



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-Kowalczyk 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-Kowalczyk 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-Kowalczyk 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-Skjerstadvfjord 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 Skjerstadvfjord (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 Skjerstadvfjord 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-Skjerstadvfjord.

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 Skjerstadvfjord 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 Skjerstadvfjord 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 Skjerstadvfjord) 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 m² Van Veen grab samples were taken at each sampling station. Coordinates and

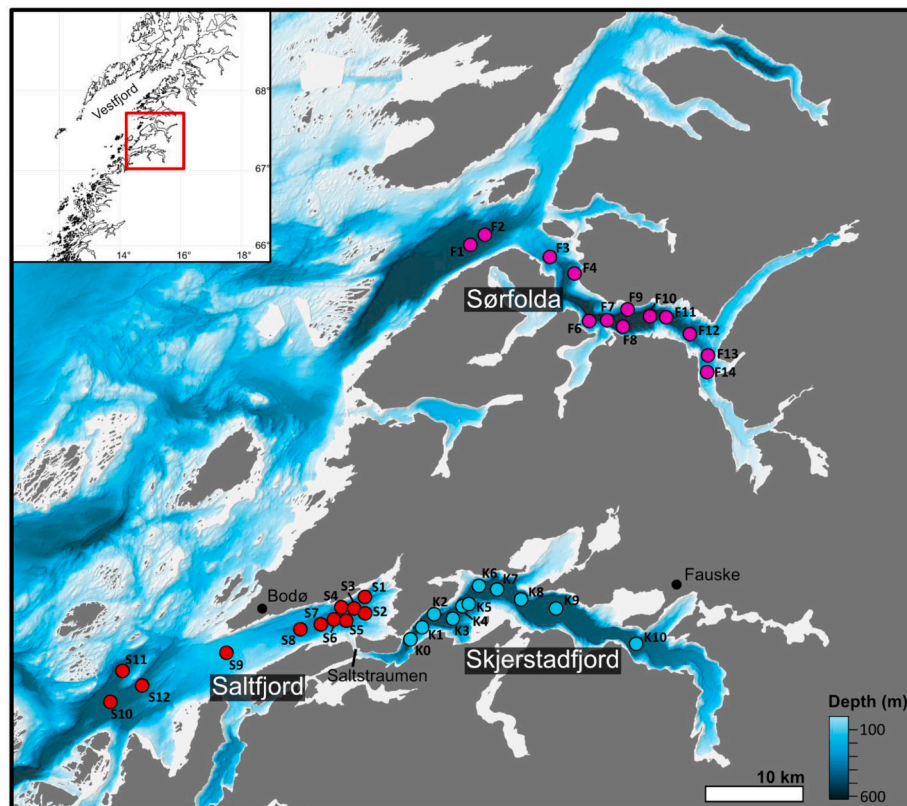


Fig. 1. Map of the study area. Stations denoted the following: S – Saltfjord transect (red), K – Skjerstadvfjord transect (blue), F – Sørfolda transect (purple). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

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 weighed without tubes. However, for Sørfolda stations, a calculated mean of 1 mg per *Spiochaetopterus typicus* individual (based on specimens weighed 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 $<63\ \mu\text{m}$ 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 ($\delta^{13}\text{C}/\delta^{15}\text{N}$) relative to VPDB (Vienna PeeDee Belemnite standard) and atmospheric nitrogen. Percent of terrigenous organic matter (% C_{terr}) was estimated based on $\delta^{13}\text{C}_{\text{org}}$ 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 $\delta^{15}\text{N}$ 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 Skjerstadjord.

2.5. Modelling of water exchange between Saltfjord and Skjerstadjord

The effects of a shallow sill on the hydrodynamic regime of the Saltfjord-Skjerstadjord 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) (Dufrene 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, Skjerstadjord and Sørfolda) and sediment (% TOC, %N, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C:N and % of three granulometric fractions: 125 μm , 63 μm and $<63\ \mu\text{m}$). 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, $\delta^{15}\text{N}$, 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, $<63\ \mu\text{m}$) was dominating the sediment composition and the size fractions below $250\ \mu\text{m}$ contributed with more than 90% of the sediment at most stations of all fjords ([Fig. 2A–C](#)). While the fraction of $63\text{--}125\ \mu\text{m}$ consisted mostly of very fine sand, the $125\text{--}250\ \mu\text{m}$ 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 $\delta^{15}\text{N}$ 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 Skjerstadjord 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 Skjerstadjord, 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 $\delta^{15}\text{N}$. Skjerstadjord 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 Skjerstadjord. Also, in Skjerstadjord, the lowest $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ ($r = -0.39$, $p < 0.05$).

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 Skjerstadjord 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 Skjerstadjord 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 Skjerstadjord, where the water has approximately the same density. The advection of surface water from Saltfjord into the greater depths of Skjerstadjord, together with further vertical mixing, are the main processes contributing to the deep water renewal of Skjerstadjord. During falling tides, the less saline and lighter surface water from Skjerstadjord flows over the sill and then mixes with the surface waters of Saltfjord. Thus, water flow from Skjerstadjord 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 Skjerstadjord 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

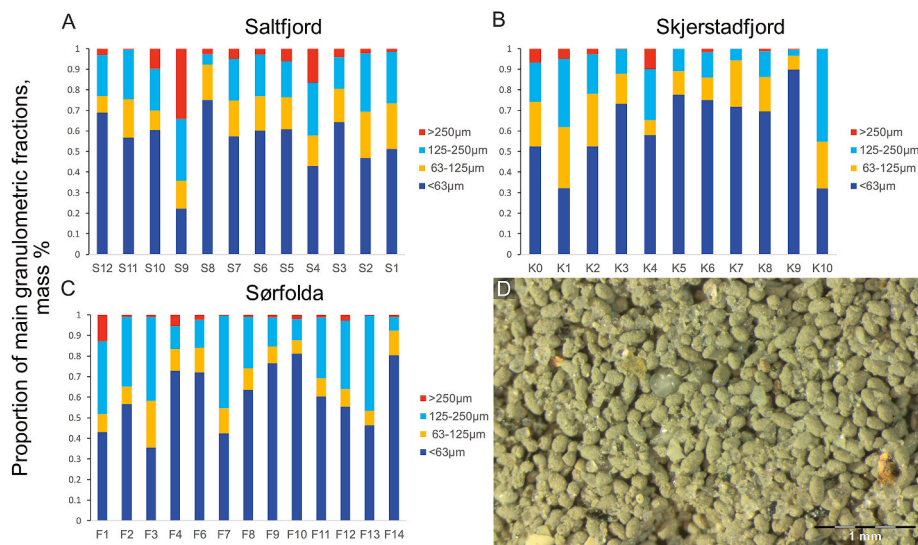


Fig. 2. Results of granulometry for three fjords: A Saltfjord, B Skjerstadjord, C Sørfolda. For each station, the contribution of the three main fractions are shown: $>250\ \mu\text{m}$, $125\text{--}250\ \mu\text{m}$, $63\text{--}125\ \mu\text{m}$ and $<63\ \mu\text{m}$. D: a macrophotograph of the $125\ \mu\text{m}$ 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.

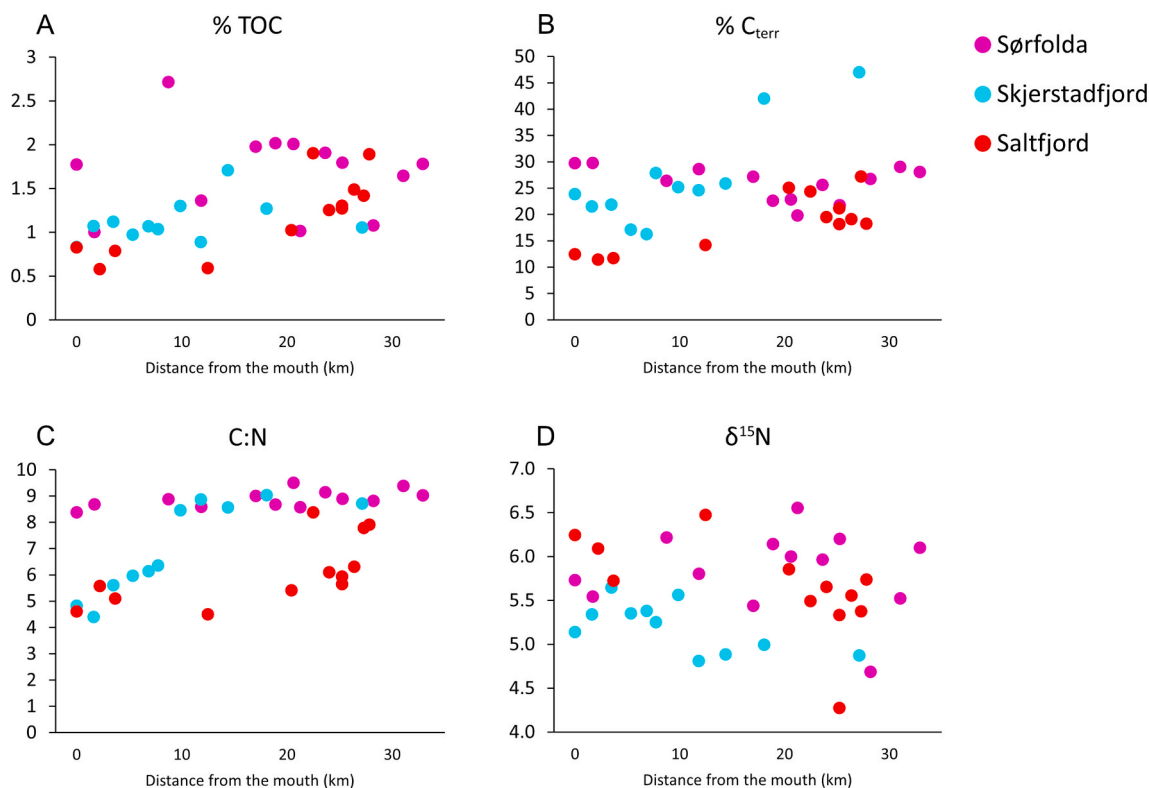


Fig. 3. Characteristics of organic matter in surface sediments: A, % of total organic carbon (% TOC); B, % of terrigenous organic matter (% C_{terr}); C, C:N ratio and D, δ¹⁵N (‰).

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
Skjerstadsfjord	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).

Skjerstadsfjord 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 Skjerstadsfjord 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).

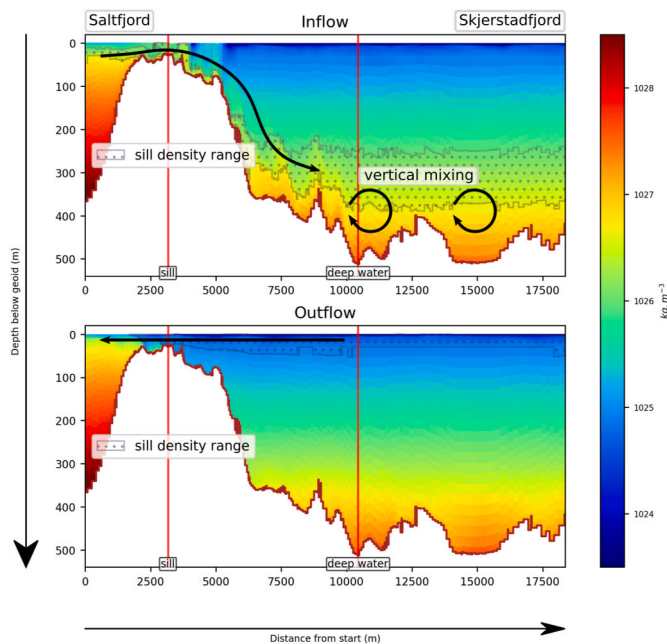


Fig. 4. Seawater density along Saltstraumen, modelled for the 1st June 2013 during both the rising tide (top) and the falling tide (bottom). The shaded area highlights the depth of the water masses which have a density that falls within the density range of the water flowing over the sill.

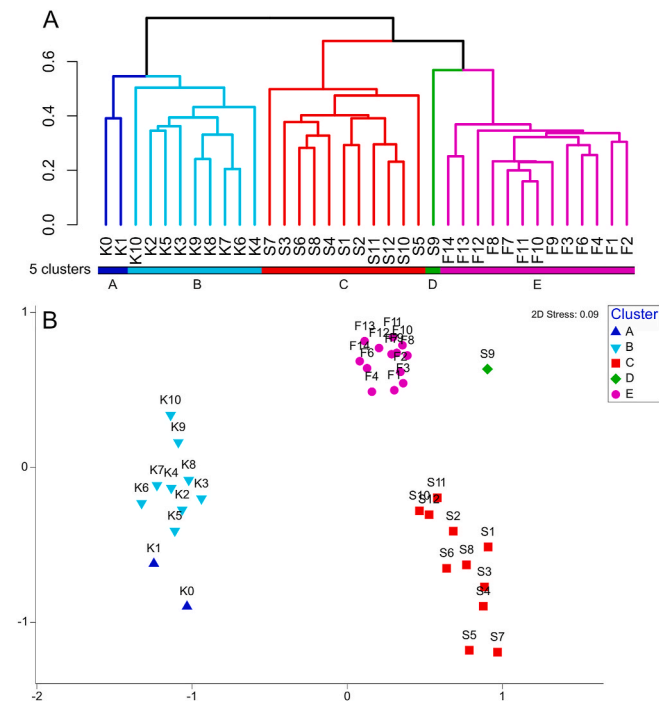


Fig. 5. The results of UPGMA clustering (A) and nMDS ordination diagram (B) based on Bray-Curtis dissimilarity matrix calculated from square root-transformed standardized species abundance data. Cluster A = Skjerstadfjord/Saltstraumen, Cluster B = Skjerstadfjord, Cluster C = Saltfjord and adjacent basin, 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 $\delta^{15}\text{N}$. 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: $\delta^{15}\text{N}$ for Saltfjord, C:N and $\delta^{13}\text{C}$ for Skjerstadfjord and $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}_{\text{org}}$), C:N and $\delta^{15}\text{N}$ 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, $\delta^{15}\text{N}$ values appeared to change independently from these two parameters. The low $\delta^{15}\text{N}$ 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). $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$ values. However, $\delta^{15}\text{N}$ 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.

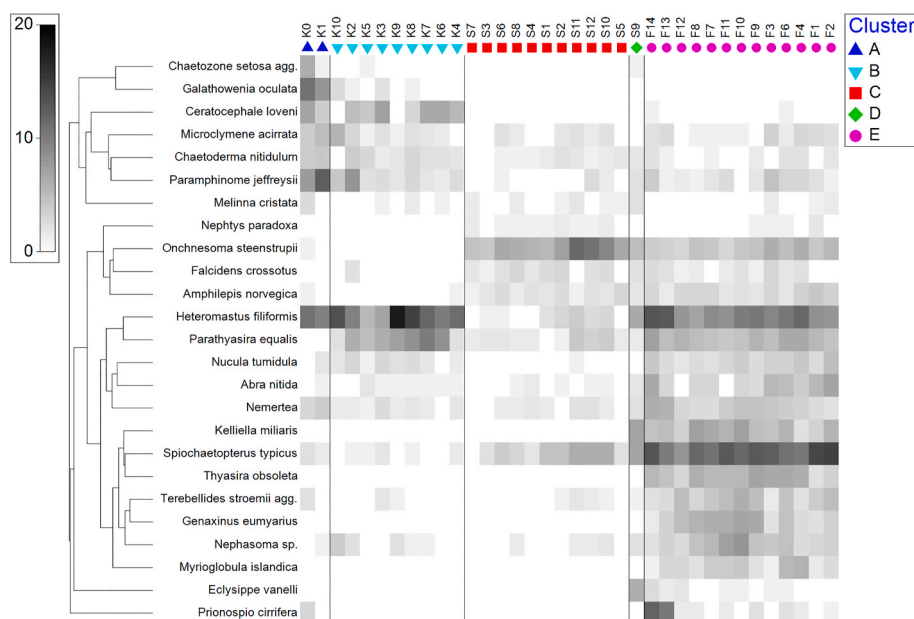


Fig. 6. Shade plot of square root transformed abundances (per 0.2 m²) for the 25 most abundant species. Species grouped using UPGMA clustering based on index of association. Cluster A = Skjerstadjord/Saltstraumen, Cluster B = Skjerstadjord, Cluster C = Saltfjord and adjacent basin, Cluster D = Saltfjord sill, Cluster E = Sørfolda and adjacent basin.

Table 2

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

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

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-Kowalczyk, 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

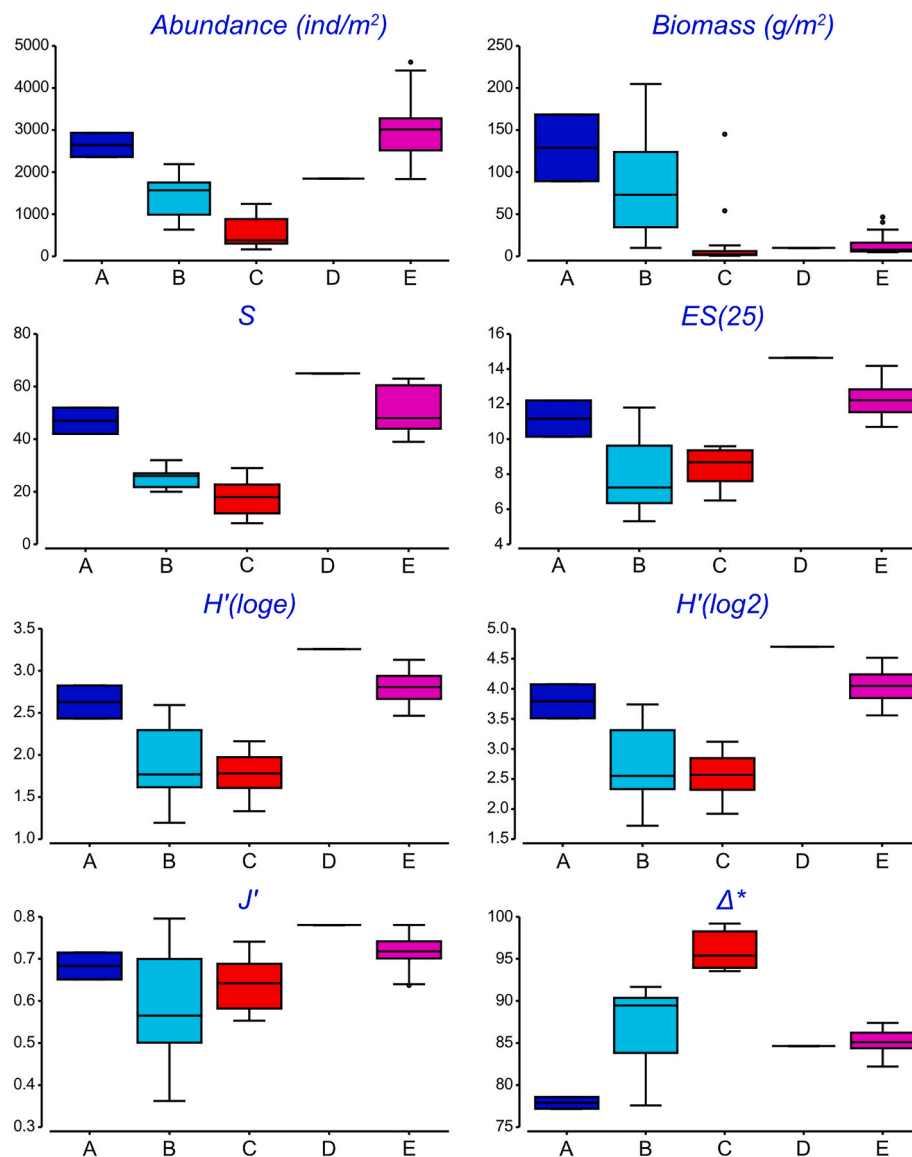


Fig. 7. Univariate characteristics of identified clusters: Abundance (individuals per square meter), Biomass (gram wet weight per square meter), number of species per station (S), expected number of species per 25 individuals ES(25), Shannon index (H') Pielou's evenness (J') and average taxonomic distinctness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

In general, sediments were dominated by the mud (silt and clay) fraction ($<63 \mu\text{m}$). 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. Skjerstadsfjord 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 Skjerstadsfjord 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

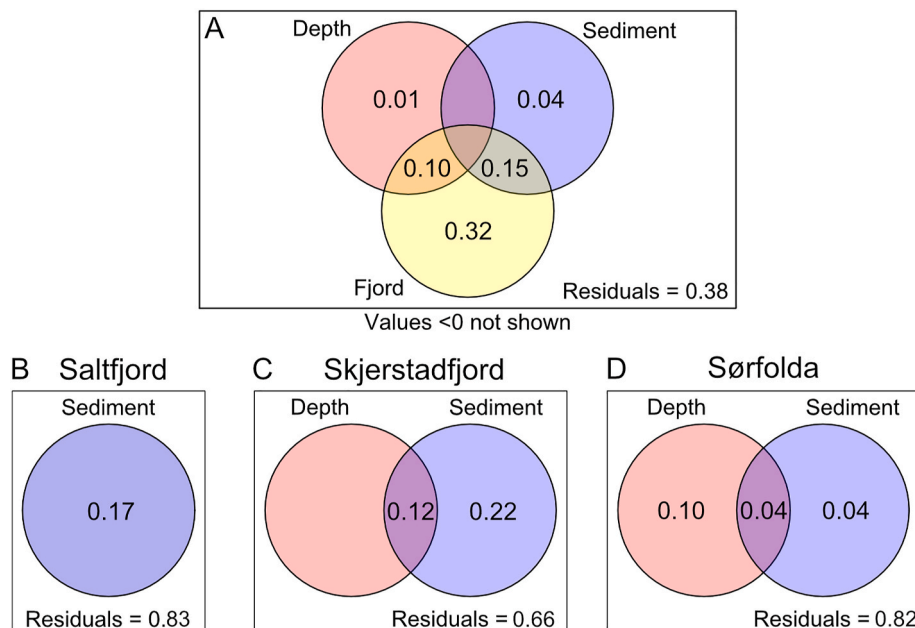


Fig. 8. Venn diagram showing the results of variation partitioning: A – all fjords, B – Saltfjord, C – Skjerstadvfjord, D – Sørfolda. Numbers indicate the proportion of variation explained (Adjusted R²) independently and jointly by three groups of factors: Depth, Fjord and Sediment.

community (most stations of cluster C) was characterised by relatively low total abundances (<1000 ind./m²) 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./m²), 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 Skjerstadvfjord also differed

significantly from the two other fjords, and was characterised by intermediate levels of total abundance, biomass and diversity compared to Saltfjord and Skjerstadvfjord. 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 Skjerstadvfjord (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 benthic-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 overlying water layer. These differences are likely related to the dynamic environmental conditions close to Saltstraumen, where water masses from Saltfjord are advected into Skjerstadvfjord by tidal currents (Fig. 4). Denser surface waters from Saltfjord sink to the deeper layers of Skjerstadvfjord, enhancing benthic-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 (Zaboraska 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 Skjerstadvfjord (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-Kowalczyk 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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