MASTER THESIS

Marthe Austad
BI309F MSc in Marine Ecology

Differences in macrofauna communities among three north Norwegian fjords

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Bodø, May 2016
Marthe Austad

Abstract

Fjords come in a vast range of geomorphologies and environmental conditions, and hydrodynamics vary greatly from fjord to fjord as well as within fjord systems. Similar to the physical properties of fjords, species composition has been shown to be equally different among fjords in addition to variability within fjord basins. In particular, a decline in diversity going from the sill and towards the inner parts of fjords has been shown. This study focuses on the differences in soft-bottom macrofauna distribution patterns in the deep basins of three north Norwegian fjords: Sørfolda, Saltfjorden and Skjerstadfjorden. Saltfjorden and Skjerstadfjorden belong to the same fjord system, separated by a narrow tidal inlet (Saltstraumen), and have very different hydrographic regimes. Sørfolda is also a part of a larger fjord system, however there are no narrow constriction in this fjord similar to Saltstraumen. Macrofauna (>1 mm) was sampled using a Van Veen grab (0.1 m^2) in May 2015 from 20 stations. In addition, sediment characteristics (Redox, pH) were measured at every station and oceanographic data (temperature, salinity, oxygen saturation) measured at selected stations to represent the hydrodynamic conditions of the different fjord regions. The majority of stations were sampled in Sørfolda, whereas six stations were sampled in a transect from the inner part of Skjerstadfjorden to outside the sill in Saltfjorden. Macrofauna was identified down to family level, and univariate measurements (total and relative abundance, taxa richness, Shannon-Wiener diversity index and Pielou's evenness index) and multivariate variables (taxa abundances per station and environmental variables) were analysed to reveal spatial changes. The findings of this study show that there were clear differences in the macrofauna communities among the fjords in this study, as well as small-scale differences within the fjord basins. The differences among fjords were, however, larger than the differences found within the fjords.

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1. Introduction

Fjords are classified as estuaries, partly enclosed from the coastal water and with a significant amount of freshwater runoff. Their basins, which can be relatively deep (e.g. Sognefjorden: 1300 meters deep), are often separated from the coastal water by shallow submarine sills created by glacial deposits. The hydrodynamics in a fjord is a result of several processes, defined by Pedersen (1978; cited in Brattegard, 1980) as follows: 1) fjord geometry such as sill depth, basin depth, length and width; 2) hydrology of watershed; 3) oceanographic conditions outside a fjord (e.g. level of stratification and tides); and 4) meteorological conditions. As fjords come in a vast range of geomorphologies and environmental conditions, the processes observed within a given fjord are defined by the respective interactions between these processes (Inall & Gillibrand, 2010). These processes vary greatly from fjord to fjord as well as within fjord systems. One example of a variable fjord system is the tidally energetic Saltfjorden-Skjerstadfjorden system, south/south-east of Bodø, northern Norway. Saltfjorden and Skjerstadfjorden are separated by a narrow sill, at the shallowest only 26 m, and with deep basins on either side. Saltfjorden is the outer basin and has only one source of runoff, whereas Skjerstadfjorden is the endpoint of two large rivers as well as drainage from two lakes (Eliassen et al., 2001). This causes Saltfjorden to have relatively homogenous water masses, whereas Skjerstadfjorden shows a high degree of stratification (Eliassen et a., 2001; Busch et al., 2014).

In sill fjords, the vertical structure is usually controlled by salinity stratifications from freshwater runoff from land, and this stratification may cause the basin water below sill level to become isolated for longer periods of time. Between periods of basin water renewal the isolated water masses may become eutrophied and depleted of dissolved oxygen (hypoxia). Persisting hypoxia may eventually lead to increased mortality of the basin fauna, either from low oxygen content, the presence of hydrogen sulphide (Levin et al., 2009), or behavioural changes causing the organisms to be more easily preyed upon (Wu, 2002).

Similar to the physical properties of fjords, species composition has been shown to be equally different between fjords (e.g. Fosså & Brattegard, 1990; Holte et al., 2005; Gaidukov, 2014; Pedersen et al., 2015). Fosså & Brattegard (1990) found a correlation to depth in the epibenthic mysid fauna of several west Norwegian fjords, but only down to 350 m. Below this depth, the fauna showed a higher variation between fjords than within fjords. In addition, a high variability in species composition and diversity has been observed also within fjord basins. In particular, a decline in diversity going from the entrance and towards the inner parts of the fjord (e.g. Hansen & Ingolfsson, 1993; Buhl-Mortensen & Høisæter, 1993; Wlodarska-Kowalczuk

& Pearson, 2004; Renaud et al., 2007; Wlodarska-Kowalczuk et al., 2012). Hansen & Ingolfsson (1993) found a decrease in species richness going into the inner parts of Icelandic fjords, and suggested the increased temperature fluctuations observed in the inner parts as an explanation for this pattern. In fjords on Spitsbergen, Svalbard, Wlodarska-Kowalczuk et al. (2012) found that the inner and outer parts of the fjords hosted significantly different communities in terms of species composition and diversity, and a severe depletion in species richness in the inner parts of the fjords. Similarly, Gaidukov (2014) found a decrease in macrofaunal richness on family level in the inner parts of the Saltfjorden-Skjerstadfjorden system, in addition to significant differences in the community composition between the two fjords. Pedersen et al. (2015) showed a similar pattern, with differences in species diversity in the fjord system of Ullsfjord-Sørfjord in Troms, northern Norway.

This study focuses on soft-bottom macrofauna distribution patterns, community structure and diversity of the deep basins of three northern Norwegian fjords: Sørfolda, Saltfjorden and Skjerstadfjorden. Little is known about the benthic communities in this region, and the master project of Gaidukov (2014) was the first extensive study of deep soft-bottom macrofauna in Saltfjorden and Skjerstadfjorden. Therefore, the objectives of this study were to 1) determine differences and/or similarities among the benthic communities in these three fjords, and 2) how the spatial community patterns in Sørfolda differ from the patterns observed in the tidally energetic system of Saltfjorden-Skjerstadfjorden potentially influenced by the tidal inlet Saltstraumen.

2. Materials and methods

2.1 Study area

In this study two fjord systems located in Nordland, northern Norway were investigated. These two systems comprise three fjords: Sørfolda and the system of Saltfjorden and Skjerstadfjorden. Both are relatively large systems, opening towards Vestfjorden in the west. Saltfjorden-Skjerstadfjorden is approximately twice as long as Sørfolda (91 km and 46 km, respectively). The sills connecting the two systems to Vestfjorden are of approximately similar depths, at 265 m (Sørfolda) and 200 m (Saltfjorden). However, Sørfolda is a part of a larger fjord system with a sister fjord, Nordfolda, and they both drain into Karlsøyfjorden before passing over a second sill into Vestfjorden at 240 m. Saltfjorden is the shallowest fjord, with a maximum depth of 375 m. Sørfolda and Skjerstadfjorden are considerably deeper, with maximum depths of 574 m and 544 m, respectively.

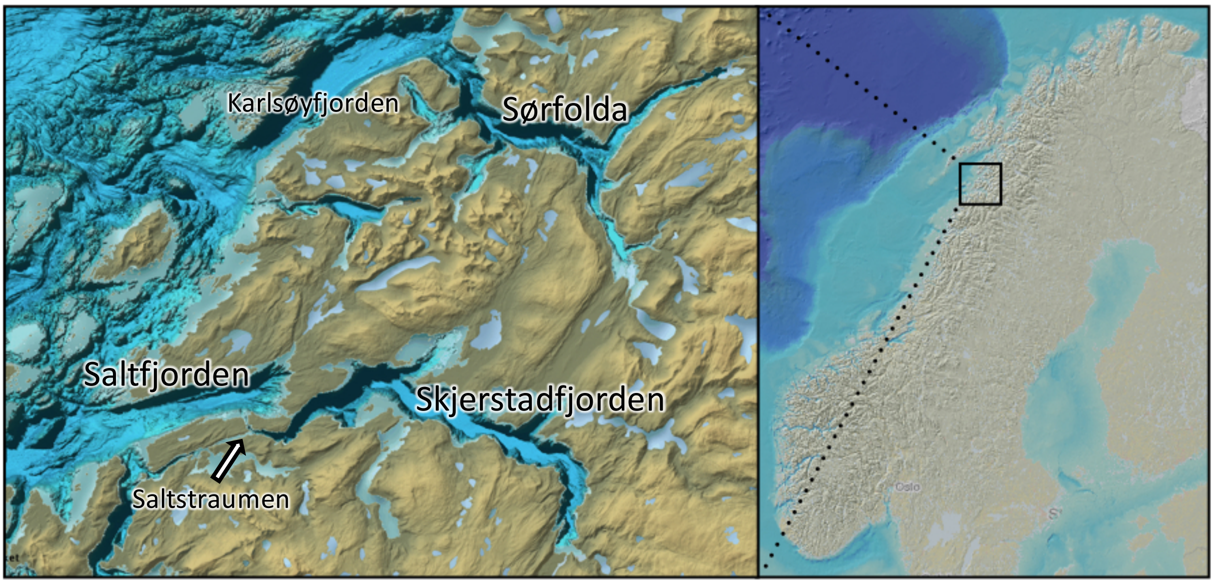

Figure 1: Map of study area showing the two fjord systems investigated in this study (source: norgeskart.no).

The hydrography of the two systems vary, although Sørfolda is largely similar to Saltfjorden is terms of both temperature (6.5 – 7.5 °C) and salinity (34.7 – 35.5)(Skreslet, 2002; Aure & Pettersen, 2004; Gaidukov, 2014; Busch et al., 2014). This indicates water masses originating from Atlantic waters, whereas Skjerstadfjorden has been shown to contain colder (4 – 4.9 °C) and less saline (33.5 – 33.9 psu) bottom water (Eliassen et al., 2001; Skreslet, 2002; Gaidukov, 2014; Busch et al., 2014) of local origin. Not many measurements have been done in Sørfolda, but Aure & Pettersen (2004) obtained relatively low oxygen saturations in Sørfolda, around 50-60%, in november/december at a time with presumed stagnating conditions in the deep basin. In Saltfjorden the oxygen saturation of the deep water has been measured to be relatively stable, between 75 and 90%, whereas Skjerstadfjorden appears to have more variable saturations, between 57 and 90% (Eliassen et al., 2001; Skreslet, 2002; Gaidukov, 2014; Busch et al., 2014).

The most noticeable difference in morphology when comparing the two systems is the narrow trench Saltstraumen separating Saltfjorden from Skjerstadfjorden. At the narrowest, Saltstraumen is only 26 m deep and 60 m wide. Saltstraumen accounts from the majority of water exchange between Skjerstadfjorden and Saltfjorden, with 2.7 x 10^8 m^3 of water flowing through at every tidal cycle. It is often reported about anoxic conditions in fjords with shallow sills (Inall & Gillibrand, 2010), nevertheless Skjerstadfjorden appears to have a sufficient exchange of deep water (e.g. Skreslet, 1994; Gaidukov, 2013). This happens because of the less saline water masses found in Skjerstadfjorden, allowing the more saline, and thus denser, water masses dragged up from ~100 meters in Saltfjorden by Saltstraumen to penetrate into the deep basin and displacing the deep water in Skjerstadfjorden (Eliassen et al., 2001).

2.2 Sampling strategy and processing

The sampling took place in May 2015. In total 20 stations were sampled in the three fjords (Fig. 2, Table 1) with the UiN research boat «Tanteyen» using a 0.1 m^2 Van Veen grab. Five stations representing the inner and outer parts of the deep basins of Saltfjorden and Skjerstadfjorden were selected based on the work of Gaidukov (2014), as well as one outside the sill in the adjacent basin of Vestfjorden. In Sørfolda no previous studies of the macrofauna in the deep basin has been done, so the locations were chosen at random along the deepest parts of the basin covering the length of the fjord up to ~350 meters depth. At each station three grab samples were taken.

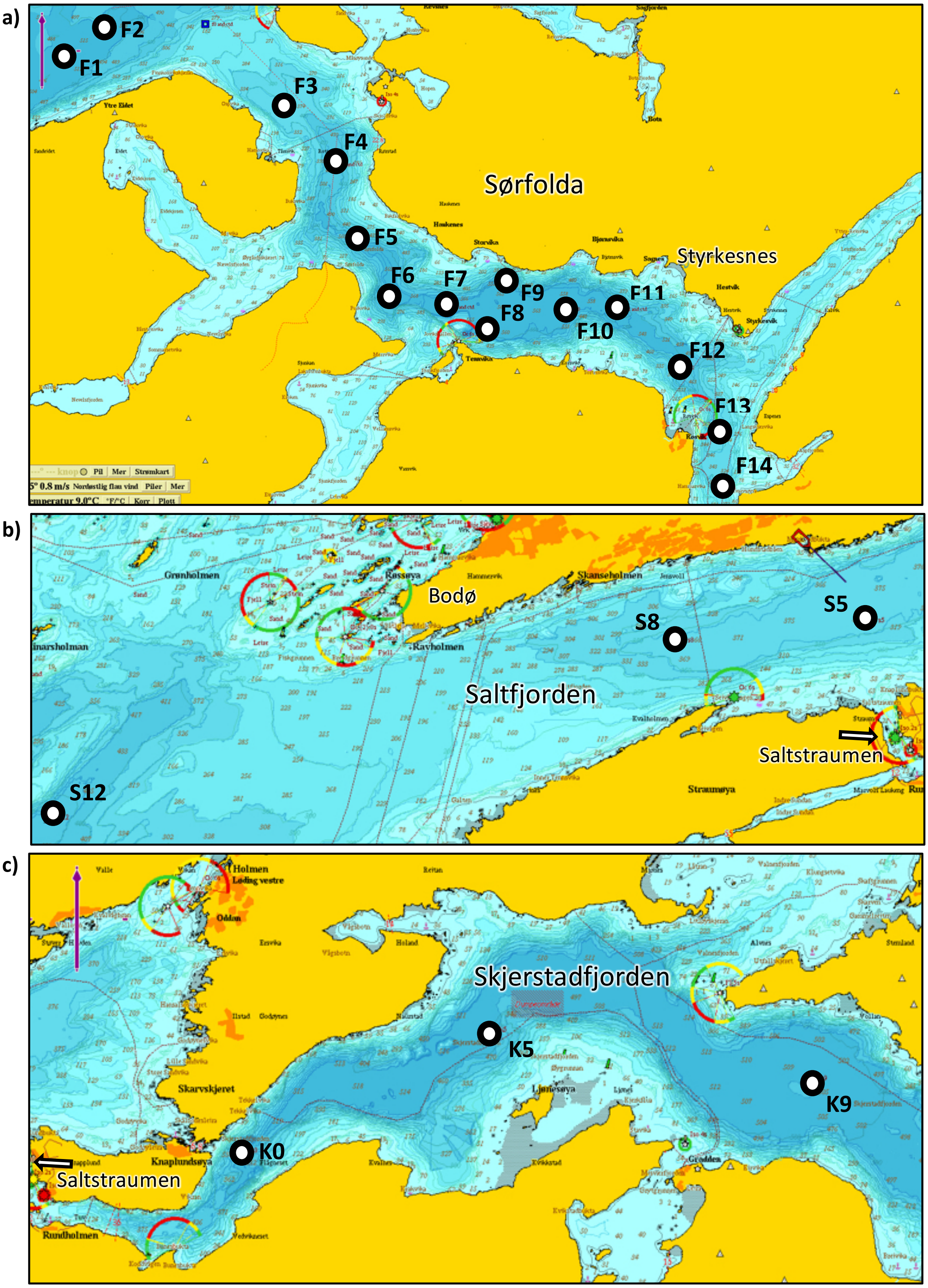

Figure 2: Overview of sampling stations in a) Sørfolda, b) Saltfjorden and c) Skjerstadfjorden (source: Olex software)

Table 1: Sampling data for each station. Stations F1-F2 in Sørfolda and S12 in Saltfjorden were taken outside the fjord basins. For station K0, one grab sample for macrofauna and CTD measurements were taken on the 12.05.2015. Stations go from the inner Sørfolda basin, through the outer stations and into Saltfjorden and Skjerstadfjorden

Fjord	Station	Date	Depth (m)	Latitude (N)	Longitude (E)
Sørfolda	F14	19.05.2015	349	67° 27.836	15° 29.778
	F13	19.05.2015	359	67° 28.837	15° 30.103
	F12	19.05.2015	403	67° 30.053	15° 27.688
	F11	19.05.2015	551	67° 31.152	15° 24.715
	F10	19.05.2015	557	67° 31.215	15° 22.435
	F9	19.05.2015	551	67° 31.666	15° 19.328
	F8	19.05.2015	558	67° 30.767	15° 18.307
	F7	19.05.2015	566	67° 31.236	15° 16.234
	F6	20.05.2015	558	67° 31.322	15° 13.611
	F4	18.05.2015	488	67° 33.950	15° 11.934
	F3	18.05.2015	361	67° 35.067	15° 05.463
	F2	18.05.2015	505	67° 36.531	14° 59.542
	F1	18.05.2015	516	67° 35.999	14° 57.618
Saltfjorden	S12	18.05.2015	457	67° 12.723	14° 05.933
	S5	07.05.2015	365	67° 15.472	14° 35.601
	S8	07.05.2015	370	67° 15.241	14° 28.771
Skjerstadfjorden	K0	21.05.2015	542	67° 14.190	14° 44.628
	K5	12.05.2015	512	67° 15.901	14° 53.619
	K9	12.05.2015	504	67° 15.312	15° 05.334

2.2.1 Sampling and processing of macrofauna

The first two grabs at each station were taken for the analyses of benthic communities. The sediment was sieved over a 1mm mesh sieve and fixed in 4% formaldehyde buffered with borax. The benthos samples were further processed in the laboratory by rinsing the samples with running water for at least two hours to remove the formaldehyde. Then the sample was dyed using Rose Bengal to ease the sorting process, before the specimens were identified to the lowest possible taxonomic level, counted, and stored in 70% ethanol. For some taxa (e.g. Nemertea) identification was possible only to higher taxonomic levels of phyla, class or order.

2.2.2 Sediment characteristics and oceanographic data

Sediment redox potential, pH and temperature were measured from the third grab sample. For this, VWR pH10 and ORP15 pens (except station S5, where Hach Lange HQ11D, MTC10101 and SOTA-1 pH electrode were used) for pH and redox potential, respectively. At selected stations CTD profiles of the water column was taken using a SAIV SD204 CTD profiler, which measured conductivity, temperature, pressure (depth), density, dissolved oxygen, fluorescence and salinity (calculated from conductivity, temperature and pressure). The stations were selected to represent the hydrodynamic conditions of the different fjord regions (inner, outer and middle regions).

2.3 Statistical analyses

2.3.1 Univariate measurements and analyses

Total abundance, number of taxa (richness), relative abundances, Shannon-Wiener diversity index (H') and Pielou's evenness index (J') were used as univariate characteristics of the macrofauna communities in the study area, reported in the sample size of 0.1 m^{-2}. All values for community characteristics were calculated as the mean of both replicates from each station. The relative abundance refers to the number of individuals of a given taxon as a percentage of all individuals in the sample.

Shannon-Wiener diversity index determines the organisation of an assemblage by the number of species and the number of individuals per species (Gray & Elliott, 2009):

$$H' = -\sum_i p_i \log_2 p_i$$

where $p_i = n_i/N$ (n_i being the number of individuals of the *i*th species and N the total number of individuals). Species diversity incorporates species richness and species evenness, the latter can be acquired by dividing the observed diversity value (H') by the maximum possible value if each individual belonged to a different species (H'_{max}):

$$J' = H'/H'_{max}$$

where $H'_{max} = \log_e s$, and s is the number of species. Both indices were calculated using Primer v6 (Clarke & Gorley, 2006).

To test the effect of station or fjord on total abundance, taxa richness, H' and J', parametric Analyses of Variance (ANOVA) or non-parametric Kruskal-Wallis one-way analysis of variance was conducted using R version 3.2.2 (R Core Team, 2015). Prior to these analyses, the assumptions of parametric data (normal distribution and homogeneity of variance) were checked with the Shapiro-Wilk normality test and the Fligner-Killeen test for equality of variances. For data meeting the assumptions of parametric data Analyses of Variance (ANOVA) was conducted, and for data not meeting the assumption Kruskal-Wallis H one way analyses of variance was used. Where ANOVA gave significant results, Tukey's HSD (Honestly Significant Difference) test was used as a post-hoc analysis to identify means that are significantly different from each other (Zar, 2010). In the case of a significant Kruskal-Wallis, a multiple comparison test was conducted using the function 'kruskal' from the agricolae package (de Mendiburu, 2015).

Oceanographic data was analysed using R (R Core Team, 2015) with OCE: An Analysis of Oceanographic Data version 0.9-17 (Kelley & Richards, 2015) in combination with GSW: Gibbs Sea Water Functions version 1.0-3 (Kelley, Richards & WG127 SCOR/IAPSO, 2015).

2.3.2 Multivariate analyses

The abundance of macrofauna taxa and environmental variables were compared to reveal spatial changes in the community structure using multivariate analyses. All multivariate analyses were conducted using PRIMER v6 (Clarke & Gorley, 2006).

To decrease the influence of the most abundant taxa, abundance data was square-root transformed prior to analyses, and a similarity matric was constructed using the Bray-Curtis measure of similarity. Analysis of Similarity (ANOSIM) was used to test for significant differences in the macrofauna communities of fjords. Subsequently, a hierarchical clustering analysis was performed, including 'similarity profile' (SIMPROF) permuatation tests identifying clusters between the stations. The output from SIMPROF was then overlayed on a non-metric Multidimensional Scaling (nMDS) plot (100 restarts). SIMPER (similarity percentages) then identifies the contribution from each taxa to the dissimilarities between fjords and clusters identified with SIMPROF.

The Bio-Env procedure in PRIMER was used to identify the best matches between multivariate among-sample patterns of the taxa assemblage and environmental variables associated with those samples. Prior to the analyses, the environmental variables were normalised before a triangular distance matrix was constructed using Euclidean distance. The Bio-Env procedure was then carried out comparing the environmental variable matrix with the species assemblages (Spearman rank-correlation; maximum number of trial variables: 10). Finally, an nMDS was constructed for the environmental variables in the same manner as for the macrofaunal assemblages.

3. Results

3.1 Abiotic parameters

The three fjords showed to have quite different vertical structures in the time of the sampling, in terms of both salinity and temperature. In Sørfolda the profiles did not vary considerably between the stations (Fig. 3a, c), with a surface layer stratified in salinity (increasing with depth) and temperature (decreasing with depth).

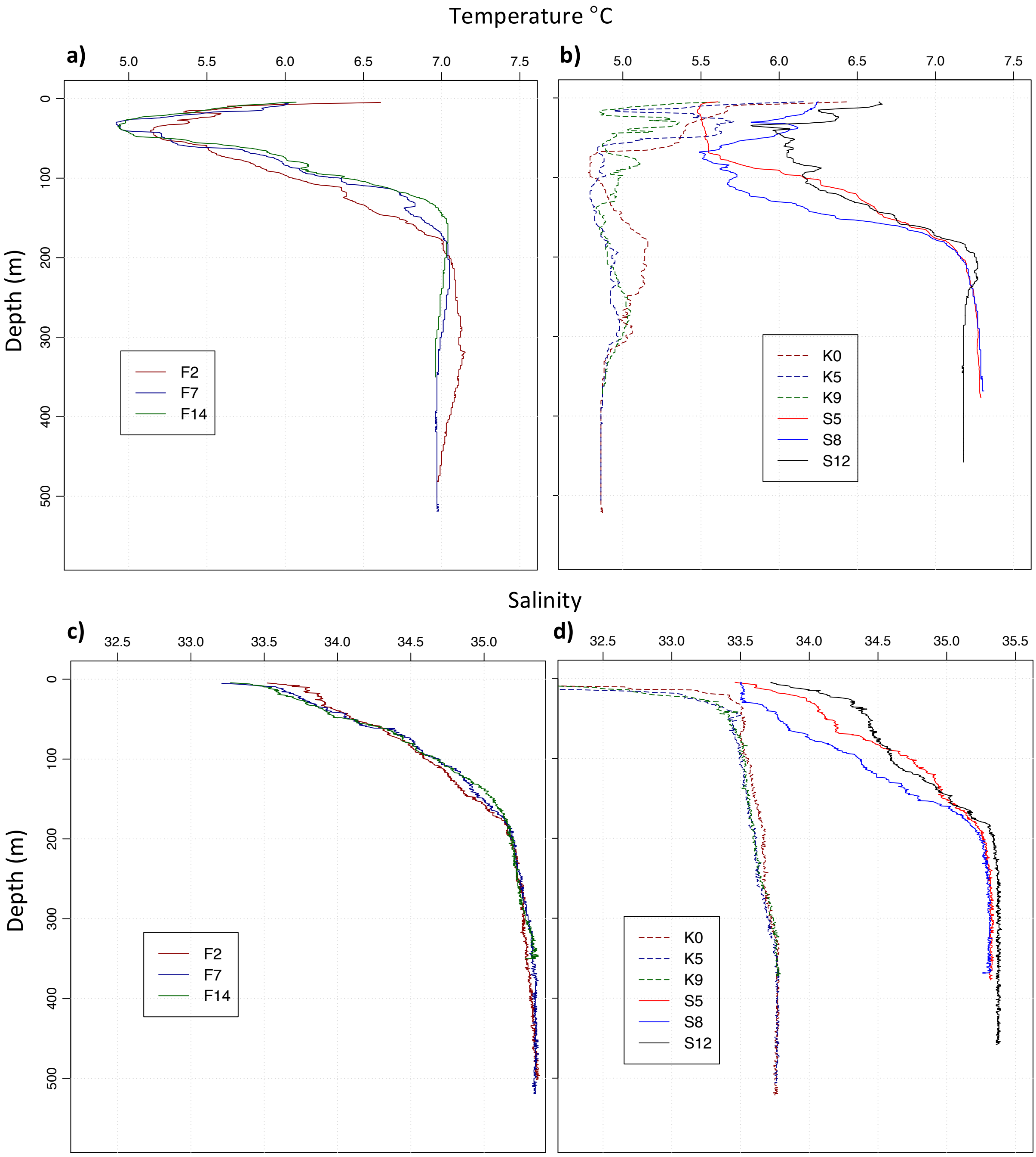

Figure 3: Temperature (upper panes) and salinity (lower panes) profiles for a, c) Sørfolda (F) and b, d) Saltfjorden (S) and Skjerstadfjorden (K).

In Saltfjorden-Skjerstadfjorden the effect of Saltstraumen was evident both in the heavy mixing of surface water as well as clearly different water masses of the deep basin. Below sill depth both temperature and salinity is very homogenous within the fjord as well as outside the sill. Also in Saltfjorden and Skjerstadfjorden the deep water is very homogenous, but Skjerstadfjorden is considerably less saline and colder than both Saltfjorden and Saltfjorden, indicating the formation of local water masses in this fjord as a result of the large runoff from rivers and lakes. The salinity down to 200-300 m in Skjerstadfjorden is similar to the surface salinity in Saltfjorden, indicating the denser water from Saltfjorden sinking down to greater depths when entering Skjerstadfjorden.

Table 2: Sediment characteristics from sediment probes as well as oxygen saturation and salinity of bottom water from CTD. Stations go from the inner Sørfolda basin, through the outer stations and into Saltfjorden and Skjerstadfjorden.

Station	Depth (m)	Temperature (°C)	Oxygen (%)	Salinity	pH	Eh (mv)
F14	349	7.7	71	35.3	7.8	274
F13	359	7.5	-	-	7.7	302
F12	403	7.3	69	35.3	7.8	264
F11	551	7.7	68	35.3	7.8	193
F10	557	7.7	-	-	7.8	343
F9	551	7.6	-	-	7.9	271
F8	558	7.7	-	-	7.9	269
F7	566	7.5	68	35.3	7.8	19
F6	558	7.3	-	-	7.9	204
F4	488	7.4	69	35.4	7.8	120
F3	361	7.7	-	-	7.9	184
F2	505	7.8	74	35.4	7.9	340
F1	516	8.0	-	-	7.8	290
S12	457	7.7	84	35.4	7.7	-55
S8	365	7.4	78	35.4	7.9	-135.7
S5	370	7.7	80	35.3	7.8	-260.7
K0	542	5.7	71	33.8	8.0	-95
K5	512	5.5	71	33.8	7.7	-101
K9	504	5.7	73	33.8	7.8	-24

The bottom water in each fjord showed no differences along the length of the fjord in terms of salinity and temperature. Sørfolda and Saltfjorden had average bottom water temperatures of 7 °C and 7.3 °C, respectively. In Skjerstadfjorden, the bottom water mass was slightly colder, averaged at 4.9 °C. The stations outside the fjord basins, S12 and F2, measured 7.2 °C and 7 °C, respectively, showing no difference from their respective fjords. Temperature measurements from the sediments were slightly warmer than the bottom water (Table 2), but this may assigned to small differences in the calibration of the different measuring instruments. Bottom water salinity show the same trends as temperature, with Sørfolda and Saltfjorden having similar measures at 35.4 and 35.3, respectively. Skjerstadfjorden is less saline, averaging at 33.8. Stations S12 anf F2, outside the sills, also have measurements close to their respective fjords, both at 35.4.

The oxygen content is relatively high in all basins, the lowest measurements from the inner parts of the Sørfolda deep basin (68-69%). Both measurements taken outside the deep basins, at stations F2 (Sørfolda) and S12 (Saltfjorden) showed higher levels of dissolved oxygen than in the deep basins of the fjords, S12 having the highest saturation (84%).

Both redox potential (Eh) and pH give an idea of the biological condition of and the degree of organic loading to the sediment (Pearson & Stanley, 1979; Carroll et al., 2003; Matijeric et al., 2007; Black et al., 2008), negative Eh values (< -125) and low pH (< 6.9) are associated with anaerobic microbial processes and reduced conditions (Pearson & Stanley, 1979; Black et al., 2008) and as a proxy for oxygen levels in the sediment. The pH is close to 8 at all stations, showing no noticeable differences. The Eh values on the other hand, varied considerably. Sørfolda showed positive values throughout the deep basin of the fjord, as well as outside the sill. Both Saltfjorden and Skjerstadfjorden had negative Eh values, but only Skjerstadfjorden had considerable negative values.

3.2 General community composition

In total, 12 302 individuals were found in the 38 grab samples collected in the study area, belonging to 81 macrofaunal taxa (77 on family level, one on phylum level, two on class level and one on order level). These taxa were representative of 13 classes beloning to 8 phyla. Numerically dominant phyla at all stations were Annelida (Polychaeta) and Mollusca, in terms of both taxa richness and abundance. Sipuncula was the third most abundant phylum, whereas Arthropoda was the third most taxa rich phylum. Table 3 lists the taxa found during the study.

Table 3: List of taxa found in the study area (* = taxon not further determined)

Phylum	Class	Order	Family
Annelida			
	Polychaeta		
			Paraonidae
			Capitellidae
			Amphinomidae
			Trichobranchidae
			Nephtyidae
			Maldanidae
			Flabelligeridae
			Ampharetidae
			Terebellidae
			Pectinariidae
			Cirratulidae
			Chaetopteridae
			Oweniidae
			Onuphidae
			Lumbrineridae
			Dorvilleidae
			Oenonidae
			Aphroditidae
			Polynoidae
			Sigalionidae
			Syllidae
			Phyllodocidae
			Hesionidae
			Nereididae
			Pholoidae
			Pilargidae
			Opheliidae
			Spionidae
			Glyceridae
			Sabellidae
			Orbiniidae
			Scalibregmatidae
			Cossuridae
Nemertea*			
Cephalorhynca			
	Priapulida		
			Priapulidae

Table 3 *continued*

Phylum	**Class**	**Order**	**Family**
Sipuncula			
	Sipunculidea		
		Golfingiida	
			Sipunculidae
			Golfingiidae
			Phascolionidae
Arthropoda			
	Malacostraca		
		Cumacea	
			Leuconidae
			Diastylidae
			Nannastacidae
		Amphipoda	
			Eriopisidae
			Oedicerotidae
			Ampeliscidae
			Aoridae
			Phoxocephalidae
			Eusiridae
		Tanaidacea*	
		Decapoda	
			Axiidae
		Isopoda	
			Desmosomatidae
Echinodermata			
	Ophiuroidea		
		Ophiurida	
			Amphilepididae
			Amphiuridae
			Ophiuridae
	Asteroidea		
		Paxillosida	
			Astropectinidae
			Ctenodiscidae
	Holothuroidea		
		Apopida	
			Synaptidae
	Echinoidea		
		Spatangoida	
			Schizasteridae
			Loveniidae
Mollusca			
	Bivalvia		
			Semelidae
			Cardiidae
			Nuculanidae
			Thyasiridae
			Arcidae
			Pectinidae
			Arcticidae
			Nuculidae
			Limidae

Table 3 *continued*

Phylum	Class	Order	Family
			Cuspidariidae
	Scaphopoda*		
	Caudofoveata*		
	Gastropoda		Skeneidae
			Pyramidellidae
			Buccinidae
		Cephalaspidea	
			Philinidae
			Cylichnidae
Cnidaria			
	Anthozoa		
		Alcyonacea	
			Isididae
		Spirularia	
			Cerianthidae
		Actinaria	
			Edwardsiidae

3.3 Spatial changes in community composition

3.3.1 Spatial changes in total abundance

Kruskal-Wallis one-way analysis of variance revealed no significant differences in the total mean abundance between the three fjords. The mean abundances for the deep basins and stations outside the fjords were as follows: Sørfolda, 304 (±23) ind. 0.1 m^{-2}; outer Sørfolda, 265 (±21) ind. 0.1 m^{-2}; outer Saltfjorden, 373 (±11) ind. 0.1 m^{-2}; Salfjorden, 236 (±32) ind. 0.1 m^{-2}; Skjerstadfjorden, 497 (±258) ind. 0.1 m^{-2}. Skjerstadfjorden has a very high variability, which is accounted for by the extremely high abundance observed close to Saltstraumen (station K0).

Significant differences were found between stations (Fig. 4; p=0.03; see appendix A, Table 1 for all Kruskal-Wallis multiple comparisons). In Sørfolda, a significant decrease in abundance was found from the sill and into the middle part of the fjord (F3 to F8, p=0.01). Furthermore, station F12 had the lowest abundance in the study area (186±14 ind. 0.1 m^{-2}), significantly lower than the preceding station F12 (p=0.03) and the suceeding stations F13-F14 (ps<0.001). No significant differences were found between the stations on opposite sides of the sill in Sørfolda. In Salfjorden, the station outside the sill (S12) had a higher abundance than the two stations in the deep basin (S8, S5, ps <0.05). Outside the sills of both Sørfolda and Saltfjorden (F1-F2, S12) the abundances were also found to be significantly different (ps <0.05). The outermost station in Skjerstadfjorden (closest to Saltstraumen, K0) had a very high abundance with 1012 (±38) ind. 0.1 m-2, whereas the rest of the study area had abundances between 168 and 465 ind. 0.1 m^{-2}. Within Skjerstadfjorden, the middle and inner stations (K5, K9) were not significantly different from each other, but both were significantly different from K0 (*p*s <0.001). K0 was also significantly different from the greater part of the rest of the study area. The exceptions were the stations with highest abundance: F3, F6, F13-F14 and S12.

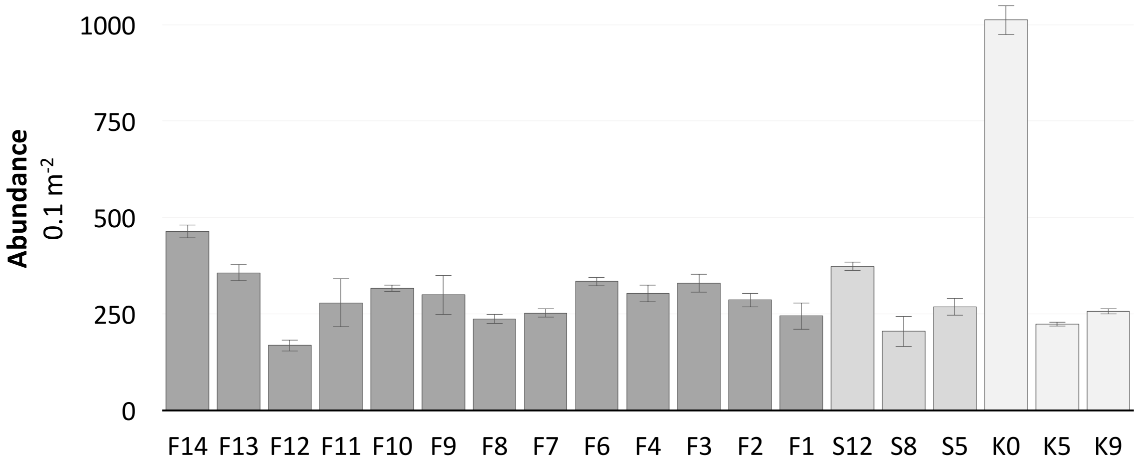

Figure 4: Spatial changes of total abundance (ind. 0.1 m^{-2}) going from the inner part of Sørfolda (F14) through the outer regions F1 – F2 and S12 going into Saltfjorden (S8, S5) and Skjerstadfjorden (K0, K9) (±SE).

3.3.2 Spatial changes in taxa richness, diversity and evenness

The Kruskal-Wallis test showed that there was a significant difference between fjords in terms of both diversity (Shannon-Wiener diversity index, H'; *p*=0.02) and evenness (Pielou's evenness index, J'; *p*=0.04) (Table 4). No significant differences in taxa richness between fjords were shown by ANOVA. Pairwise comparisons of diversity and evenness showed that Sørfolda was significantly different from outer Sørfolda (F1-F2) and Skjerstadfjorden. In addition, Sørfolda was shown to be different from outer Saltfjorden (S12) in terms of diversity.

A significant difference was also found between stations for taxa richness (Kruskal-Wallis, *p*=0.04), but no differences in diversity (H') or evenness (J') were found (Fig. 5a; appendix A, Table 1). In Sørfolda, the middle basin had a significantly lower taxa richness than the outer (F3, F6) and inner (F13-F14) parts (*p*s <0.05). From the outer station in Saltfjorden (S12) the richness increases both towards Sørfolda (F2, *p*=0.045) as well as into the deep basin in Saltfjorden (S5, *p* <0.05). In the inner and middle parts of Skjerstadfjorden (K5, K9) no differences were found, but this region had the lowest taxa richness in the study area and was significantly lower than, among others, K0 (*p*s <0.001). Kruskal-Wallis did not show any significant differences in diversity or evenness, however the innermost station in Skjerstadfjorden (K9) has visibly lower diversity and evenness (Fig. 5b, c).

Table 4: Kruskal-Wallis pairwise comparisons of Shannon-Wiener diversity index (H') and Pielou's evenness index (J') between fjords. Statistically significant results are emboldened.

	p-value	
Fjord area	Diversity (H')	Evenness (J')
Outer Saltfjorden – Outer Sørfolda	0.860	0.628
Outer Saltfjorden – Saltfjorden	0.307	0.531
Outer Saltfjorden – Skjerstadfjorden	0.709	1.000
Outer Saltfjorden – Sørfolda	**0.039**	0.147
Outer Sørfolda – Saltfjorden	0.300	0.179
Outer Sørfolda – Skjerstadfjorden	0.813	0.516
Outer Sørfolda – Sørfolda	**0.013**	**0.009**
Saltfjorden – Skjerstadfjorden	0.367	0.402
Saltfjorden – Sørfolda	0.215	0.320
Skjerstadfjorden – Sørfolda	**0.009**	**0.023**

3.3.3 Spatial changes in relative abundance

In terms of relative abundance of taxa, the macrofaunal composition showed clear differences along a spatial gradient and the three fjords could clearly be differentiated (Fig. 6). In both Sørfolda and Saltfjorden, the benthic community was dominated by the polychaete families Chaetopteridae and Capitellidae, as well as the bivalve family Thyasiridae. At the innermost stations in Sørfolda (F13-F14) a difference in the community composition was observed, accounted for by the higher proportions of the polychaete family Spionidae. In Saltfjorden the sipunculan Phascolionidae is also a dominant taxon together with Chaetopteridae. Skjerstadfjorden deviates from the rest of the study area in the relative abundance of taxa, and the three stations also clearly differed from each other. At the outermost part of Skjerstadfjorden (K0) the polychaete Oweniidae (33%) dominated the benthic community, a taxon not exceeding 6% relative abundance in the rest of the study area. In the middle part of the deep basin in Skjerstadfjorden Thyasiridae and Capitellidae were dominating, similarly to what was observed in Saltfjorden and Sørfolda, and the innermost part of the basin showed a very high domination of Capitellidae (56%). It is worth noting that the proportion of 'other' taxa is considerably higher in the outer and middle part of the deep basin in Skjerstadfjorden (K0 and K5), caused by, among others, a high abundance of Phoxocephalidae at K0 and a more even distribution of individuals among the taxa.

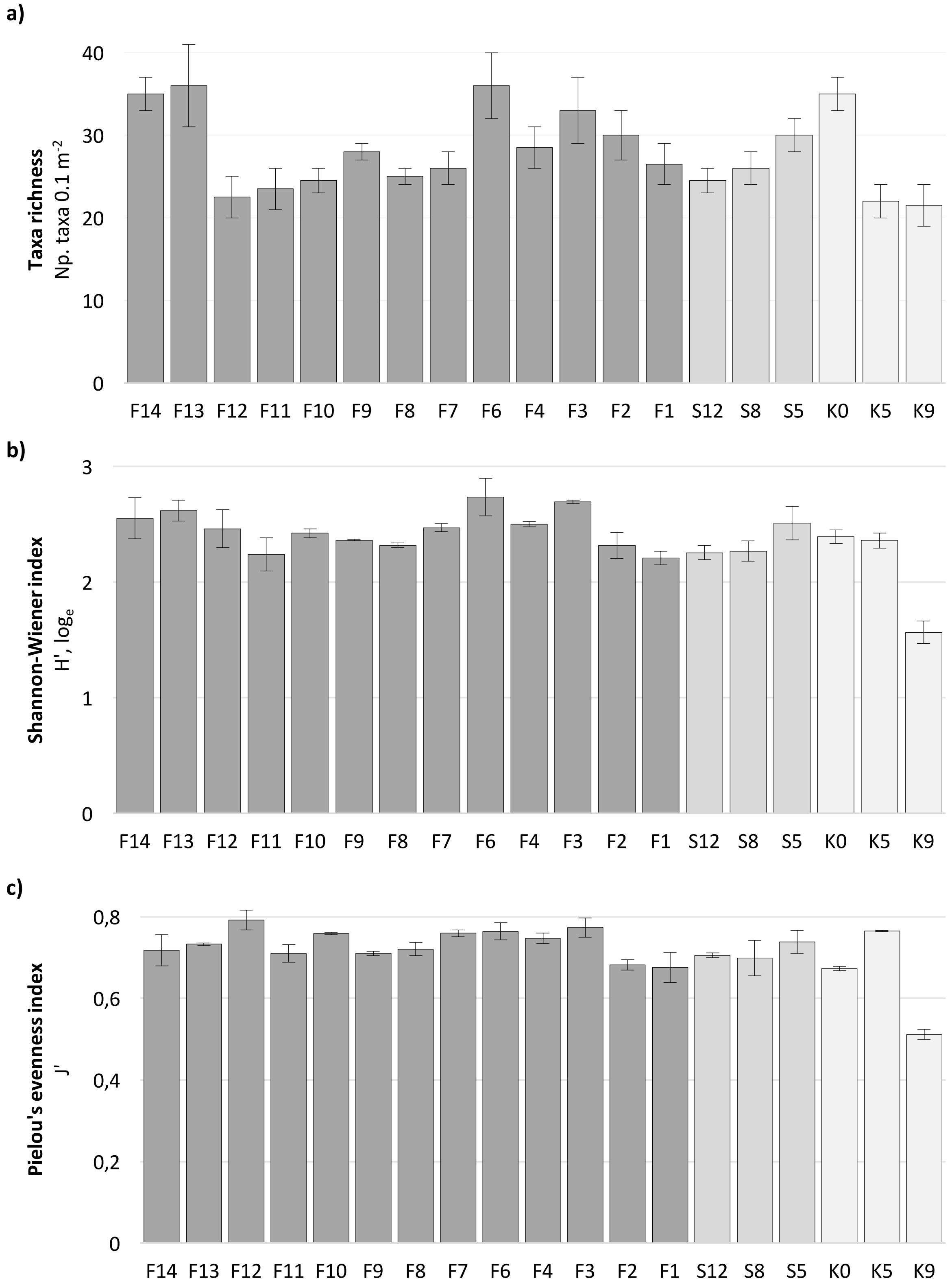

Figure 5: Spatial changes of a) mean number of taxa (0.1 m2), b) Shannon-Wiener diversity index (H’), and c) Pielou’s evenness index (J’) going from the inner part of Sørfolda (F14) through the outer regions F1 – F2 and S12 going into Saltfjorden (S8, S5) and Skjerstadfjorden (K0, K9)(±SE).

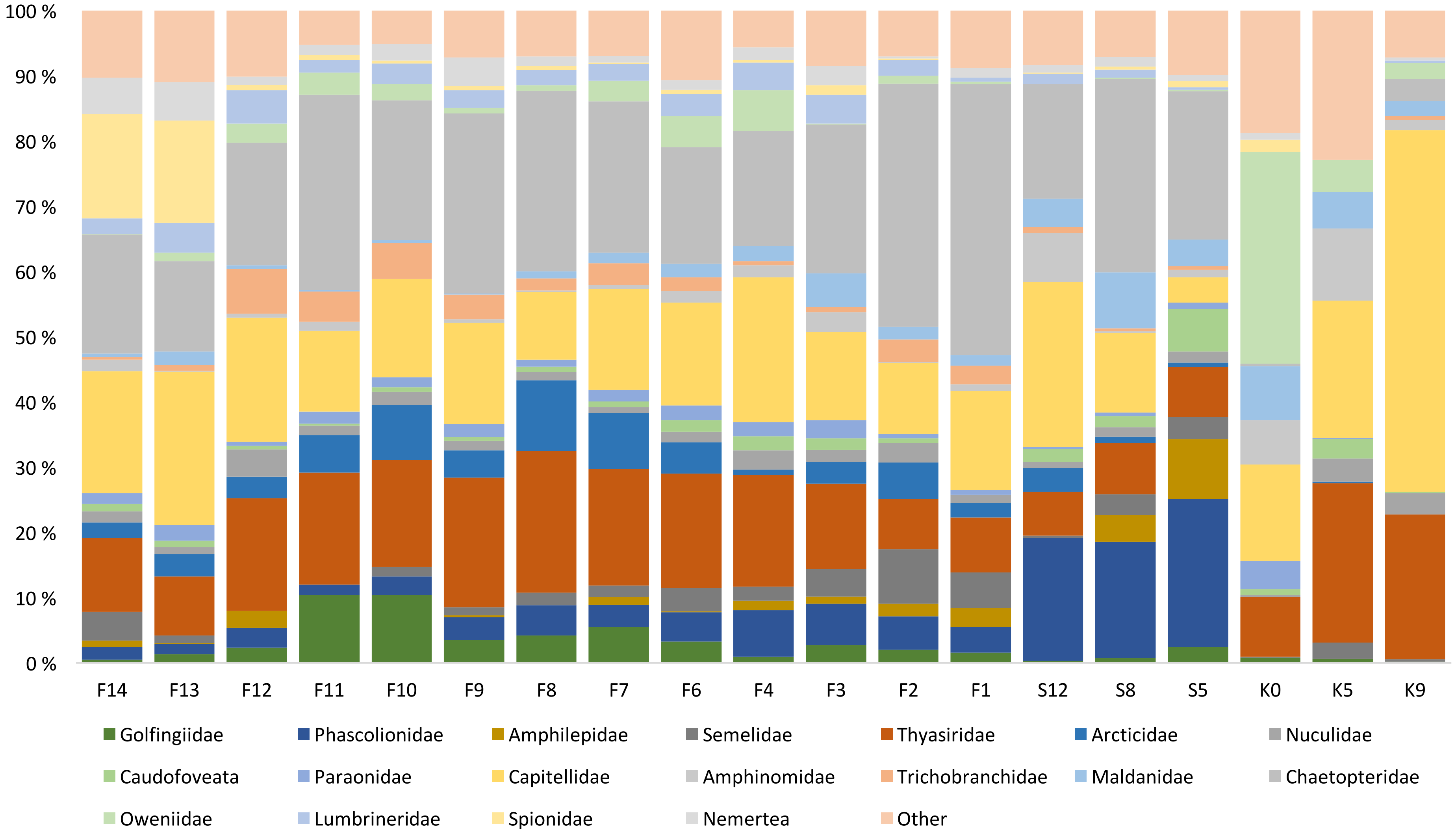

Figure 6: Relative abundance of taxa contributing more than 1% to the total abundance across stations. Left to right: inner part of Sørfolda (F14) through the outer regions F1 – F2 and S12 going into Saltfjorden (S8, S5) and Skjerstadfjorden (K0, K9).

3.4 Spatial changes in community structure

The multi-dimensional scaling (MDS) ordination show clear differences in the community composition of the three fjords (Fig. 7). Between the deep basins of Sørfolda and Saltfjorden, significant differences were shown (ANOSIM, R=0.862, p=0.013) but with a relatively low dissimilarity of 38%. Sørfolda was also shown to be significantly different from Skjerstadfjorden (ANOSIM, R=0.973, p=0.003) with a dissimilarity of 55%, and, even though not significantly different (ANOSIM, R=0.75, p=0.2), Skjerstadfjorden had a high dissimilarity of 57% to Saltfjorden. High dissimilarities were also found between Skjerstadfjorden and the outer parts of Saltfjorden (S12) and Sørfolda (F1-F2) (52% and 58% dissimilarity, respectively), although not significant according to ANOSIM (Table 5). Furthermore, the outer parts of Sørfolda and Saltfjorden were not significantly different from either of the respective deep basins of Sørfolda and Saltfjorden and with low dissimilarities (Outer Sørfolda vs Sørfolda, 30%; Outer Saltfjorden vs Saltfjorden, 33%).

Table 5: Pairwise test from Analysis of Similarities (ANOSIM, R statistic and p-value) and average dissimilarity from SIMPER. Significant results are emboldened.

Fjord	**R statistic**	**p-value**	**Average diss.**
Outer Sørfolda vs Sørfolda	0.330	0.090	30.05
Outer Sørfolda vs Saltfjorden	1.000	0.333	30.15
Outer Sørfolda vs outer Saltfjorden	1.000	0.333	37.00
Outer Sørfolda vs Skjerstadfjorden	0.830	0.100	58.37
Sørfolda vs Saltfjorden	0.862	**0.013**	37.98
Sørfolda vs outer Saltfjorden	0.874	0.083	37.41
Sørfolda vs Skjerstadfjorden	0.973	**0.003**	54.71
Saltfjorden vs outer Saltfjorden	1.000	0.333	32.45
Saltfjorden vs Skjerstadfjorden	0.750	0.200	57.19
Outer Saltfjorden vs Skjerstadfjorden	0.330	0.500	51.70

In addition to clear dissimilarities between fjord basins, nine clusters of macrofauna were identified (SIMPROF) within the basins of each fjord (Fig. 7): inner (F13-F14 and F12) middle (F7-F11) and outer (F3-F4, F6) deep basin in Sørfolda, outer Sørfolda beyond the sill (F1-F2), outer Saltfjorden (S12), Saltfjorden deep basin (S5, S8), outer Skjerstadfjorden (K0) and inner/middle Skjerstadfjorden (K5, K9). No significant differences between the clusters were identified with ANOSIM, and the high R values (R=1) indicate that ANOSIM might not be able to distinguish between the groups because of the low sample sizes within each cluster.

Most conspicuous was the separation of the outer part of Skjerstadfjorden (K0) and the middle and inner part (K5 and K9) (Fig. 7). The middle and inner deep basin of Skjerstadfjorden (K5, K9) had a similarity of 66%, and a dissimilarity of 52% with the outer station (K0) (Table B in appendix B), mainly contributed by Oweniidae (8%), Paraonidae (3%) and Maldanidae (3%). Both clusters in Skjerstadfjorden were also considerably different from both Saltfjorden and Skjerstadfjorden.

In Saltfjorden, the deep basin (S5, S8) had a similarity of 77% and was distinguished from K0 with a 63% dissimilarity and from the outer station (S12) with a 33% dissimilarity. Oweniidae (8%), Capitellidae (4%), Amphinomidae, Nereididae and Phascolionidae (3%) were mainly responsible for the dissimilarity between Saltfjorden (S5, S8) and K0 in Skjerstadfjorden.

Three main clusters were identified in the deep basin of Sørfolda: inner (F13-F14; 79% similarity), middle (F7-F11; 82% similarity) and outer (F3-F4, F6; 80% similarity). In addition, station F12 had a community composition slightly different from the inner and middle cluster in Sørfolda (40% and 30% dissimilarity, respectively). The stations outside the sill, F1-F2, were also identified as a separate group with 28% dissimilarity to the outer part of Sørfolda (F3-F4, F6). Overall, the dissimilarity between clusters in Sørfolda was relatively low, between 26% and 40%.

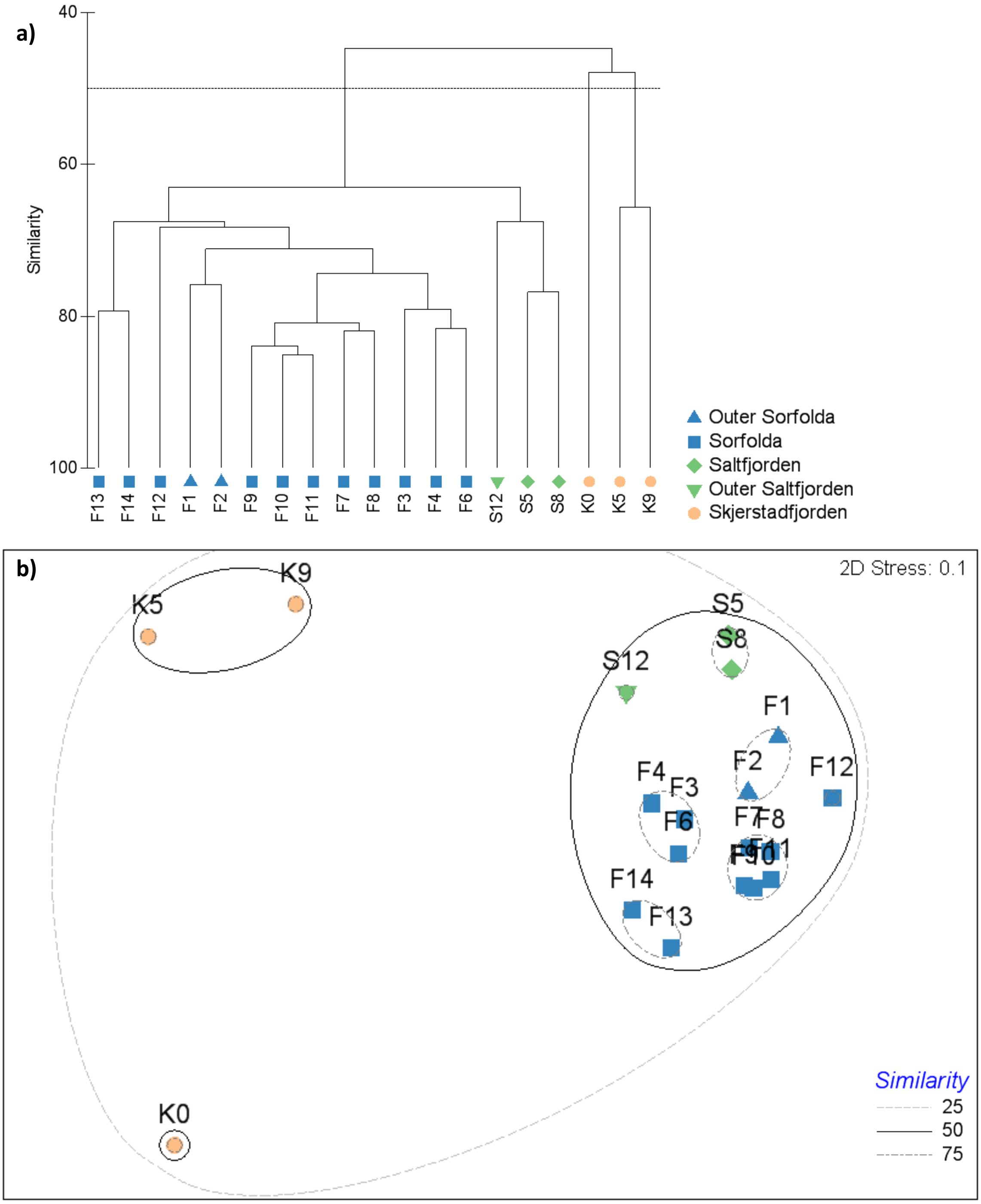

Figure 7: a) Hierarchical clustering and b) two-dimensional non-metric multi-dimensional scaling (nMDS) of taxa abundance (based on square-root transformed data in a Bray-Curtis similarity matrix).

3.5 Spatial changes in characteristic and dominant taxa

In Sørfolda, Chaetopteridae (Polychaeta; Fig. 8a) was a dominant taxa throughout the deep basin as well as in the outer stations (F1-F2). The deep basin did, however, have a lower abundance than than the outer stations, and so Chaetopteridae was the most contributing taxa to the dissimilarity between Sørfolda and outer Sørfolda (5% dissimilarity contribution). In Saltfjorden-Skjerstadfjorden, Chaetopteridae was also a dominant taxa outside Saltfjorden and in the Saltfjorden deep basin but was only found in small numbers in Skjerstadfjorden.This contributed to 8% dissimilarity between Saltfjorden and Skjerstadfjorden.

Throughout the study area, Capitellidae (Polychaeta; Fig 8b) was one of the most dominating taxa. The innermost station in Skjerstadfjorden, K9, was highly dominated by this taxon. High abundances were also recorded at K0 in Skjerstadfjorden, S12 in outer Saltfjorden and F13-F14 in Sørfolda, but was not the single most dominating taxon in either of theses stations. Relatively stable abundances were seen from outer Sørfolda and in the deep basin up to F12. In contrast, 12% of the dissimilarity between outer Saltfjorden (S12) and Saltfjorden (S5, S8) was explained by the considerable decrease in both total and relative abundance of Capitellidae. The clustering of F13-F14 and F7-F11 in Sørfolda was also explained by a higher abundance of Capitellidae in the innermost stations (F13-F14; 7% dissimilarity contribution).

Occurring at very high abundances, Oweniidae (Polycheta; Fig. 8c) dominated station K0 in Skjerstadfjorden. Throughout the rest of the study area, this taxon did not contribute markedly to total or relative abundances. Oweniidae was identified as the most contrubuting taxon to the division of K0 from the middle and inner stations in Skjerstadfjorden (K5, K9), with 15% of the dissimilarity contribution. Similarly, 13% of the dissimilarity between K0 and the deep basin of Saltfjorden (S5, S8) was accounted for by the abundance of Oweniidae.

Spionidae (Polychaeta; Fig 9) was a characteristic taxon for the innermost stations in Sørfolda (F13-F14) and contributed 11-13% of the dissimilarity between F13-F14 and the other clusters in Sørfolda. Compared to the rest of the study area, Spionidae was also found at a comparable high abundance at station K0 in Skjerstadfjorden, but did not contribute significantly to the dissimilarity of K0 from the rest of the study area.

The most abundant mollusc in the study area was Thyasiridae (Bivalvia; Fig. 10a). The communities in both Sørfolda and Skjerstadfjorden was characterised by high relative abundances of Thyasiridae. The total abundance showed a higher variance, with low abundances in Saltfjorden and correspondingly low relative abundance. Thyasiridae was responsible for 4% of the dissimilarity between Saltfjorden and Skjerstadfjorden.

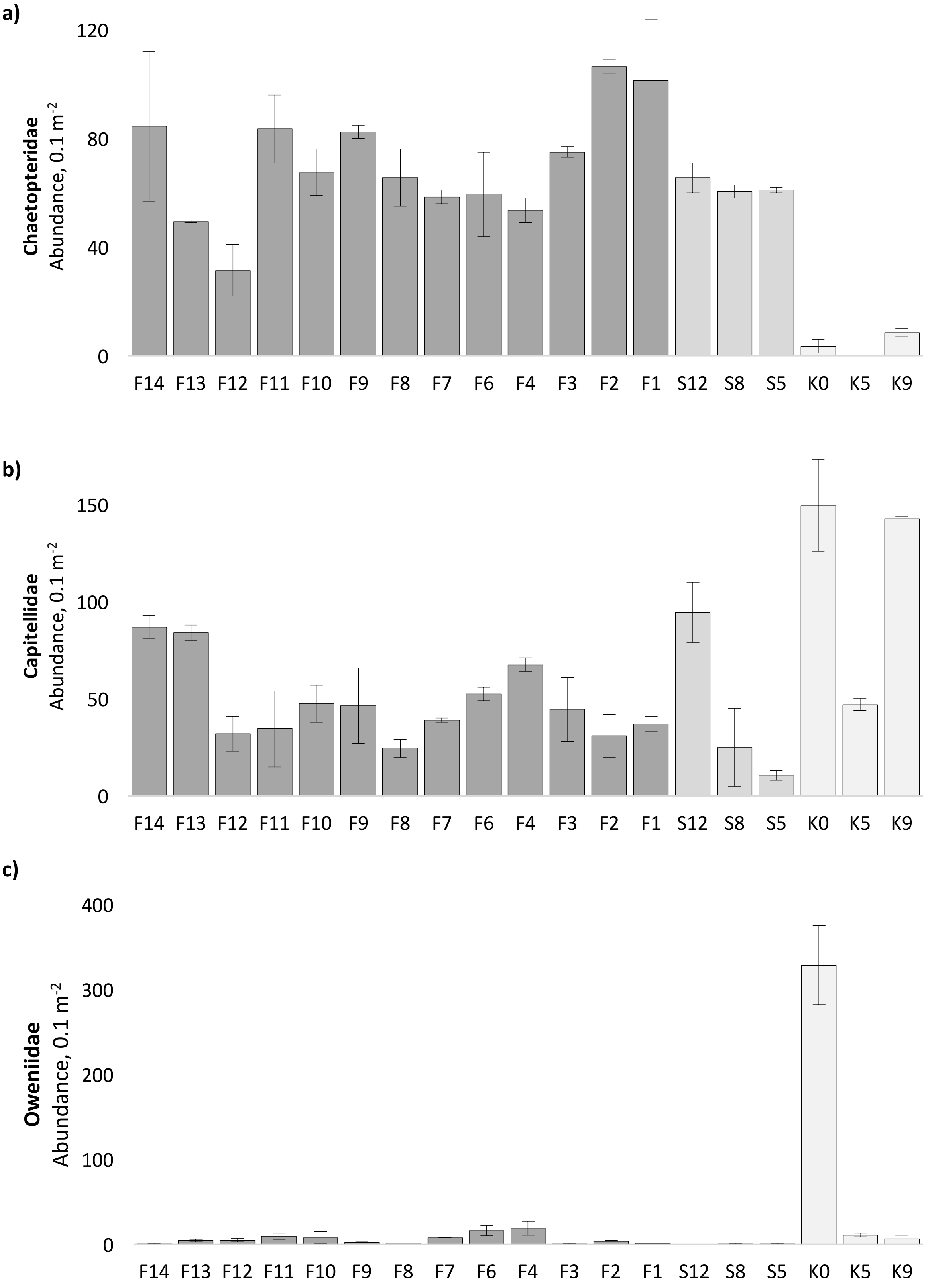

Figure 8: Abundance of a) Chaetopteridae, b) Capitellidae and c) Oweniidae (abundance 0.1 m^{-2} ±SE) going from the inner part of Sørfolda (F14-F3) through the outer regions F1-F2 and S12 going into Saltfjorden (S8, S5) and Skjerstadfjorden (K0, K5, K9).

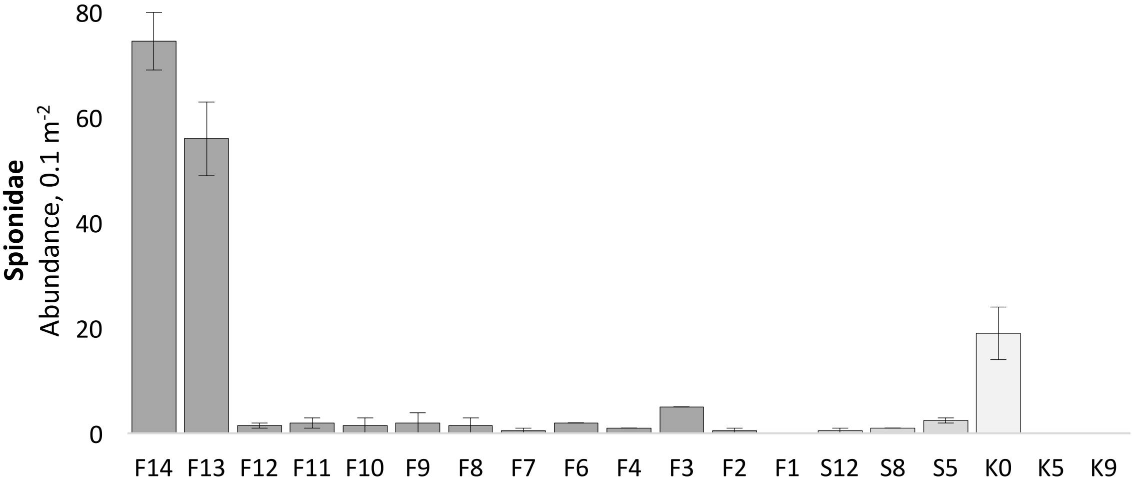

Figure 9: Abundance of Spionidae (abundance 0.1 m^{-2} ±SE) going from the inner part of Sørfolda (F14-F3) through the outer regions F1-F2 and S12 going into Saltfjorden (S8, S5) and Skjerstadfjorden (K0, K5, K9).

Through most of the study area, Semelidae (Bivalvia; Fig. 10b) was found in low to moderate abundances. This taxon was also a contributing taxa to dissimilarities between Sørfolda and outer Sørfolda (5% contribution), outer Sørfolda and outer Saltfjorden (6% contribution) and outer Saltfjorden and Saltfjorden (3% contribution). This taxon was not found at stations F12 and F11 in Sørfolda.

A characteristic taxon of Saltfjorden was Phascolionidae (Sipunculida; Fig. 10c), both in the deep basin (S5, S8) and outside the sill (S12). Consequently, the dissimilarities between Saltfjorden and the two other fjords were explained by relatively high contributions from this taxa: Sørfolda and Saltfjorden (7% contribution), outer Sørfolda and outer Saltfjorden (9% contribution), Saltfjorden and Skjerstadfjorden (8% contribution). In Skjerstadfjorden, Phascolionidae was not found, and in Sørfolda only with small abundances compared to Saltfjorden.

Phoxocephalidae (Amphipoda; Fig. 11) was only found in Saltfjorden-Skjerstadfjorden, and in particularly high abundances at K0. The high abundances at K0 contributes to 4-5% of the dissimilarity between this station and the rest of Skjerstadfjorden (K5, K9) and the deep basin of Saltfjorden.

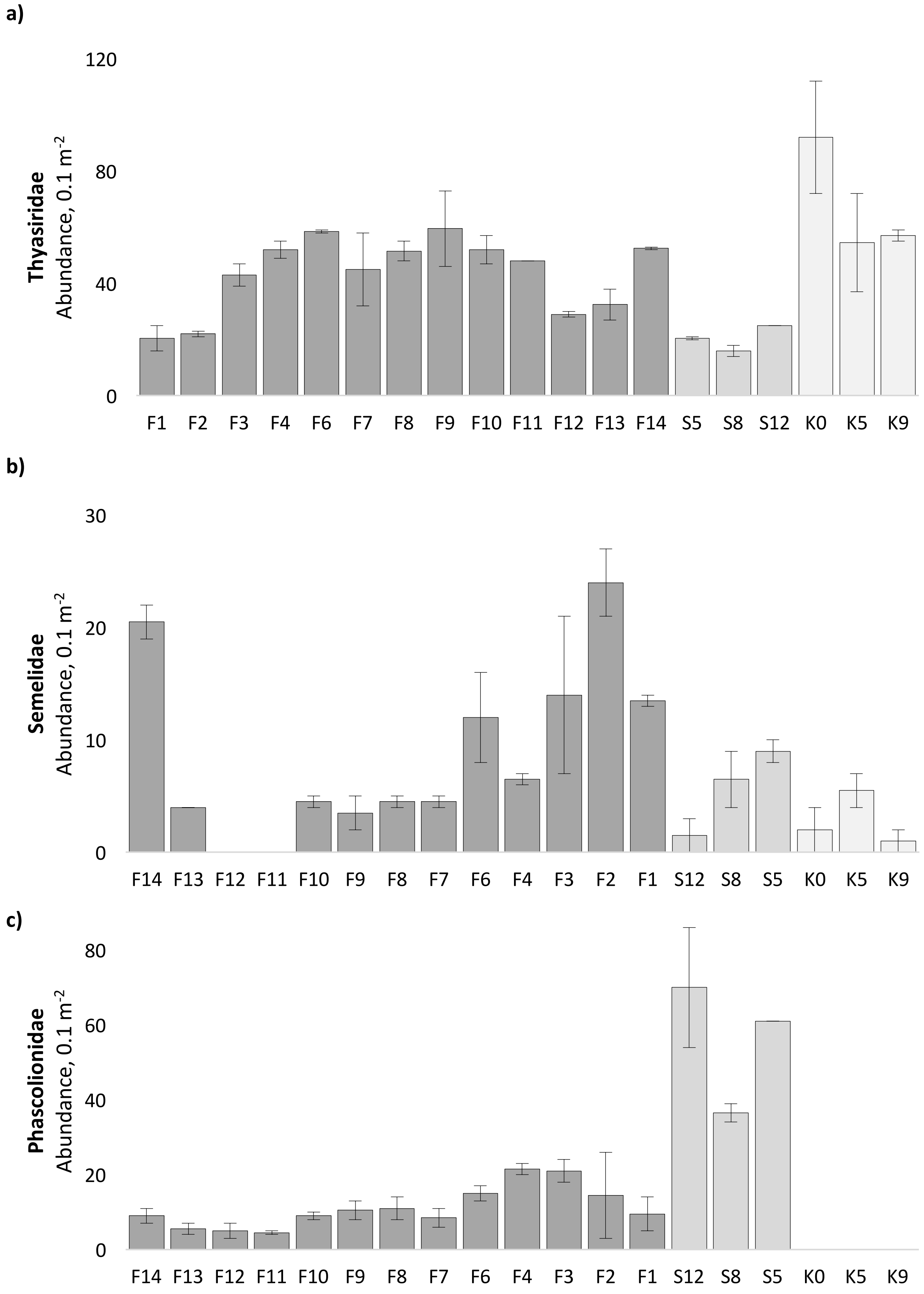

Figure 10: Abundance of a) Thyasiridae, b) Semelidae and c) Phascolionidae (abundance 0.1 m^{-2} ±SE) going from the inner part of Sørfolda (F14-F3) through the outer regions F1-F2 and S12 going into Saltfjorden (S8, S5) and Skjerstadfjorden (K0, K5, K9).

Figure 11: Abundance of Phoxocephalidae (abundance 0.1 m^{-2} ±SE) going from the inner part of Sørfolda (F14-F3) through the outer regions F1-F2 and S12 going into Saltfjorden (S8, S5) and Skjerstadfjorden (K0, K5, K9).

3.6 Linking macrofauna assemblages to the environment

Bio-Env revealed correlations (r_s) close to 0.8 between taxa assemblages and environmental variables (Table 6; Appendix C). Salinity and temperature had the highest single-variable correlations of 0.68 and 0.65, respectively, with taxa assemblages. The other environmental variables had low single-variable correlations, not exceeding r_s=0.165. Hierarchical clustering and nMDS of environmental variables (Fig. 12) was a very good match with the clustering analysis and nMDS of macrofauna assemblages (Fig. 7). The three fjords are clearly separated from each other, and clusters within each fjord were also identified. In Sørfolda, clusters of the outer station (F2), outer deep basin (F4), middle deep basin (F7, F11) and inner deep basin (F12, F14) were identified, corresponding to the clustering observed in the macrofauna. In Saltfjorden, the outer station (S12) appears to be more similar to the innermost station (S5), with the middle station clustered alone (S8). Skjerstadfjorden shows the same pattern as for macrofauna, with K0 separated from K5 and K9.

Table 6: Best correlations from Bio-Env analysis in relation to taxa assemblages (unranked environmental variables). A combination of four environmental variables (salinity, temperature, oxygen saturation and pH) provided the best match to the patterns observed in the biological data.

No. variables	Variable combination	Correlation r_s
4	Salinity-Temperature-Oxygen-pH	0.798
	Salinity-Temperature-Redox-pH	0.782
5	Salinity-Temperature-Redox-pH-Depth	0.782
	Salinity-Temperature-Oxygen-Redox-pH	0.775
	Salinity-Temperature-Oxygen-pH-Depth	0.773
6	Salinity-Temperature-Oxygen-Redox-pH-Depth	0.762

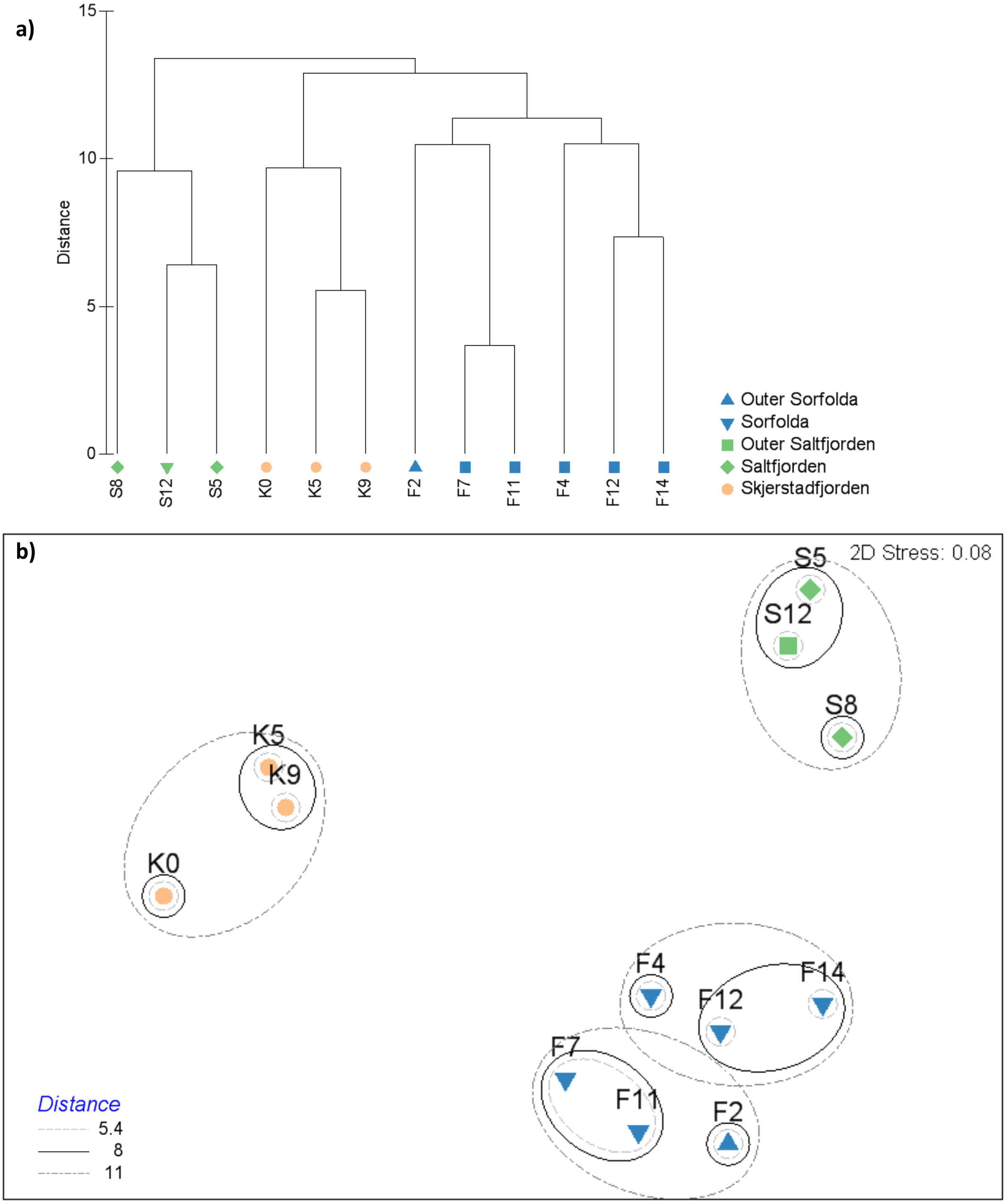

Figure 12: a) Hierarchical clustering and b) two-dimensional non-metric multi-dimensional scaling (nMDS) of environmental variables at selected stations (based on normalised data in a Euclidean distance similarity matrix).

4. Discussion

Fjords exist in a vast range of geomorphologies and environmental conditions, and the hydrodynamics in a given fjord is defined by the interactions between several processes (as defined by Pedersen, 1978; cited in Brattegard, 1980) which vary greatly from fjord to fjord as well as within fjord systems. Mirroring the physical variations in fjords, species composition has been shown to vary significantly between fjord systems as well a within fjords (e.g. Hansen & Ingolfsson, 1993; Holte et al., 2005; Wlodarska-Kowalczuk et al., 2012; Gaidukov, 2014; Pedersen et al., 2015). In this study the distribution patterns, community structure and diversity of the deep basins of three north Norwegian fjords were investigated.

The results showed clear differences between the benthic communities in the fjords investigated. In addition, differences in the community composition were observed within the fjord systems. Large differences between Saltfjorden and Skjerstadfjorden was evident in both the macrofauna communities and environmental parameters, showing the potential effect of the Saltstraumen inlet. Small-scale differences were also identified in Sørfolda, with three main clusters of macrofauna in the deep basin. The macrofauna at the stations sampled outside the fjord systems were also shown to be slightly different from the main fjord basins.

4.1 Differences in the benthic communities of Sørfolda and Saltfjorden-Skjerstadfjorden

The spatial patterns of diversity, abundance and community composition in Arctic glacial fjords have been well studied, showing a clear decrease in both abundance and diversity towards the innermost parts of the fjords, as well as a clear distinction between communities at the inner and outer regions of the fjords (Holte et al., 1996; Wlodarska-Kowalczuk et al., 2005; Wlodarska-Kowalczuk et al., 2012; Grzelak & Kotwicki, 2012). Species richness has also been reported to decrease towards the inner parts of fjords on Iceland and Spitsbergen (Svalbard), and it has been suggested that a less diverse habitat regarding food resources and sediment composition as well as fluctuating physichochemical characteristics can explain this observation (Buhl-Mortensen & Høisæter, 1993; Hansen & Ingolfsson, 1993). In contrast, no significant changes in diversity and evenness were observed in Sørfolda or Saltfjorden in this study, whereas Skjerstadfjorden had a decrease in both diversity and evenness at the innermost station (K9). Both taxa richness and abundance inceased from the outer parts of Sørfolda (F1-F2) and over the sill into the deep basin (F3). From the sill (F3) and further into the fjord (F12) a decrease was observed, in accordance with previous studies from Arctic fjords. At station F12 both richness and abundance reach a minima, and then increased significantly to the innermost parts of the deep basin (F13-F14). In Saltfjorden, richness increases significantly from the outer station (S12) and into Saltfjorden. On the other hand, abundance decreases over the same distance. The station closest to Saltstraumen in Skjerstadfjorden, K0, had a significantly higher abundance than the rest of the study area, and a significant decrease in richness was observerd from K0 towards the inner parts of the fjord basin (K5, K9).

Gaidukov (2014) covered the entire deep basin length of the Saltfjorden-Skjerstadfjorden system, and showed a different pattern than what is presented here. Overall, the present study had a considerably higher abundance and taxa richness than what was found in Saltfjorden and Skjerstadfjorden by Gaidukov in 2014. In addition, a clear increase in taxa richness was found form Saltfjorden to Skjerstadfjorden by Gaidukov (2014), which was not found in this study. In another north Norwegian fjord (Balsfjord, Troms), Oug (2000) found a temporal increase in macrofauna abundance and species richness but with a relatively constant community structure. A covariation between temporeal differences in macrofauna community structure and interannual oceanographic variations has been shown in the Chukchi Sea (Blanchard et al., 2013) as well as in deep sea meiofauna (Guidi-Guilvard & Dallot, 2014). These observations were explained by oceanographic variations possibly altering food suppy (Oug, 2000; Guidi-Guilvard & Dallot, 2014) as well as macrofauna survival and larval recruitment and survival (Blanchard et al., 2013). It is therefore possible that interannual variations in the oceanographic conditions in Saltfjorden and Skjerstadfjorden could have caused the observed differences in abundance and taxa richness between 2013 (Gaidukov, 2014) and 2015 (this study).

As shown by the relative abundances (Fig. 6) and nMDS of taxa assemblages (Fig. 7), there were clear differences in the community composition among the three fjords. These results correspond to differences found among fjords in western Norway (Fosså & Brattegard, 1990) and northern Norway (Larsen, 1997; Holte et al., 2005). In the system of Saltfjorden-Skjerstadfjorden, a substantial dissimilarity was found between the two fjords, with Saltfjorden more similar to Sørfolda than Skjerstadfjorden.

Polychaeta was the dominant taxa in all fjords, followed by Bivalvia and Sipunculida, with different characteristic families among the fjords. Both Polychaeta and Bivalvia has been shown to be the dominant macrobenthic taxa in sill basins of north Norwegian fjords (Larsen, 1997) and Arctic fjords (Renaud et al., 2007; Wlodarska-Kowalczuk et al., 2012). Sørfolda was dominated by a polychaete-bivalvia community (Chaetopteridae-Capitellidae-Thyasiridae), whereas Saltfjorden was characterised by a polychaeta-sipunculida community

(Chaetopteridae-Capitellidae-Phascolionidae). Skjerstadfjorden was subdivided into two very different communities based on the three stations from this study. Closest to Saltstraumen, K0 was largely dominated by Oweniidae (Polychaeta), compared to the middle and inner stations (K5 and K9) which were dominated by Capitellidae and Thyasiridae. These findings are in agreement with the findings of Gaidukov (2014) for this area, where Phascolionidae was dominating in Saltfjorden and Capitellidae in Skjerstadfjorden.

There was also considerable within-fjord differences, especially in Sørfolda and Skjerstadfjorden. In Sørfolda, three main clusters were identified: inner, middle and outer basin macrofauna clusters. In Skjerstadfjorden, Gaidukov (2014) revealed a similar pattern of macrofauna clusters, and also in Arctic fjords this pattern has been shown (Wlodarska-Kowalczuk et al., 2012). In this study, only two clusters were identified in Skjerstadfjorden. However, the inner and middle cluster identified by Gaidukov (2014) had a relatively low dissimilarity compared to K0 as well. Comparing the clustering observed in Skjerstadfjorden with the clustering in Sørfolda showed a considerably higher dissimilarity between the clusters in Skjerstadfjorden than between the clusters in Sørfolda. In Saltfjorden only one cluster was identified, and the two stations included in this study was also identified within the same cluster by Gaidukov (2014). An additional cluster was found in 2014 by Gaidukov, consisting of two stations on opposite sides of the deep basin – close to the sill and close to the inner part of the deep basin.

The findings of this study show that there were clear differences in the macrofauna communities among the two fjord systems in this study, Sørfolda and Saltfjorden-Skjerstadfjorden. Skjerstadfjorden was very different from Saltfjorden, and the latter fjord was more similar to Sørfolda. The effects of Salstraumen thus appear to affect the macrofauna communities in the system of Saltfjorden-Skjerstadfjorden. No such differences were shown in Sørfolda, apart from small clusters of relatively small dissimilarities between the inner, middle and outer basin communities. Considering the three fjords as separate systems thus agrees with the findings of Fosså & Brattegard (1990) and Gaidukov (2014), with larger between-fjord differences than within-fjord differences.

4.2 The link between macrofauna and the environment: Hydrodynamics and physichochemical characteristics

Sill fjords generally have stratified water on either side of the sill, causing the deep water of fjord basins to be largely isolated (Inall & Gillibrand, 2010). Below sill depth, the deep water in both Sørfolda, Saltfjorden and Skjerstadfjorden was homogenous with stable salinity and temperature throughout the length of the deep basins (Fig. 3). In Saltfjorden-Skjerstadfjorden the effect of Saltstraumen was evident both in the heavy mixing of surface water as well as clearly different water masses of the deep basin. Skjerstadfjorden receives runoff from two large rivers as well as drainage from two lakes whereas Saltfjorden only have one source of runoff (Eliassen et al., 2001). Therefore, it has often been reported of highly stratified water masses in Skjerstadfjorden and more homogenous water masses in Saltfjorden (Eliassen et al., 2001; Busch et al., 2014). The temperature and salinity profiles presented here does, however, show that Skjerstadfjorden had a less pronounced stratification than Saltfjorden. The vertical profile in Saltfjorden was largely similar to Sørfolda, with a surface layer stratified in salinity (increasing with depth) and temperature (decreasing with depth). In Skjerstadfjorden the surface water was clearly affected by freshwater runoff, with a thin layer of low salinity the upper 20-30 m. The temperature fluctuated greatly between the stations in Skjerstadfjorden, but a small decrease with depth could be seen. Outside Sørfolda the vertical profile did not deviate from the vertical structure in the fjord, with a stratification in both salinity and temperature. S12 outside Saltfjorden also shows the same structure, however a less pronounced temperature stratification was present.

Salinity is the major constituent in density in northerly latitudes caused by the considerable runoff during spring and summer from snow and/or glacier melting, which can be seen in the deep water of Skjerstadfjorden. The whole water column in Saltfjorden is heavier than the water in Skjerstadfjorden, so when the tide flushes water from Saltfjorden into Skjerstadfjorden this water sinks into the deep basin of Skjerstadfjorden. Usually the water sinking down in Skjerstadfjorden comes from the upper 100 m of Saltfjorden (Eliassen et al., 2001), replenishing the deep water in Skjerstadfjorden with oxygen-rich water causing the high oxygen saturations observed in Skjerstadfjorden (Table 2; Eliassen et al., 2001; Skreslet, 2002; Gaidukov, 2014; Busch et al., 2014). In comparison, Sørfolda has no such exchange of deep water and a consequently lower oxygen saturation in the deep basin has been reported during stagnant conditions with saturations as low as 50-60% (Aure & Pettersen, 2004). The measurements presented here represent a time of the year where advection has been sufficiently strong through the winter to break down stratification and to ventilate into the depths of the fjord basin, and so the oxygen saturations reported in this study were considerably higher than the reported measurements of Aure & Pettersen (2004). When sill fjords are highly stratified, density gradients may isolate the deep water and between periods of renewal the water masses may therefore become eutrophied and depleted of dissolved oxygen (hypoxia). Although there were no indications of hypoxia events in Sørfolda in this study, with relatively high oxygen saturations and high redox (Eh) measurements, the observed decrease in macrofauna abundance and taxa richness may be an indicator of seasonal hypoxia. For example, the bivalves *Abra alba* and *A. nititda* (family Semelidae) have been shown to exhibit increased mortality when at low oxygen saturations (Rosenberg et al., 1991). The Semelidae was found at considerably lower relative abundances in the middle deep basin of Sørfolda and was even completely absent from two stations (Fig. 10b). Coupled with the lower taxa richness and overall abundances, the distribution of Semelidae may be a further indication of seasonal hypoxia events.

Close to Saltstraumen in Skjerstadfjorden (station K0), extremely high abundances were found compared to the other stations (Fig. 4). Also Gaidukov (2014) found the highest abundances in Saltfjorden-Skjerstadfjorden at the stations closest to Saltstraumen, and it is possible that as an effect of currents and bathymetry this area receives a higher supply of organic matter. The polychaete Oweniidae was the most abundant taxa at K0, a family of suspension and surface deposit feeders (Jumars et al., 2015), as well as conspicuous abundances of the scavenging amphipods Phoxocephalidae (Fig. 11; Dauby et al., 2001; De Broyer et al., 2003). Another taxa that was found in relatively high abundances at K0 was the polychaete family Spionidae (Fig. 9). Many spionid species are passive suspension feeders, relying on water movement to bring food particles within reach of their feeding structures (Jumars et al., 2015). This family was also found at high relative abundances at the innermost stations in Sørfolda (F13-F14). In Skjerstadfjorden, the occurrences of Oweniidae and Phoxocephalidae in combination with Spionidae may further indicate bottom currents in the area, as well as for the innermost stations in Sørfolda. Both taxa richness and abundance was significantly higher at these stations, which may also be explained by higher current velocity compared to the middle basin. In comparison, the innermost station in Skjerstadfjorden (K9) had significantly lower taxa richness, as well as lower diversity and evenness owed to a domination of Capitellidae (Fig. 8b). Capitellidae is a family of opportunistic species, with high tolerance to natural and anthropogenic disturbances and organically enriched sediments (Gray & Elliott, 2009; Kutti et al., 2008). It is therefore possible that the physical environment here is much less affected by Saltstraumen, with lower currents and a higher deposition rate of organic matter.

The results from the Bio-Env analysis showed that environmental varibles such as sediment characteristics (pH, redox), bottom water chemical characteristics (oxygen saturation, temperature, salinity) as well as depth may play a role in structuring the macrofauna communities in the deep basins of Sørfoda and Saltfjorden-Skjerstadfjorden. This is especially evident when looking at the considerable fauna dissimiliarities between the deep basins of Skjerstadfjorden and the fauna dissimilarities between the deep basin of Skjerstadfjorden and the deep basin of Sørfolda and Saltfjorden. Skjerstadfjorden had temperature and salinity measurements considerably lower than both Saltfjorden and Sørfolda. Saltfjorden, although belonging to the same fjord system as Skjerstadfjorden, was more similar to Sørfolda both in environmental variables as well as macrofauna assemblages. The environmental variables formed clusters very similar to the clustering found for the macrofauna (Fig. 7, 12). Redox potential (Eh) was the only sediment parameter which varied between all three fjords, and together with salinity and temperature showed a relatively high correlations with the macrofauna assemblages. Eh can indicate the degree of organic loading to the sediment (Pearson & Stanley, 1979; Carroll et al., 2003; Matijeric et al., 2007; Black et al., 2008), and is also a proxy for the oxygen levels in the sediment. The negative Eh values in Saltfjorden-Skjerstadfjorden may therefore indicate a degree of organic loading and oxygen consumption, in contrast to Sørfolda which had relatively high Eh values.

The environmental variables in the three fjords formed clusters very similar to the clustering found for macrofauna in this study, with a larger differences among the fjords than within the fjord basins. Skjerstadfjorden was very different from Saltfjorden in temperature and salinity, Saltfjorden being more similar to Sørfolda. On the other hand, Sørfolda had relatively high Eh values, whereas Saltfjorden and Skjerstadfjorden both had negative measurements. The highest single-variable correlations were found in salinity and temperature, but it was the combining effect of environmental variables that gave the best correlations between the environment and the taxa assemblages (Table 6). However, these results to not give a cause-effect relationship between the similar clustering of environmental variables and macrofauna asseblages. Unfortunately, neither organic matter or granulometry was measured for this study, which could have given more information about the sediment environment. The hydrodynamic regime determines sedimentation rates (Gray & Elliott, 2009) as well as food and larval supply, and sediments with higher particle-size diversity has been linked to higher macrofauna diversity (Etter & Grassle, 1992; Snelgrove & Butman, 1994; Leduc et al., 2012). When considering the differences in abundance, taxa richness and characteristic taxa that was found in the study area, measurements of grain size and organic matter could have given a better resolution of the observed differences in macrofauna communities in Sørfolda, Saltfjorden and Skjerstadfjorden.

4.3 Conclusion

The findings of this study show that there were clear differences in the macrofauna communities among the two fjord systems in this study, Sørfolda and Saltfjorden-Skjerstadfjorden. In addition, there were considerable differences in the measured environmental variables among the fjords and differences in the hydrodynamic regimes were detected. The effects of Saltstraumen appear to affect the macrofauna communities in the system of Saltfjorden-Skjerstadfjorden, as well as the water masses in each fjord. In Sørfolda, no such spatial pattern is observed. Small-scale differences in the macrofauna communities were found within the fjord basins of Sørfolda and Skjerstadfjorden, possibly caused by variations in the bottom current velocity. Previous studies from northerly and Arctic fjords have also shown such clustering within fjord basins. Polychaeta and Mollusca were the numerically dominant taxa in this study, and both Sørfolda and Skjerstadfjorden were dominated by taxa from these phyla whereas Saltfjorden was characterised by a co-dominance between Polychaeta and Sipunculida.

To conclude, there were significant differences in the soft-bottom benthic communities among the deep basins of Sørfolda and Saltfjorden-Skjerstadfjorden. There is a clear effect of the tidal inlet Saltstraumen on the macrofauna communities in Saltfjorden and Skjerstadfjorden, and although small-scale patterns were detected in Sørfolda these differences were not comparable with the spatial pattern in Saltfjorden-Skjerstadfjorden. The among-fjord differences were therefore larger than within-fjord differences.

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Appendix A

Results from Kruskal-Wallis multiple comparison test

Table 1: Kruskal-Wallis pairwise comparisons of total abundance, taxa richness, Shannon-Wiener diversity index (H’) and Pielou’s evenness index (J’) between stations. Statistically significant results are emboldened.

	p-value	
Stations	Total abundance	Taxa richness
F1 – F10	0.0504	0.3633
F1 – F11	0.3878	0.3119
F1 – F12	0.1644	0.1893
F1 – F13	**0.0065**	**0.0387**
F1 – F14	**0.0009**	**0.0311**
F1 – F2	0.2140	0.2381
F1 – F3	0.0222	0.0834
F1 – F4	0.0802	0.5267
F1 – F6	0.0222	**0.0334**
F1 – F7	0.8740	0.8321
F1 – F8	0.8429	0.5267
F1 – F9	0.1160	0.4824
F1 – K0	**0.0004**	**0.0311**
F1 – K5	0.5280	0.1234
F1 – K9	0.5280	0.1018
F1 – S12	**0.0022**	0.3633
F1 – S5	0.4784	0.2381
F1 – S8	0.4316	0.8321
F10 – F11	0.2429	0.9155
F10 – F12	**0.0022**	0.6721
F10 – F13	0.3471	**0.0052**
F10 – F14	0.0802	**0.0041**
F10 – F2	0.4316	**0.0447**
F10 – F3	0.6924	**0.0125**
F10 – F4	0.8121	0.1315
F10 – F6	0.6924	**0.0045**
F10 – F7	0.0689	0.4824
F10 – F8	**0.0336**	0.7775
F10 – F9	0.6635	0.1158
F10 – K0	**0.0429**	**0.0041**
F10 – K5	**0.0132**	0.5043
F10 – K9	0.1644	0.4403
F10 – S12	0.1644	1.0000
F10 – S5	0.1879	**0.0447**
F10 – S8	**0.0093**	0.4824
F11 – F12	**0.0310**	0.7505
F11 – F13	**0.0429**	**0.0041**
F11 – F14	**0.0065**	0.0032
F11 – F2	0.6924	0.0360
F11 – F3	0.1245	**0.0099**
F11 – F4	0.3471	0.1086
F11 – F6	0.1245	**0.0035**
F11 – F7	0.4784	0.4202
F11 – F8	0.2916	0.6979
F11 – F9	0.4546	0.0953

Table 1 *continued*

	p-value	
Stations	Total abundance	Taxa richness
F11 – K0	**0.0032**	**0.0032**
F11 – K5	0.1433	0.5732
F11 – K9	0.8121	0.5043
F11 – S12	**0.0157**	0.9155
F11 – S5	0.8740	**0.0360**
F11 – S8	0.1079	0.4202
F12 – F13	**0.0002**	**0.0020**
F12 – F14	**0.0000**	**0.0016**
F12 – F2	**0.0132**	**0.0184**
F12 – F3	**0.0009**	**0.0048**
F12 – F4	**0.0038**	0.0593
F12 – F6	**0.0009**	**0.0017**
F12 – F7	0.1245	0.2659
F12 – F8	0.2281	0.4824
F12 – F9	**0.0060**	0.0515
F12 – K0	**0.0000**	**0.0016**
F12 – K5	0.4316	0.8047
F12 – K9	0.0504	0.7241
F12 – S12	**0.0001**	0.6721
F12 – S5	**0.0429**	**0.0184**
F12 – S8	0.5280	0.2659
F13 – F14	0.3878	0.9155
F13 – F2	0.0932	0.3284
F13 – F3	0.5804	0.6979
F13 – F4	0.2429	0.1315
F13 – F6	0.5804	0.9436
F13 – F7	**0.0093**	**0.0249**
F13 – F8	**0.0042**	**0.0099**
F13 – F9	0.1758	0.1489
F13 – K0	0.2429	0.9155
F13 – K5	**0.0015**	**0.0011**
F13 – K9	**0.0262**	**0.0009**
F13 – S12	0.6352	**0.0052**
F13 – S5	**0.0310**	0.3284
F13 – S8	**0.0011**	**0.0249**
F14 – F2	**0.0157**	0.2806
F14 – F3	0.1644	0.6217
F14 – F4	0.0504	0.1086
F14 – F6	0.1644	0.9718
F14 – F7	**0.0013**	**0.0198**
F14 – F8	**0.0006**	**0.0078**
F14 – F9	**0.0336**	0.1234

Table 1 *continued*

	p-value	
Stations	Total abundance	Taxa richness
F14 – K0	0.7514	1.0000
F14 – K5	**0.0002**	**0.0009**
F14 – K9	**0.0038**	**0.0007**
F14 – S12	0.6924	**0.0041**
F14 – S5	**0.0046**	0.2896
F14 – S8	**0.0001**	**0.0198**
F2 – F3	0.2429	0.5497
F2 – F4	0.5804	0.5732
F2 – F6	0.2429	0.2959
F2 – F7	0.2746	0.1681
F2 – F8	0.1536	0.0780
F2 – F9	0.7217	0.6217
F2 – K0	**0.0078**	0.2806
F2 – K5	0.0689	**0.0107**
F2 – K9	0.5280	**0.0084**
F2 – S12	**0.0365**	**0.0447**
F2 – S5	0.5804	1.0000
F2 – S8	0.0504	0.1681
F3 – F4	0.5280	0.2517
F3 – F6	1.0000	0.6467
F3 – F7	**0.0310**	0.0553
F3 – F8	**0.0144**	**0.0231**
F3 – F9	0.4094	0.2806
F3 – K0	0.0932	0.6217
F3 – K5	**0.0055**	**0.0027**
F3 – K9	0.0802	**0.0022**
F3 – S12	0.3093	**0.0125**
F3 – S5	0.0932	0.5497
F3 – S8	**0.0038**	0.0553
F4 – F6	0.5280	0.1158
F4 – F7	0.1079	0.4006
F4 – F8	0.0545	0.2126
F4 – F9	0.8429	0.9436
F4 – K0	**0.0262**	0.1086
F4 – K5	**0.0222**	**0.0360**
F4 – K9	0.2429	**0.0289**
F4 – S12	0.1079	0.1315
F4 – S5	0.2746	0.5732
F4 – S8	**0.0157**	0.4006
F6 – F7	**0.0310**	**0.0214**
F6 – F8	**0.0144**	**0.0084**
F6 – F9	0.4094	0.1315

Table 1 *continued*

	p-value	
Stations	Total abundance	Taxa richness
F6 – K0	0.0932	0.9718
F6 – K5	**0.0055**	**0.0010**
F6 – K9	0.0802	**0.0007**
F6 – S12	0.3093	**0.0045**
F6 – S5	0.0932	0.2959
F6 – S8	**0.0038**	**0.0214**
F7 – F8	0.7217	0.6721
F7 – F9	0.1536	0.3633
F7 – K0	**0.0006**	**0.0198**
F7 – K5	0.4316	0.1785
F7 – K9	0.6352	0.1489
F7 – S12	**0.0032**	0.4824
F7 – S5	0.5804	0.1681
F7 – S8	0.3471	1.0000
F8 – F9	0.0802	0.1893
F8 – K0	**0.0003**	**0.0078**
F8 – K5	0.6635	0.3465
F8 – K9	0.4094	0.2959
F8 – S12	**0.0014**	0.7775
F8 – S5	0.3671	0.0780
F8 – S8	0.5539	0.6721
F9 – K0	**0.0172**	0.1234
F9 – K5	**0.0336**	**0.0311**
F9 – K9	0.3278	**0.0249**
F9 – S12	0.0744	0.1158
F9 – S5	0.3671	0.6217
F9 – S8	**0.0241**	0.3633
K0 – K5	**0.0001**	**0.0009**
K0 – K9	**0.0018**	**0.0007**
K0 – S12	0.4784	**0.0041**
K0 – S5	**0.0022**	0.2806
K0 – S8	**0.0001**	**0.0198**
K5 – K9	0.2141	0.9155
K5 – S12	**0.0005**	0.5043
K5 – S5	0.1879	**0.0107**
K5 – S8	0.8740	0.1785
K9 – S12	**0.0093**	0.4403
K9 – S5	0.9368	**0.0084**
K9 – S8	0.1644	0.1489
S12 – S5	**0.0111**	**0.0447**
S12 – S8	**0.0004**	0.4824
S5 – S8	0.1433	0.1681

Appendix B

Results from Similarity Percentages (SIMPER) routine

Table 1: Taxa contributions to dissimilarities between fjords identified with SIMPER. Cut-off at 50% contribution.

Fjords	Average diss.	Taxa	Diss. contrib. %
Outer Sørfolda vs. Sørfolda	30.05	Chaetopteridae	5.10
		Thyasiridae	5.06
		Semelidae	5.00
		Spionidae	4.59
		Amphilepididae	3.14
		Nemertea	3.06
		Capitellidae	2.97
		Golfingiidae	2.85
		Oweniidae	2.82
		Lumbrineridae	2.80
		Arcticidae	2.66
		Scaphopoda	2.56
		Caudofoveata	2.51
		Paraonidae	2.15
		Amphinomidae	2.06
		Maldanidae	2.04
Outer Sørfolda vs. Saltfjorden	30.15	Phascolionidae	8.24
		Chaetopoteridae	5.75
		Caudofoveata	5.45
		Trichobranchidae	4.29
		Arcticidae	4.14
		Capitellidae	3.98
		Maldanidae	3.86
		Semelidae	3.60
		Amphilepididae	3.28
		Phoxocephalidae	2.28
		Spionidae	2.23
		Onuphidae	2.08
		Lumbrineridae	1.91
Sørfolda vs. Saltfjorden	37.98	Phascolionidae	6.71
		Amphilepididae	5.01
		Capitellidae	4.97
		Thyasiridae	4.71
		Arcticidae	4.11
		Maldanidae	3.61
		Lumbrineridae	3.23
		Oweniidae	3.02
		Golfingiidae	2.90
		Trichobranchidae	2.77
		Caudofoveata	2.67
		Spionidae	2.54
		Nuculanidae	2.17
		Semelidae	2.15
Outer Sørfolda vs. outer Saltfjorden	37.00	Phascolionidae	9.08
		Amphinomidae	7.60
		Capitellidae	7.15
		Semelidae	5.60
		Nuculanidae	5.39

Table 1 *continued*

Fjords	Average diss.	Taxa	Diss. contrib. %
		Amphilepididae	4.60
		Chaetopteridae	3.86
		Caudofoveata	3.78
		Maldanidae	3.37
Sørfolda vs. outer Saltfjorden	37.41	Phascolionidae	9.03
		Amphinomidae	6.50
		Nuculanidae	5.93
		Capitellidae	4.90
		Oweniidae	4.12
		Maldanidae	3.77
		Golfingiidae	3.49
		Thyasiridae	3.21
		Spionidae	2.92
		Semelidae	2.44
		Orbiniidae	2.35
		Paraonidae	2.23
Saltfjorden vs. outer Saltfjorden	32.45	Capitellidae	11.82
		Amphinomidae	8.73
		Amphilepididae	8.25
		Arcticidae	4.81
		Nuculanidae	4.76
		Semelidae	3.27
		Phascolionidae	3.18
		Orbiniidae	3.01
		Lumbrineridae	1.43
Outer Sørfolda vs. Skjerstadfjorden	58.37	Chaetopteridae	10.07
		Oweniidae	5.85
		Capitellidae	4.99
		Phascolionidae	4.02
		Amphinomidae	3.97
		Thyasiridae	3.92
		Nereididae	3.81
		Phoxocephalidae	3.54
		Arcticidae	3.37
		Semelidae	3.12
		Amphilepididae	2.93
		Trichobranchidae	2.82
Sørfolda vs. Skjerstadfjorden	54.71	Chaetopteridae	7.58
		Oweniidae	5.39
		Capitellidae	4.30
		Arcticidae	3.08
		Nereididae	3.87
		Amphinomidae	3.81
		Phascolionidae	3.79
		Phoxocephalidae	3.62
		Maldanidae	3.29
		Lumbrineridae	3.21
		Spionidae	3.04
		Paraonidae	2.96
		Trichobranchidae	2.57
Saltfjorden vs. Skjerstadfjorden	57.19	Phascolionidae	8.34
		Chaetopteridae	7.54

Table 1 *continued*

Fjords	Average diss.	Taxa	Diss. contrib. %
		Capitellidae	7.19
		Oweniidae	6.91
		Amphilepididae	4.70
		Thyasiridae	4.50
		Amphinomidae	4.08
		Nereididae	3.94
		Phoxocephalidae	2.51
		Paraonidae	2.35
Outer Saltfjorden vs. Skjerstadfjorden	51.70	Phascolionidae	10.59
		Chaetopteridae	8.24
		Oweniidae	8.19
		Arcticidae	4.31
		Nereididae	3.95
		Phoxocephalidae	3.84
		Thyasiridae	3.75
		Nuculanidae	3.33
		Capitellidae	3.20
		Amphinomidae	2.69

Table 2: Taxa contributions to cluster dissimilarities identified with SIMPROF. Cut-off at 50% contribution.

Station cluster	**Average diss.**	**Taxa**	**Diss. contrib. %**
F1-F2 vs. F3-F4, F6	28.24	Thyasiridae	5.74
		Chaetopteridae	5.24
		Oweniidae	4.75
		Cadofoveata	4.08
		Lumbrineridae	3.83
		Capitellidae	3.55
		Amphinomidae	3.38
		Paraonidae	3.05
		Spionidae	2.71
		Nemertea	2.59
		Syllidae	2.55
		Arcticidae	2.49
		Semelidae	2.40
		Trichobranchidae	2.34
		Maldanidae	2.19
F1-F2 vs. F7-F11	29.20	Semelidae	6.41
		Thyasiridae	6.20
		Golfingiidae	4.96
		Amphilepidae	4.79
		Chaetiopteridae	4.30
		Arcticidae	3.48
		Scaphopoda	3.01
		Ophiurida juv.	2.97
		Scalibregmatidae	2.71
		Oweniidae	2.61
		Ampharetidae	2.43
		Nemertea	2.43
		Nephtyidae	2.32
		Maldanidae	2.24

Table 2 *continued*

Fjords	**Average diss.**	**Taxa**	**Diss. contrib. %**
F3-F4, F6 vs. F7-F11	25.54	Maldanidae	4.74
		Oweniidae	4.47
		Golfingiidae	4.08
		Arcticidae	4.05
		Amphinomidae	4.05
		Semelidae	4.01
		Phascolionidae	3.67
		Trichobranchidae	3.61
		Capitellidae	3.29
		Amphilepididae	3.05
		Caudofoveata	3.00
		Glyceridae	2.58
		Lumbrineridae	2.43
		Terebellidae	2.33
		Ampharetidae	2.23
F1-F2 vs. F12	29.97	Chaetopteridae	12.12
		Semelidae	11.28
		Pyramidellidae	4.58
		Scaphopoda	4.37
		Eriopisidae	3.27
		Phascolionidae	3.16
		Maldanidae	3.08
		Diastylidae	3.07
		Cuspidariidae	2.84
		Lumbrineridae	2.67
F3-F4, F6 vs . F12	36.11	Semelidae	6.33
		Chaetopteridae	4.45
		Phascolionidae	4.19
		Maldanidae	4.17
		Oweniidae	3.55
		Paraonidae	3.44
		Thyasiridae	3.43
		Capitellidae	3.41
		Pyramidellidae	3.39
		Amphinomidae	3.22
		Trichibranchidae	2.99
		Caudofoveata	2.91
		Syllidae	2.87
		Eriopisidae	2.66
F7-F11 vs. F12	29.75	Chaetopteridae	7.55
		Golfingiidae	6.01
		Arcticidae	5.72
		Thyasiridae	4.71
		Pyramidellidae	4.64
		Semelidae	4.40
		Amphilepididae	4.23
		Ophiurida juv.	4.23
		Glyceridae	3.35
		Paraonidae	2.99
		Scalibregmatidae	2.97
F1-F2 vs. F13-F14	34.93	Spionidae	13.07
		Capitellidae	5.79

Table 2 *continued*

Fjords	**Average diss.**	**Taxa**	**Diss. contrib. %**
		Nemertea	5.75
		Chaetopteridae	3.59
		Synaptidae	3.40
		Thyasiridae	3.13
		Lumbrineridae	3.03
		Semelidae	2.50
		Paraonidae	2.40
		Caudofoveata	2.40
		Trichibranchidae	2.24
		Scaphopoda	2.22
		Glyceridae	2.10
F3-F4, F6 vs. F13-F14	27.39	Spionidae	12.91
		Nemertea	4.46
		Oweniidae	4.14
		Capitellidae	3.67
		Phascolionidae	3.39
		Onuphidae	2.73
		Glyceridae	2.69
		Nuculanidae	2.58
		Semelidae	2.51
		Amphinomidae	2.37
		Synaptidae	2.31
		Chaetopteridae	2.13
		Ampharetidae	2.09
		Maldanidae	2.02
		Pyramidellidae	1.99
F7-F11 vs. F13-F14	33.02	Spionidae	12.34
		Capitellidae	5.60
		Nemertea	4.41
		Golfingiidae	4.20
		Ampharetidae	3.15
		Semelidae	2.99
		Trichobranchidae	2.98
		Synaptidae	2.56
		Nuculanidae	2.51
		Cirratulidae	2.40
		Ophiurida juv.	2.19
		Amphinomidae	2.13
		Oweniidae	2.10
		Terebellidae	2.04
F12 vs. F13-F14	39.49	Spionidae	11.21
		Capitellidae	5.90
		Nemertea	5.62
		Semelidae	5.30
		Chaetopteridae	4.06
		Synaptidae	3.86
		Paraonidae	3.01
		Trichobranchidae	2.98
		Glyceridae	2.60
		Syllidae	2.46
		Terebellidae	2.32
		Cirratulidae	2.19

Table 2 *continued*

Fjords	**Average diss.**	**Taxa**	**Diss. contrib. %**
F1-F2 vs. S5, S8	30.15	Phascolionidae	8.24
		Chaetopteridae	5.75
		Caudofoveata	5.45
		Trichobranchidae	4.29
		Arcticidae	4.14
		Capitellidae	3.98
		Maldanidae	3.86
		Semelidae	3.60
		Amphilepididae	3.28
		Phoxocephalidae	2.28
		Spionidae	2.23
		Onuphidae	2.08
		Lumbrineridae	1.91
F3-F4, F6 vs. S5, S8	33.73	Capitellidae	6.23
		Thyasiridae	5.57
		Phascolionidae	4.83
		Oweniidae	4.51
		Lumbrineridae	4.43
		Amphilepididae	4.42
		Arcticidae	2.91
		Paraonidae	2.86
		Amphinomidae	2.80
		Onuphidae	2.67
		Nuculanidae	2.66
		Terebellidae	2.33
		Synaptidae	2.29
		Caudofoveata	2.17
F7-F11 vs. S5, S8	39.34	Phascolionidae	7.29
		Amphilepididae	6.14
		Arcticidae	5.65
		Thyasiridae	5.34
		Maldanidae	4.66
		Golfingiidae	4.42
		Trichobranchidae	3.91
		Capitellidae	3.64
		Caudofoveata	3.07
		Oweniidae	3.02
		Ophiurida juv.	2.91
F12 vs. S5, S8	38.95	Phascolionidae	9.60
		Maldanidae	5.76
		Semelidae	5.72
		Trichobranchidae	4.74
		Chaetopteridae	4.52
		Caudofoveata	4.04
		Amphilepididae	3.61
		Lumbrineridae	3.33
		Oweniidae	3.17
		Capitellidae	3.06
		Scaphopoda	2.92
F13-F14 vs. S5, S8	40.53	Spionidae	10.03
		Capitellidae	7.53
		Phascolionidae	6.26

Table 2 *continued*

Fjords	**Average diss.**	**Taxa**	**Diss. contrib. %**
		Nemertea	4.70
		Amphilepididae	3.69
		Lumbrineridae	3.55
		Synaptidae	3.48
		Thyasiridae	3.26
		Arcticidae	2.93
		Maldanidae	2.36
		Paraonidae	2.30
F1-F2 vs. S12	37.00	Phascolionidae	9.08
		Amphinomidae	7.60
		Capitellidae	7.15
		Semelidae	5.60
		Nuculanidae	5.39
		Amphilepididae	4.60
		Chaetopteridae	3.86
		Caudofoveata	3.78
		Maldanidae	3.37
F3-F4 vs. S12	33.20	Phascolionidae	7.41
		Nuculanidae	6.71
		Oweniidae	5.65
		Amphinomidae	4.91
		Capitellidae	4.31
		Thyasiridae	3.97
		Semelidae	3.73
		Paraonidae	3.26
		Amphilepididae	2.94
		Syllidae	2.73
		Golfingiidae	2.66
		Cuspidariidae	2.39
F7-F11 vs. S12	38.67	Phascolionidae	9.63
		Amphinomidae	7.52
		Nuculanidae	6.55
		Capitellidae	6.34
		Golfingiidae	5.34
		Maldanidae	4.86
		Oweniidae	4.14
		Thyasiridae	3.79
		Ophiurida juv.	2.79
F12 vs. S12	41.45	Phascolionidae	11.18
		Amphinomidae	7.82
		Capitellidae	7.41
		Nuculanidae	5.82
		Maldanidae	5.47
		Chaetopteridae	4.52
		Oweniidae	4.08
		Amphilepididae	3.87
F13-F14 vs. S12	38.53	Spionidae	10.89
		Phascolionidae	8.47
		Amphinomidae	5.28
		Nemertea	4.03
		Synaptidae	3.49
		Nuculanidae	3.44

Table 2 *continued*

Fjords	**Average diss.**	**Taxa**	**Diss. contrib. %**
		Ampharetidae	3.01
		Semelidae	2.97
		Paraonidae	2.72
		Maldanidae	2.71
		Glyceridae	2.35
		Syllidae	2.22
S5, S8 vs. S12	32.45	Capitellidae	11.82
		Amphinomidae	8.73
		Amphilepididae	8.25
		Arcticidae	4.81
		Nuculanidae	4.76
		Semelidae	3.27
		Phascolionidae	3.18
		Orbiniidae	3.01
		Lumbrineridae	2.43
F1-F3 vs. K0	66.56	Oweniidae	11.84
		Chaetopteridae	5.90
		Amphinomidae	5.07
		Maldanidae	4.96
		Nereididae	4.94
		Capitellidae	4.53
		Phoxocephalidae	4.46
		Paraonidae	3.67
		Thyasiridae	3.53
		Opheliidae	3.19
F3-F4, F6 vs. K0	54.40	Oweniidae	12.20
		Nereididae	5.37
		Phoxocephalidae	5.08
		Maldanidae	4.88
		Chaetopteridae	4.87
		Amphinomidae	4.58
		Capitellidae	3.91
		Phascolionidae	3.54
		Opheliidae	3.41
		Paraonidae	3.10
F7-F11 vs. K0	63.72	Oweniidae	11.72
		Maldanidae	5.88
		Amphinomidae	5.40
		Nereididae	5.17
		Chaetopteridae	4.87
		Phoxocephalidae	4.67
		Capitellidae	4.52
		Opheliidae	3.39
		Arcticidae	3.33
		Paraonidae	3.32
F12 vs. K0	68.34	Oweniidae	11.79
		Maldanidae	6.06
		Amphinomidae	5.42
		Nereididae	5.17
		Capitellidae	4.87
		Phoxocephalidae	4.66
		Paraonidae	4.15

Table 2 *continued*

Fjords	**Average diss.**	**Taxa**	**Diss. contrib. %**
		Opheliidae	3.60
		Thyasiridae	3.12
		Chaetopteridae	2.78
F13-F14 vs. K0	52.62	Oweniidae	13.24
		Maldanidae	5.54
		Nereididae	5.25
		Amphinomidae	5.20
		Phoxocephalidae	4.98
		Chaetopteridae	4.93
		Opheliidae	3.05
		Paraonidae	2.99
		Lumbrineridae	2.93
		Spionidae	2.92
S5, S8 vs. K0	63.15	Oweniidae	13.15
		Capitellidae	6.09
		Amphinomidae	5.36
		Nereididae	5.26
		Phascolionidae	5.20
		Chaetopteridae	4.47
		Maldanidae	4.07
		Thyasiridae	4.03
		Phoxocephalidae	4.02
S12 vs. K0	59.36	Oweniidae	14.00
		Phascolionidae	6.46
		Phoxocephalidae	4.86
		Nereididae	4.83
		Chaetopteridae	4.81
		Paraonidae	4.32
		Maldanidae	3.99
		Opheliidae	3.75
		Thyasiridae	3.55
F1-F2 vs. K5, K9	54.28	Chaetopteridae	12.63
		Capitellidae	5.28
		Phascolionidae	4.98
		Thyasiridae	4.16
		Arcticidae	4.06
		Semelidae	3.79
		Amphilepididae	3.63
		Amphinomidae	3.30
		Trichobranchidae	3.29
		Nereididae	3.12
		Phoxocephalidae	2.98
F3-F4, F6 vs. K5, K9	48.55	Chaetopteridae	9.26
		Phascolionidae	6.34
		Lumbrineridae	4.48
		Capitellidae	3.84
		Arcticidae	3.73
		Paraonidae	3.50
		Nereididae	3.13
		Nemertea	3.01
		Phoxocephalidae	2.97
		Onuphidae	2.49

Table 2 *continued*

Fjords	Average diss.	Taxa	Diss. contrib. %
		Regularia juv.	2.47
		Golfingiidae	2.45
		Pyramidellidae	2.39
F7-F11 vs. K5, K9	53.70	Chaetopteridae	10.23
		Arcticidae	6.10
		Capitellidae	4.93
		Golfingiidae	4.85
		Phascolionidae	4.30
		Trichobranchidae	3.83
		Amphinomidae	3.54
		Nereididae	3.17
		Lumbrineridae	3.13
		Phoxocephalidae	3.02
		Nemertea	2.76
		Paraonidae	2.62
F12 vs. K5, K9	50.55	Chaetopteridae	7.24
		Capitellidae	6.73
		Trichobranchidae	4.87
		Amphinomidae	4.28
		Lumbrineridae	4.23
		Phascolionidae	3.94
		Nereididae	3.77
		Amphilepididae	3.74
		Thyasiridae	3.67
		Phoxocephalidae	3.61
		Arcticidae	3.53
		Maldanidae	3.48
F13-F14 vs. K5, K9	55.15	Spionidae	9.42
		Chaetopteridae	7.72
		Nemertea	5.07
		Lumbrineridae	3.74
		Arcticidae	3.57
		Phascolionidae	3.12
		Capitellidae	2.98
		Paraonidae	2.91
		Synaptidae	2.75
		Nereididae	2.54
		Amphinomidae	2.48
		Phoxocephalidae	2.40
		Ampharetidae	2.38
S5, S8 vs. K5, K9	54.21	Phascolionidae	10.17
		Chaetopteridae	9.32
		Capitellidae	7.84
		Amphilepididae	5.72
		Thyasiridae	4.77
		Amphinomidae	3.33
		Oweniidae	3.28
		Nereididae	3.18
		Regularia juv.	2.52
S12 vs. K5, K9	47.86	Phascolionidae	13.14
		Chaetopteridae	10.36
		Arcticidae	5.23

Table 2 *continued*

Fjords	**Average diss.**	**Taxa**	**Diss. contrib. %**
		Oweniidae	4.59
		Nuculanidae	4.23
		Capitellidae	3.98
		Thyasiridae	3.88
		Nereididae	3.41
		Phoxocephalidae	3.22
K0 vs. K5, K9	52.09	Oweniidae	14.74
		Paraonidae	6.06
		Maldanidae	5.99
		Amphinomidae	4.71
		Opheliidae	4.70
		Nereididae	4.65
		Spionidae	4.23
		Phoxocephalidae	4.11
		Cirratulidae	3.22

Appendix C

Results from Bio-Env analysis

Table 1: Bio-Env analysis correlations between environmental variables and taxa assemblages in relation to taxa assemblages (unranked environmental variables).

No. variables	Variable combination	Correlation r_s
1	Salinity	0.678
1	Temperature	0.652
1	pH	0.165
1	Redox	0.067
1	Oxygen	0.009
1	Depth	-0.007
2	Salinity-pH	0.671
2	Temperature-pH	0.667
2	Salinity-Temperature	0.656
2	Salinity-Redox	0.647
2	Temperature-Redox	0.628
2	Salinity-Depth	0.612
2	Temperature-Oxygen	0.612
2	Temperature-Depth	0.609
2	Salinity-Oxygen	0.603
2	Redox-pH	0.235
2	pH-Depth	0.151
2	Oxygen-pH	0.147
2	Oxygen-Redox	0.124
2	Redox-Depth	0.091
2	Oxygen-Depth	-0.023
3	Salinity-Temperature-Oxygen	0.754
3	Salinity-Temperature-Redox	0.732
3	Salinity-Temperature-pH	0.719
3	Salinity-Temperature-Depth	0.706
3	Salinity-Redox-pH	0.685
3	Salinity-pH-Depth	0.663
3	Temperature-Redox-pH	0.663
3	Temperature-pH-Depth	0.649
3	Salinity-Redox-pH	0.629
3	Temperature-Oxygen-pH	0.617
3	Salinity-Redox-Depth	0.592
3	Temperature-Redox-Depth	0.574
3	Salinity-Oxygen-Depth	0.522
3	Temperature-Oxygen-Depth	0.520
3	Temperature-Oxygen-Redox	0.473
3	Salinity-Oxygen-Redox	0.472
3	Redox-pH-Depth	0.219
3	Oxygen-Redox-pH	0.193
3	Oxygen-pH-Depth	0.102
3	Oxygen-Redox-Depth	0.053
4	Salinity-Temperature-Oxygen-pH	0.798
4	Salinity-Temperature-Redox-pH	0.782
4	Salinity-Temperature-pH-Depth	0.758
4	Salinity-Temperature-Redox-Depth	0.739
4	Salinity-Temperature-Oxygen-Redox	0.721
4	Salinity-Temperature-Oxygen-Depth	0.718
4	Salinity-Redox-pH-Depth	0.656

Table 1 *continued*

No. variables	**Variable combination**	**Correlation r_s**
4	Temperature-Redox-pH-Depth	0.639
4	Salinity-Oxygen-pH-Depth	0.577
4	Temperature-Oxygen-pH-Depth	0.560
4	Salinity-Oxygen-pH-Depth	0.545
4	Temperature-Oxygen-Redox-pH	0.542
4	Salinity-Oxygen-Redox-Depth	0.461
4	Temperature-Oxygen-Redox-Depth	0.446
4	Oxygen-Redox-pH-Depth	0.181
5	Salinity-Temperature-Redox-pH-Depth	0.782
5	Salinity-Temperature-Oxygen-Redox-pH	0.775
5	Salinity-Temperature-Oxygen-pH-Depth	0.773
5	Salinity-Temperature-Oxygen-Redox-Depth	0.703
5	Salinity-Oxygen-Redox-pH-Depth	0.539
5	Temperature-Oxygen-Redox-pH-Depth	0.527
6	Salinity-Temperature-Oxygen-Redox-pH-Depth	0.762