

# 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 Nordland 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 delimited 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 (Brkljačić 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<sup>2</sup>) 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

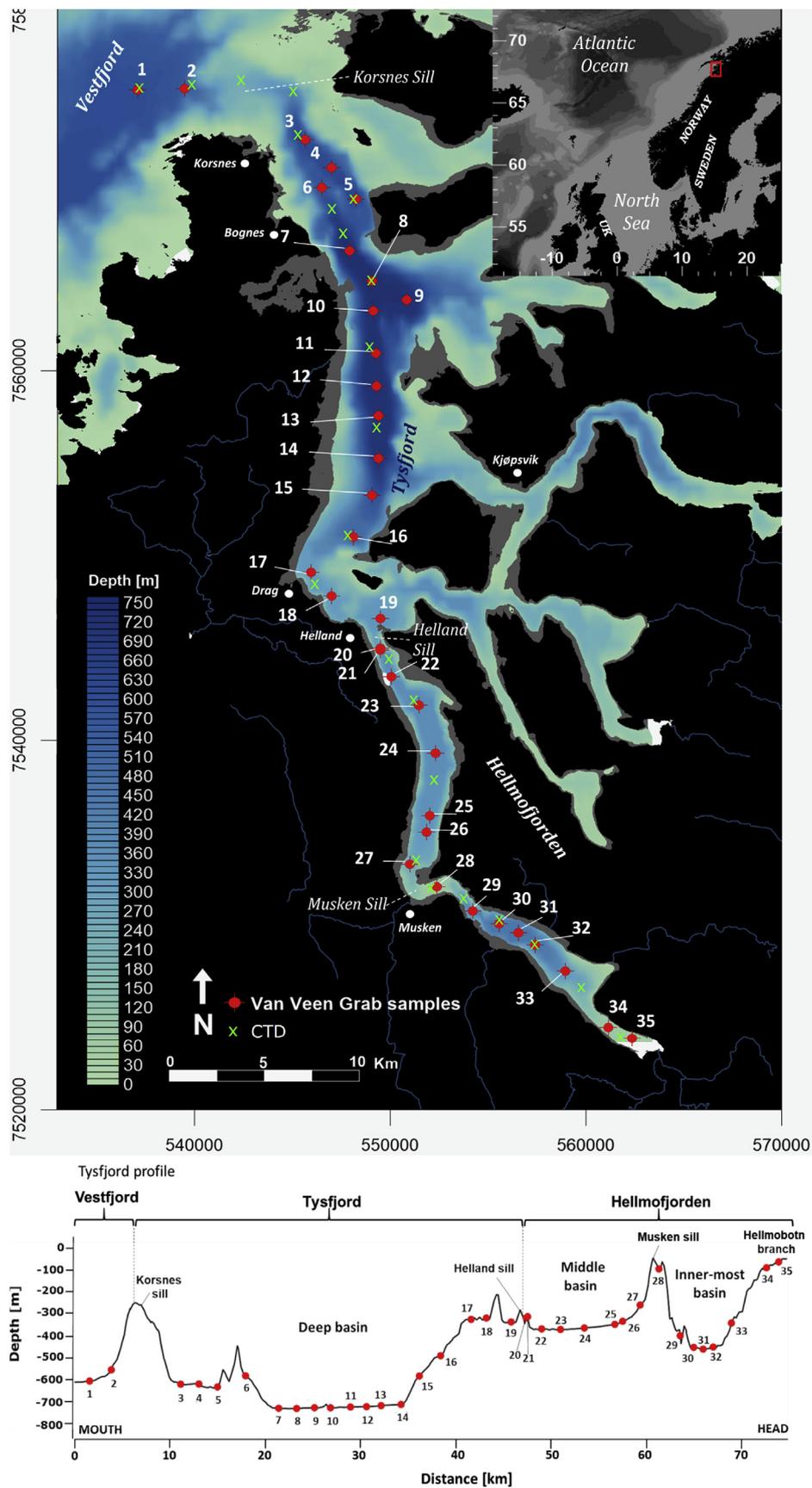


Fig. 1. Study region. *top*: Map of Tysfjord, benthos stations indicated in red, CTD stations indicated in green; *bottom*: depth profile of the sampled transect, benthos stations indicated in red. Main basins and sills are labeled. *Note*: The depicted depth profile follows the benthos stations through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

**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	<b>O<sub>2</sub> in bottom water [mg/l]</b>
	<b>Salinity of bottom water</b>
	<b>Temperature of bottom water [°C]</b>
Sediment characteristics	<b>Mud content [%]</b>
	Textural group pH of the sediment
	Redox potential of the sediment [mV]
	<b>Organic matter in the sediment [%]</b>
Depth	<b>Depth [m]</b>

series of constrained and partially constrained redundancy analysis (RDA) with a double stopping criterion (Blanchet et al., 2008), to avoid overestimation of the explained variation. In this approach, variables are added to the model in order of decreasing explanatory power until no variable adds significantly to the explanatory power or until the adj.  $R^2$  exceeds that of the full model. Following the variable selection, RDA was used to partition the variation in the faunal data set on the three sets of selected environmental variables and all combinations of them (Borcard et al., 1992; Peres-Neto et al., 2006).

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

## 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<sub>2</sub>/l). Temperature, salinity, and the oxygen content 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<sub>2</sub>/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<sub>2</sub>/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 eumyrius* (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

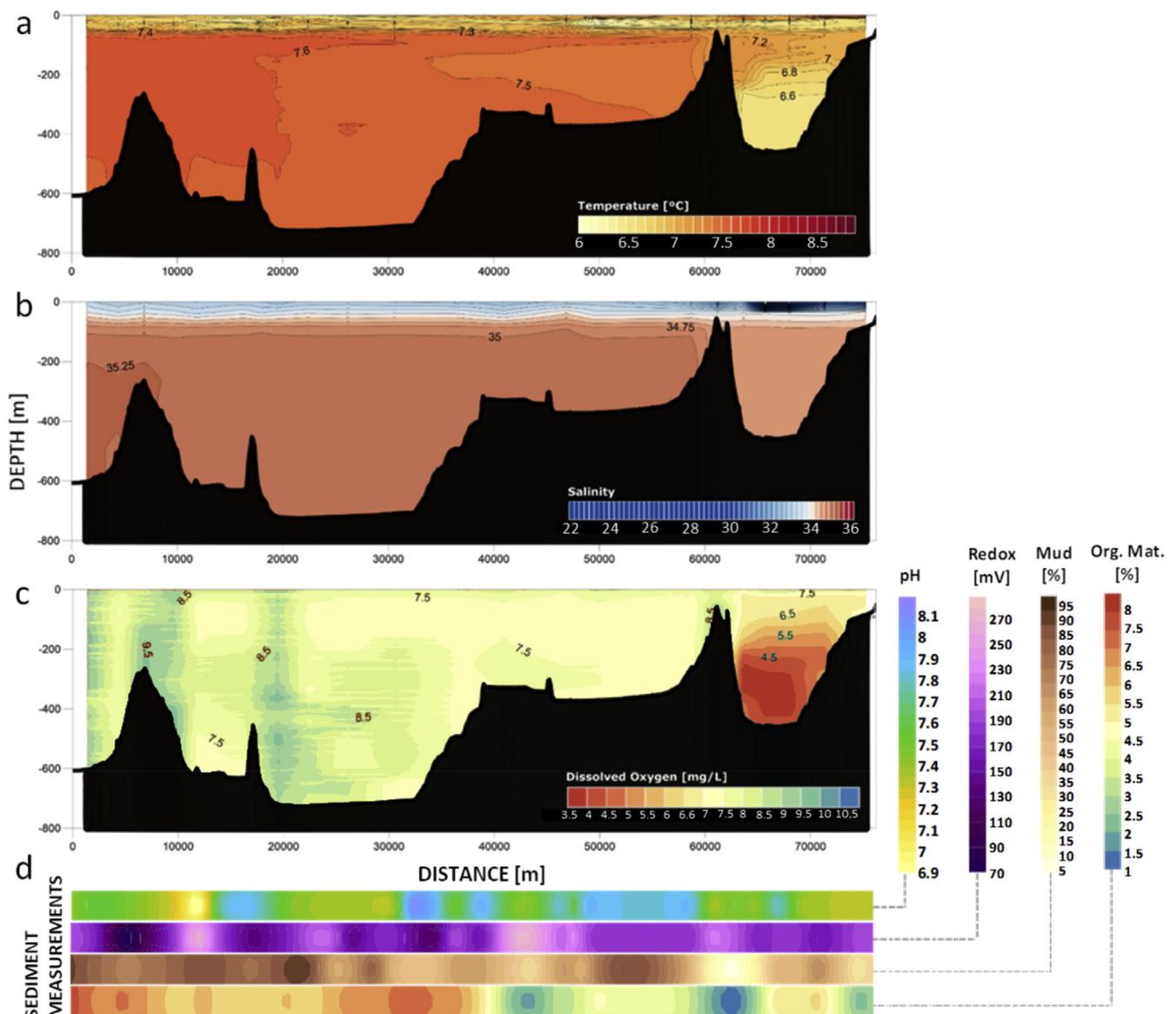


Fig. 2. Results of the CTD casts along the fjord transect showing (a) Temperature [°C], (b) Salinity and (c) Dissolved Oxygen [mg/L], and (d) the results for the sediment parameters showing from top to bottom pH, Redox potential [mV], Mud content [%], and Organic Matter content [%].

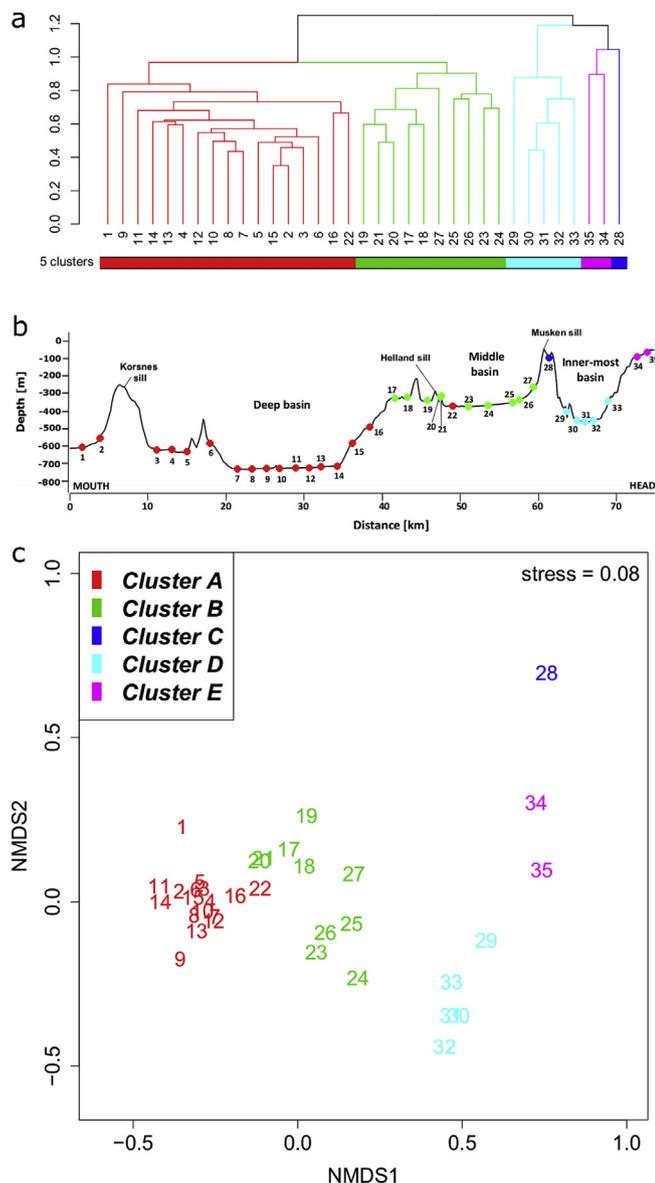
diversity characteristics (Table 2). Shannon diversity as well as the average number of species per sample, clearly identified cluster B as the most diverse community within the fjord basins. Cluster A was characterized by a lower evenness than the other clusters, which was primarily caused by the extreme 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<sup>2</sup>) 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 the benthic communities. Accordingly, basin depth seems to be an important property of northern Norwegian fjords.

##### 4.1. Depth related community structure

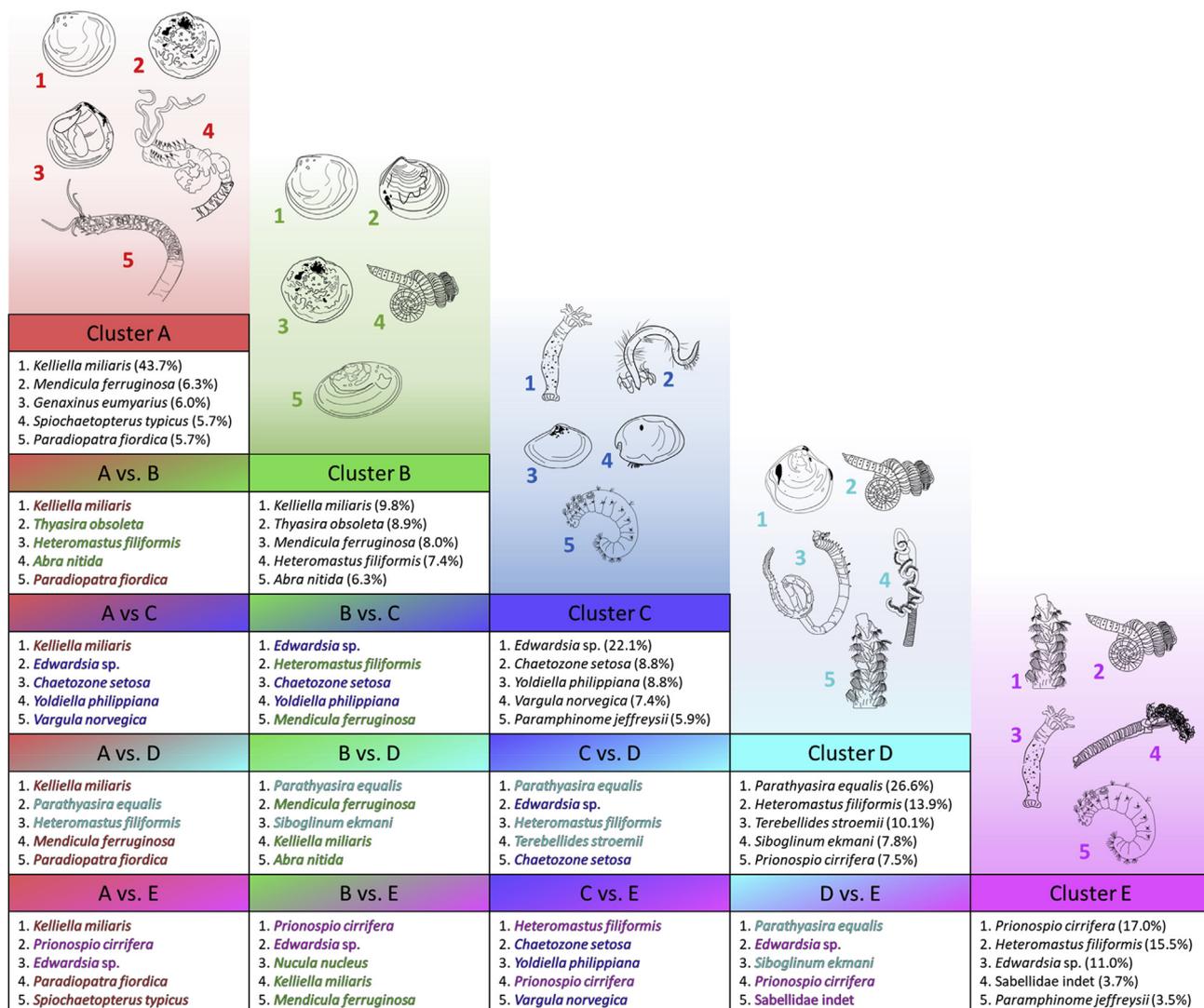
Although we report total infaunal abundances throughout the Tysfjord system that seem to vary unrelated to the sampled depth gradient (Table 2), a separation in deep (depth > 400 m; cluster A and D) and shallow (depth < 400 m; cluster B) basin community clusters became apparent regarding the applied 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 eumyrius*, 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), Hurlbert rarefaction (ES100), and species identified by the IndVal method of Dufrene 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 <sup>2</sup> ]	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	<i>Paradiopatra fiordica</i> <i>Kelliella miliaris</i> <i>Spiochaetopterus typicus</i>	<i>Nephtys hystrix</i> <i>Onchnesoma steenstrupii steenstrupii</i> <i>Nucula nucleus</i> <i>Mendicula ferruginosa</i>	-	<i>Parathyasira equalis</i>	-



**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.)

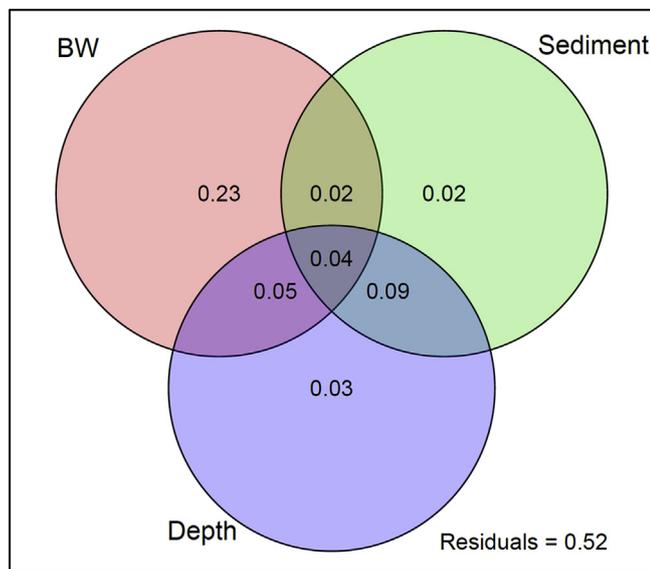


Fig. 5. Venn diagram showing the results of the variation partitioning. The explained fraction of the total variation in the Hellinger transformed abundance data is given for all three sets of environmental variables and all combinations of them. Bottom water properties (BW) includes the variables salinity, 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 ( $\approx 2.85$  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 innermost 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

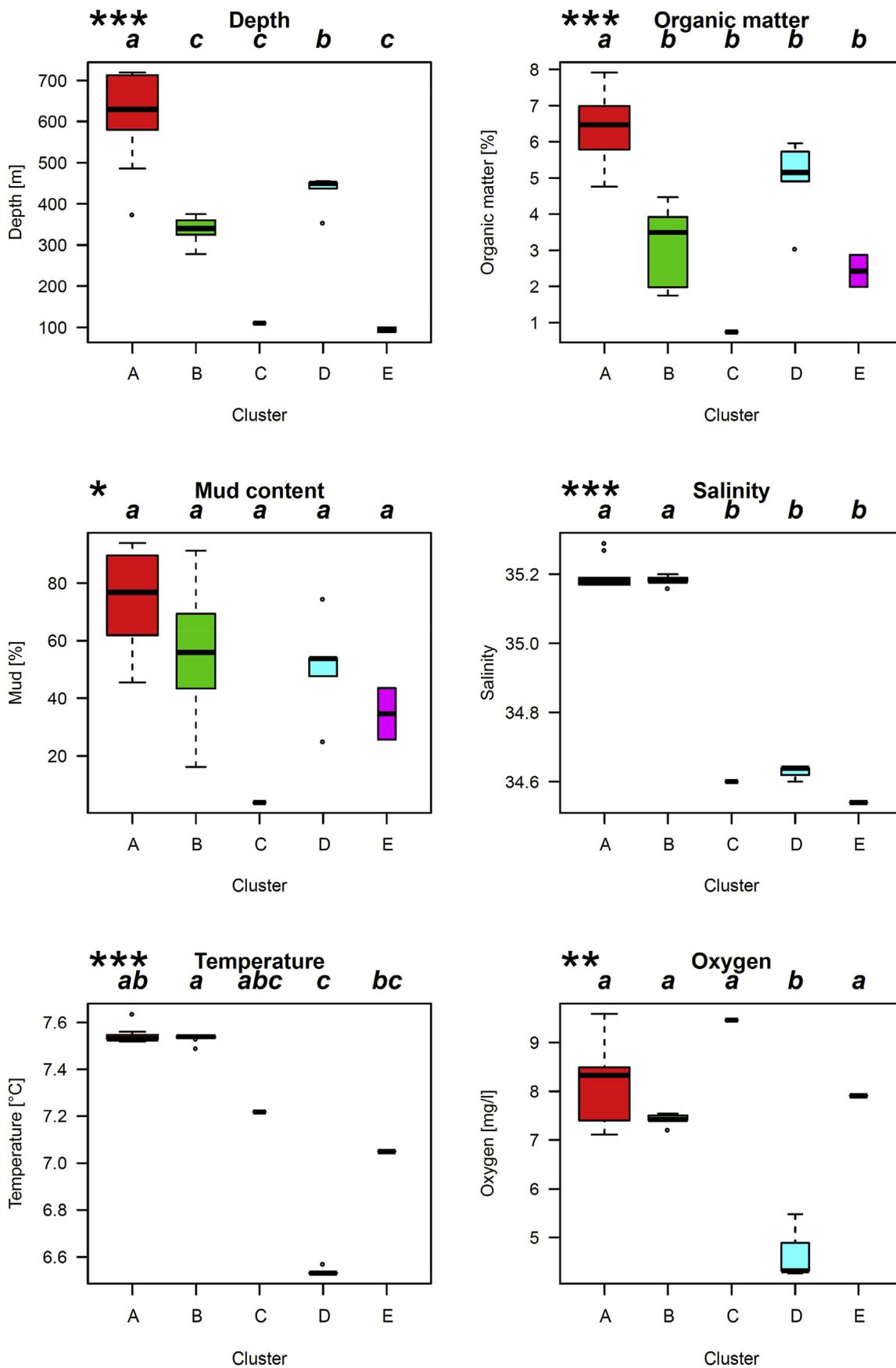


Fig. 6. Box plots for all environmental variables selected by the forward selection procedure. Stars indicate the significance of the differences among groups for each environmental variable, according to Kruskal–Wallis test. Letters indicate results of the post-hoc comparison. Groups with the same letter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