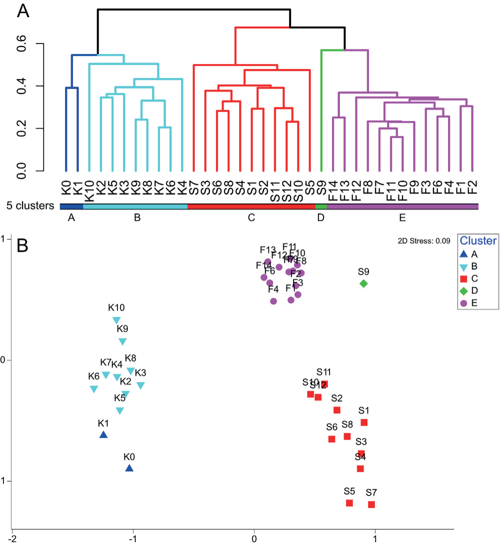

Fig. 5. The results of UPGMA clustering (A) and nMDS ordination diagram (B) based on Bray-Curtis dissimilarity matrix calculated from square root-transformed standardized species abundance data. Cluster A = Skjerstadfjord/Saltstraumen, Cluster B = Skjerstadfjord, Cluster C = Saltfjord and adjacent basin,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

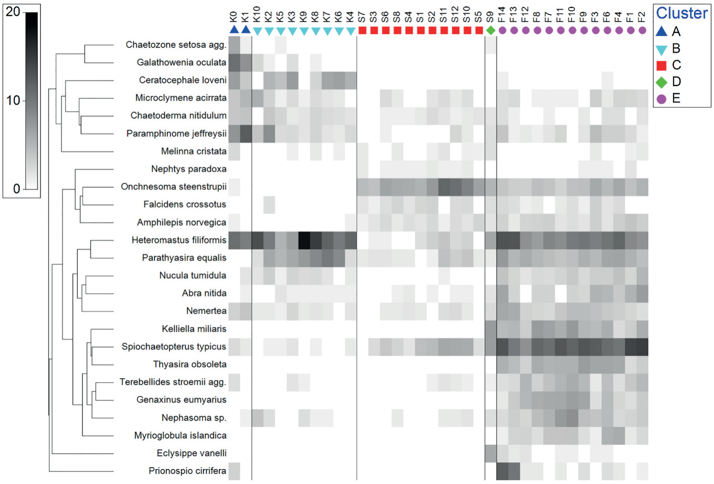

Fig. 6. Shade plot of square root transformed abundances (per 0.2 m^2) for the 25 most abundant species. Species grouped using UPGMA clustering based on index of association. Cluster A = Skjerstadfjord/Saltstraumen, Cluster B = Skjerstadfjord, Cluster C = Saltfjord and adjacent basin, Cluster D = Saltfjord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

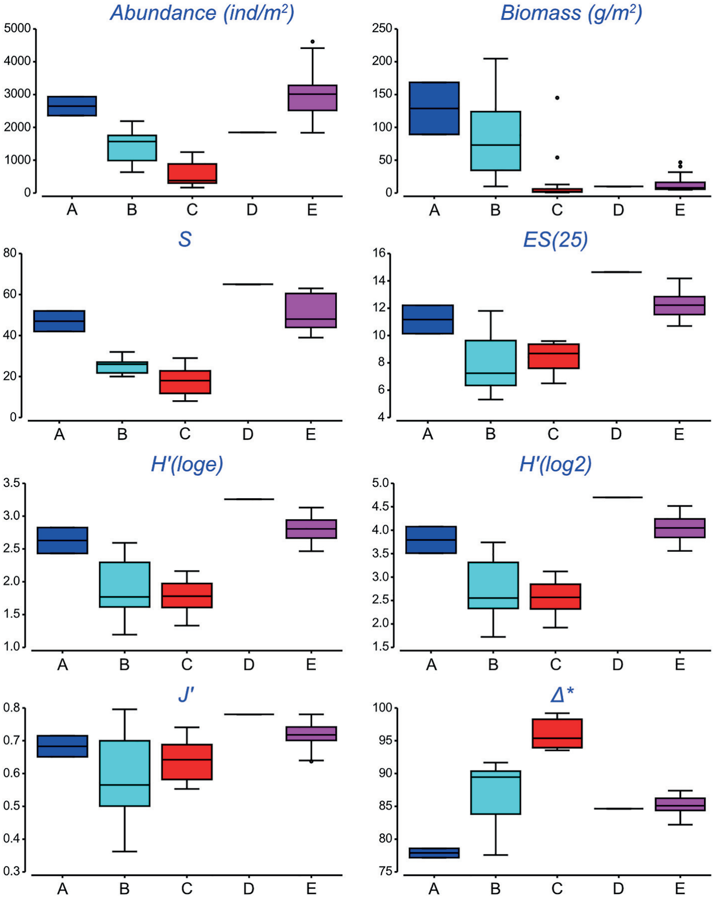

Fig. 7. Univariate characteristics of identified clusters: Abundance (individuals per square meter), Biomass (gram wet weight per square meter), number of species per station (S), expected number of species per 25 individuals ES(25), Shannon index (H′) Pielou's evenness (J′) and average taxonomic distinctness (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

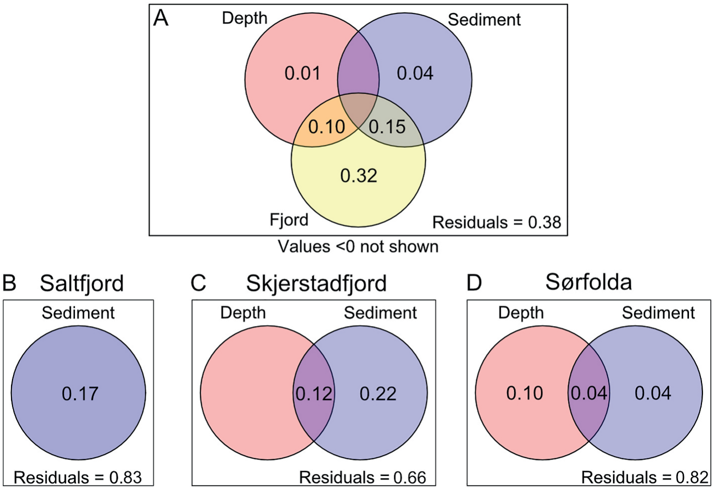

Fig. 8. Venn diagram showing the results of variation partitioning: A – all fjords, B – Saltfjord, C – Skjerstadfjord, D – Sørfolda. Numbers indicate the proportion of variation explained (Adjusted R^2) independently and jointly by three groups of factors: Depth, Fjord and Sediment.

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.

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Appendix A. Supplementary data

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

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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.

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