UNIVERSITETET I NORDLAND

MASTER THESIS

Spatial patterns of benthic communities in Saltfjorden and Skjerstadfjorden

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Table of contents

Abstract

Benthic macrofauna is important components of marine ecosystem playing a key role in nutrient cycling, detrital decomposition and as food resource for higher trophic levels (Gray 2009). In this study the benthic communities of Saltfjorden – Skjerstadfjorden fjord system were investigated to reveal the spatial patterns of benthic community distribution in relation to differences in geophysical parameters and hydrography in the two fjords.

Samples were taken at 23 stations located from outer part of Saltfjorden towards the middle of Skjerstadfjorden in April, May and June 2013. Sixty nine taxa belonging to 7 phyla were identified, with Polychaete dominance. Taxa richness showed that maximum number of taxa near the fjord mouth area declining toward inner part of Saltfjorden. Skjerstadfjorden is the study area with second high value of taxa richness and had the highest total abundance. Geophysical parameters such as depth, sediment temperature, redox potential and pH were examined for every station; moreover salinity and bottom water temperature was measured at six stations. Depth and Redox potential had the highest differences between two fjords; all other parameters were differed not that substantially.

Lecithotrophic reproductive mode was common in Saltfjorden, whereas a planktotrophic mode was typical for Skjerstadfjorden, indicating a barrier effect on larval transport by the narrow and shallow trench of Saltstraumen. Dominant feeding modes also differed between Saltfjorden (detritus feeder dominance) and Skjerstadfjorden (deposit feeder dominance) indicating differences in food supply and level of organic enrichment. Multivariate analyses revealed significant difference in the community structure between Skjerstadfjorden and Saltfjorden deep basin and outer basin. Based on all conducted analyses and measurements it can be stated that Saltstraumen, Sundstraumen and Godøystraumen play a crucial role in forming benthic community structure in Skjerstadfjorden as a dispersal barrier.

1. Introduction

Norway is a country with the great number of fjords, semi-enclosed marine inlets far embedded in the land, strongly dependent by terrestrial processes (variable terrestrial runoff, atmospheric air forcing, layers of low salinity, differential flow fields and light attenuation due to suspended particles) (Pearson 1980; Krapp-Schickel 1993). Water movements in a fjord system are significantly different from offshore processes, due to water separation and stratification by a sill between the open sea and the fjord (Cokelet 2012).

Fjords with relative wide mouth have permanent and usually strong water exchange with the open sea. More dense coastal water passing above the sill intrudes in the fjord and descends to the sea bottom. Moreover, tidal pumping raises water level above the sill and thus increases inflow of water in fjord through. In this way, new coastal water replaces deep basin water in a fjord. Coastal water has a higher salinity and is denser than fjord's basin water and a water exchange is mainly based on water density differences between an open sea and fjord. Circulation between bottom and surface layer may decline with decreasing density of coastal water that may cause pycnocline formation on more shallow depth. Period of water stagnation can cause oxygen deficiency and even anoxia near the sea bottom (Stigebrandt 2001). Tidal water infusion induces the increase of water mixing into basin, providing better water oxygen saturation. This process is occurring by replacing less dense fjord basin water by more dense coastal water initiating permanent, prolonged water exchange between coastal area and fjord (Stigebrandt 2001).

Arctic fjords are characterized as relatively homogenous and temporally stable waterbodies in their environmental conditions. This can be explained by the fact that they have no receptivity to the short-term meteorological and oceanographical events due to their great depth (Syvitski 1987). Furthermore, most fjords have strong chemical and physical gradients, affecting benthic communities and diversity (Kuklinski 2013).

Study region of this Master Thesis is Saltfjorden – Skjerstadfjorden tidally energetic fjord system situated in Northern Norway connected with each other through narrow and shallow trench Saltstraumen. These two fjords have a different hydrography by reason of distinct connection with coastal area and consequently different period of water exchange (Eliassen 2001).

Spatial distribution of benthic organisms is dependent on several abiotic factors like topographical and hydrographical features, physicochemical sediment characteristics, and biological factors, such as amount of available food resources and bioturbation (Souza et. al.

2013). Numerous articles have described correlation between biophysical ecosystem features and benthic community parameters (Blanchard et. al. 2013; Souza 2013; Bandelj 2009; Galeron 2009). Parameters such as water depth, bottom-water temperature and sediment characteristics (e.g. grain size, percentage of organic components, etc.) have a strong influence on community structure (Harriott 1999; Bandelj 2009; Galeron et.al 2009; Blanchard et.al. 2013). Fjord topography plays a key role in water exchange and circulation providing oxygen and food. Benthic communities of deep fjords are often influenced by anoxia/hypoxia events, which may be permanent or seasonal depending on nutrient input and water circulation (Pearson and Rosenberg 1992; Rosenberg 1996). The low mobility of many benthic organisms and their inability to avoid adverse conditions makes benthos a suitable indicator for such disturbance events and general changes in the ecosystem (Gray, 1979). Moreover, interannual oceanographic variations may induce short-term differences in benthic community cause by ranging food availability, macrofaunal survival, or larval recruitment (Blanchard et.al. 2013).

The benthic fauna plays an important role in marine ecosystems; it participates in nutrient cycling, decomposition and forage base for higher level consumers in the food chain (Gerlach, 1970). Thus, the spatial distribution patterns of benthos are important for understanding the underlying structuring factors. Especially the functional composition of benthos communities can reveal relationships with the environmental drivers (e.g. Bremner et al. 2004). Because fjords are mainly influenced by the hydrographic regime within the fjord, larval dispersal and feeding types are relevant functional groups. Among marine invertebrates mainly two different modes of larval development are found: benthoplanktonic and direct (or holobenthic). In benthic ecosystems the most widespread pattern of development is benthoplanktonic (80 % of species). Such "complex life cycles" (Sinclair, 1988) occur in two different environments: water column (the plankton) and sea bottom (the benthos). Within the benthoplanktonic two types of larvae can be distinguished: 1) planktotrophic development, where the species larvae feed during the planktonic phase with usually small size, long planktonic period and lack of parental care; 2) lecithotrophic development, on the contrary, have only few, relatively large non-feeding larvae with short planktonic life stage. The main target of benthoplanktonic life style is maximum species distribution in space, but currents and water turbulence can be detrimental to passive larvae transport, because planktonic organism can drift away from suitable habitats. Therefore, planktotrophic species produce large amount of larvae to increase the chance of finding suitable habitat and extend their distribution on maximal areal (M. Bhaud, 1995). In contrast, direct pattern of development occurs within relatively small spatial areas and dispersal is limited. In addition, percentage of offspring’s survival of species with direct development is much higher than in benthoplanktonic ones (M. Bhaud, 1995).

Feeding types are very informative characteristic about benthic organisms. Feeding classification is distinguishes on several feeding types: suspension or filter feeders, obtained food by filtering particles from water column (sponges, crinoids, bivalve mollusks, many polychaetes). Suspension feeders are subdivided in passive feeders with specific feeding organ trapping organic particle from current and active feeders, which create water circulation around them to enhance the filtration of organic particles. Representatives of deposit feeders group are ingest sediment feeding on the organic matter and microbial organisms within the sediment. Some taxa of Arthropoda and Echinodermata are related to herbivores feeding group that consumes seaweeds and sea grasses. Carnivores or predators consume only other animals. This group includes asteroid starfish, many fishes and nemertea worms. Another group is scavengers feeding on the remains of dead animals and plants (Levinton 2013). In fact, it is very complex to attribute one organism to specific feeding group, since many benthic organisms represent a mixture of two or three feeding types (Levinton 2013; Macdonald et.al. 2010; Fauchald 1979; Cammen, 1980; Fauchald et.al. 1977).

In this study existence of different patterns of benthic community distribution in Saltfjorden and Skerstadfjorden is expected. Distinction in feeding and reproductive mode may be caused by specific hydrographic condition in each fjord. Saltstraumen as a potential bottleneck for dispersal of benthic larvae and the large and deep opening of Saltfjorden to the open Norwegian Sea is expected to enable the exchange of benthic organisms.

The main objective of this project is to compare the species distribution patterns, community structure and diversity of the soft bottom benthic fauna of Saltfjorden and Skerstadfjorden and to relate the patterns to the differences in the water exchange with the open ocean and other environmental factors. A functional analysis of the benthic communities in relation to dispersal/reproduction traits and feeding modes is used to reveal potential effects of the special hydrography in Saltstraumen on the functional composition of the benthos. This project is the first study of deep soft bottom benthos of Saltfjorden and Skjerstadfjorden.

2. Materials and Methods

2.1. Study area

The study area of this project is located in Northern Norway and comprises two fjord systems, Saltfjorden and Skjerstadfjorden, as well as the adjacent off-shore basin outside of Saltfjorden (Fig. 2). Saltfjorden is 20 km long and it is connected to the NE Atlantic by a broad opening of 6 km width with a relatively deep sill-depth of 200 m. The basins of the fjords are relatively deep with a maximum of 374 m and 544 m in Saltfjorden (without sea outer part) and Skerstadfjorden, respectively (own data). Both fjords are connected by the narrow and shallow sill in the narrow trench Saltstraumen, which is located in 15 km from the Saltfjorden sill. Topography of Saltfjorden – Skjerstadfjorden fjord system is represented by glacially carved basins (Eliassen et al. 2001).

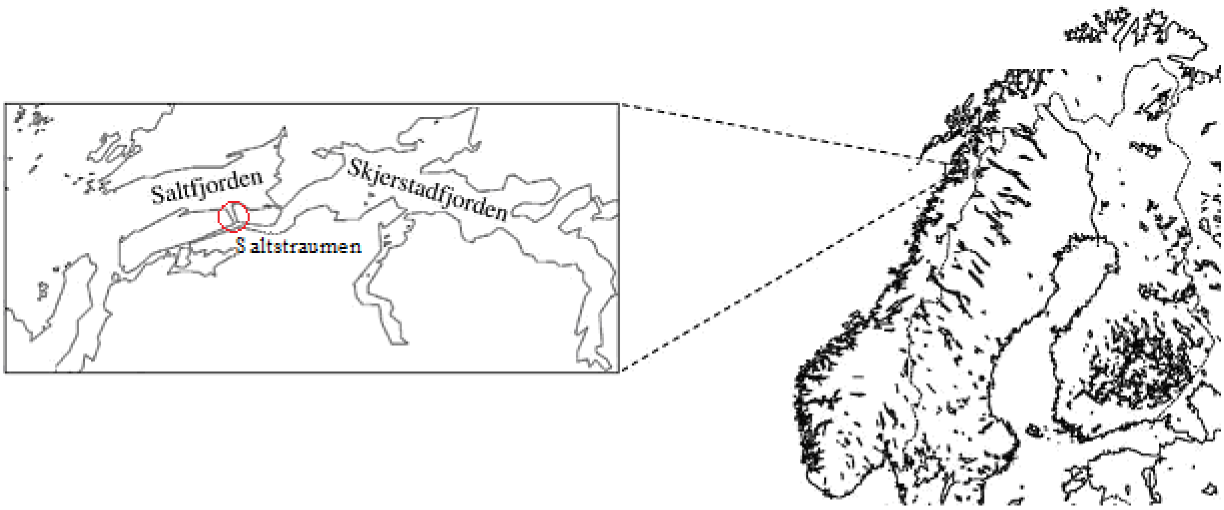

Figure 1. Saltfjorden and Skjerstadfjorden location (Eliassen et al. 2001).

The water exchange between Saltfjorden and the Norwegian Sea occurs relatively unhampered via the wide and deep sill region. In contrast, Skjerstadfjorden is connected to Saltfjorden by only two narrow channels, Godøystraumen and Saltstraumen, as well as to the open ocean by Sundstraumen (Eliassen et al. 2001). Saltstraumen is the most important pathway of water exchange between fjords and also known as a one of the energetically strongest tidal system in Norway (Table 1). Water masses from Saltfjorden flows into Skjerstadfjorden during high tide and back again during low tide twice per day. Transition of water from one fjord to another is accompanied by a development of strong currents and large number of gyres inside Saltstraumen. According to Eliassen et al. (2001) there are several permanent vortices in the fjord system. Two vortices in Saltfjorden are produced by powerful currents through Saltstraumen with strong influence of the topography on their direction. On the contrary, in

Skjerstadfjorden most of the vortices and counterclockwise circulation are dependent on stratification (Eliassen et al. 2001).

Pursuant to Skreslet's report (1996) Skjerstadfjorden has a relatively fast deepwater exchange, where deep water was lifted from one hundred (and deeper) meters for passing through the shallow trench of Saltstraumen. This process is affected by tidal current from Saltfjorden to Skjerstadfjorden. After entering to the Skjerstadfjorden, the denser water descends and thereby forming the bottom water of Skjerstadfjorden. Furthermore, less dense water from 0-20 meters depth moves from Skjerstadfjorden back to the Saltfjorden during low tide. It is important to note, that Skjerstadfjorden have relatively more permanent fresh water inflow from the lakes Valnesfjordvatnet, Nervatnet and the rivers Lakselva and Saltdalselva in comparison with Saltfjorden that has constant flux from Vatnvatnet only. Deepwater salinity is 35 and 33, 5 in Saltfjorden and Skjerstadfjorden, respectively (Eliassen et al. 2001).

Table 1. Characteristics of the trenches between Saltfjorden and Skjerstadfjorden (Eliassen et al. 2001; Van Der Meeren et al. 2013; Skreslet 2000).

Parameters	Saltstraumen	Sundstraumen	Godøystraumen
Length (km)	3	30	≈1
Width (m)	150	200-20	100
Depth (m)	26	11	1
Cross-section (m^2)	≈5000	≈500	≈120
Tidal current speed (km/h)	41	no info	no info
Drop in water level (m)	up to 1	no info	no info

The water masses in Skjerstadfjorden are year-round thermo-haline stratified, which becomes especially strong in the summer due to river discharge and sun heating. On the contrary, Saltfjorden has a less marked stratification. The absence of temperature and salinity deviation below 125 m depth was found in the both fjords (Skreslet 1996; Eliassen et al. 2001).

2.2. Sampling strategy

The surveys to fjords for the sampling purpose were conducted on the university's boat "Tantayen" in the end of April, in May and June 2013. Samples were taken in the deepest parts from 12 stations in Saltfjorden and 11 stations in Skjerstadfjorden.

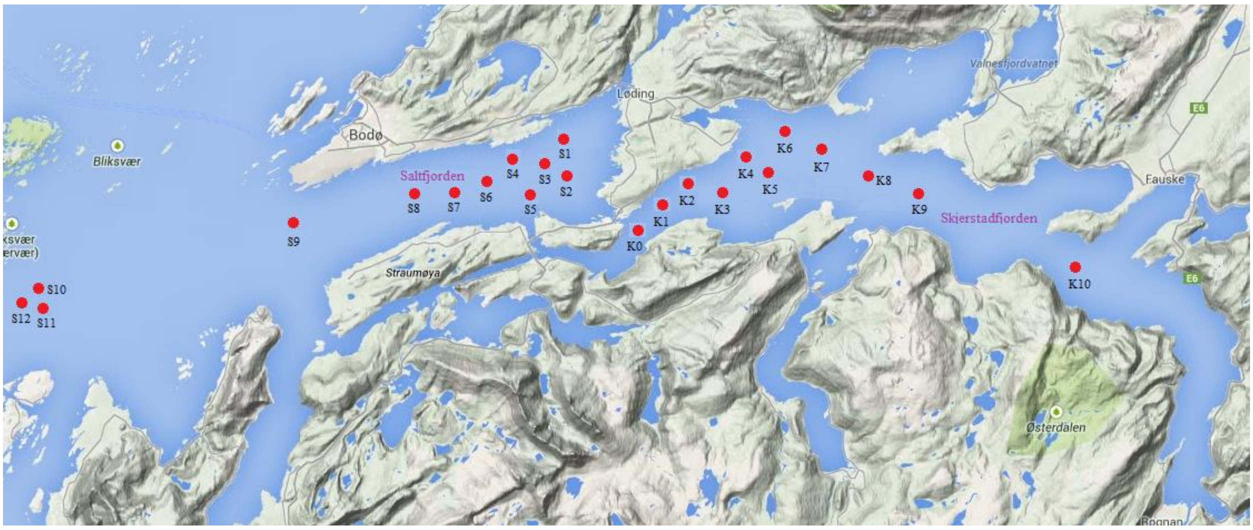

Figure 2. Location of sampling stations in Saltfjorden and Skjerstadfjorden.

In Saltfjorden the majority of stations were positioned along the full extension of the deep basins, only one station S9 was located directly on the sill. In Skjerstadfjorden the majority of stations were located in a western part of the fjord. Only one station K10 was situated in the middle of Skjerstadfjorden. In addition, in the open sea in 17 km from Saltfjorden's entrance, three more stations sampled to assess the role of the sill as a barrier of dispersal into Saltfjorden (Fig.2).

2.3. Sample processing

At each station two replicates were sampled with a Van Veen grab (0.1 m^2 surface area). Each sample was sieved through a 1 mm screen and was fixed in 4% formaldehyde buffered with Borax.

Analyses of samples took place in the Ecology Lab at UiN. Before taxonomical sorting, Rose Bengal was added to the sample for dyeing the organisms, thereby facilitating the sorting. 70% ethanol was used for sample fixation after taxonomical sorting. The benthic organisms were identified to family or higher taxonomical level if possible and all organisms were counted.

Family level was chosen for further statistical analyses in order to avoid inaccuracies in taxon determination. Individuals belonging to meiofauna, plankton and fish taxa were excluded from further analyses.

2.4. Sediment and geophysical characteristics

At each station physicochemical parameters such as pH, Eh and temperature were measured using a WTW pH - electrode Sen Tix 41 and a Schott Platinum Electrode BlueLine 31 RX, respectively. The electrodes were placed through the open hatch in the upper layer of sediment (2 cm) before emptying Van Veen grab. Depth and coordinates were obtained from GPS and depth sounder installed on board the “Tantayen” boat.

The sediment type was characterized by visual observation. After sieving sample from all sand and clay, the rest of sample’s content was subjected to visual analyses. For every replicate the sample volume and the remaining shells, gravel or algae after sieving were assessed visually to further characterize the substrate.

Furthermore, at several stations (S5, S8, S12, K0, K5 and K9) temperature, salinity and oxygen concentration were measured by a CTD (Saiv model SD204) at 2nd and 4th of the June 2014 (because of logistical reasons). Only the bottom layer data were used for this research.

2.5. Statistical analyses

2.5.1. Univariate analyses

Characteristic of benthic community like total abundance, abundance of particular taxon, total number of taxa and relative abundance with taxa number were adopted as univariate features for study area. The sample size was 0.1 m^2, therefore abundance and number of taxa was calculated for this area. Abundances of each station reported in this study thesis is given as a mean of the two replicates. Furthermore, total and mean taxa numbers as well as relative number of taxa and abundance were also calculated.

Feeding types were determined for every taxon based on Macdonald (2010) and Fauchald (1979) articles. Reproductive modes for each taxon were identified with BIOTIC (www.marlin.ac.uk/biotic) and Shanks (2002). All data were processed with the software MS Excel 2003.

Analysis of variance (ANOVA) was conducted to determine significant differences in total abundance and mean number of taxa between the main study areas (Skjerstadfjorden - 11 stations, Saltfjorden deep basin – 8 stations and outer part – 3 stations). The sill was excluded from analysis. Tukey's HSD (honestly significant difference) test was used to identify differences between the areas with a confidence level of 95%. Furthermore, the result were plotted in a box-plot displaying data scatter, including mean value, block with 90 % of values, lowest and highest values (Crawley 2007).

The univariate analyses were conducted using R version 2.15.1 (The R Foundation for Statistical Computing, 2012).

2.5.2. Multivariate analyses

All multivariate analyses were conducted with the PRIMER V6 software package performed on mean abundance values of each station. For a series of multivariate analyses (see below), square-root and fourth root transformation of abundance data were used to decrease the impact of the most numerous taxa in addition to non-transformed data. Bray-Curtis similarity matrix was constructed prior all analyses (Clarke & Warwick 2001).

Hierarchical clustering was conducted for the entire fjord system to assess the similarity between stations, displaying the grouping of samples into cluster (samples with highest percent of similarity combined in clusters). None and square root transformed data were used.

Non metric multi-dimensional scaling (MDS) represent the similarity of stations in a two-dimensional space, where distance between points indicate the relative level of dissimilarity. MDS analysis was conducted for three types of abundance data: none, square and fourth root transformed. Characteristic taxa responsible for the similarity and dissimilarity within and between the station clusters/groups were determined using SIMPER (Clarke & Warwick 2001).

ANOSIM analysis (analysis of similarities) was carried out to test for significant differences between the main fjord areas based on no transformed data (Clarke & Warwick 2001).

3. Results

3.1. Sediment characteristics

The difference between average depths of the two fjords was 129 m, with the sill as the shallowest station sampled in the fjord system with 226 meters depth. Saltfjorden deep basin was sampled in a depth range of 367 to 374 m. The outer part stations were considerably deeper than Saltfjorden basin with depth from 455 to 475 m. All stations sampled in Skjerstadfjorden had a depth of more than 500 m (except station K10 with 475 m; Table 2).

Table 2. Sediment characteristics of the study area showing depth, pH, temperature (t) and Redox potential (Eh) of the sediment.

Sampling Date	Station №	Depth (m)	pH	t (ºC)	Eh (mV)	Sample remains	Volume of remains (ml)
10.05.2013	S1	369	7.8	7.3	-95	shells	25
	S2	369	7.9	7.4	-132	shells	50
	S3	374	7.9	7.5	-137	shells	25
30.04.2013	S4	373	7.9	7.6	-121	shells	25
	S5	373	7.8	7.5	-52	shells	100
	S6	372	7.7	7.6	-131	shells+coarse sand	50
	S7	371	7.8	7.6	-77	shells	10
	S8	367	7.4	7.3	-107	shells	20
	S9	226	7.7	6.3	446	coarse sand	1250
13.06.2013	S10	475	7.9	8.2	-117	shells	30
	S11	462	7.9	9.6	-113	shells	30
	S12	455	7.8	10.3	-140	algae	50
11.06.2013	K0	544	7.9	6.1	10	shells+algae	350
	K1	514	8.0	6.5	-145	shells+algae	140
	K2	510	7.9	5.5	-118	shells+algae	20
21.05.2013	K3	516	7.7	6.7	9	shells+algae	50
	K4	512	7.9	8.3	-137	shells+algae	30
	K5	514	7.6	8.9	-110	shells+algae	50
08.05.2013	K6	510	7.7	6.0	-33	shells+algae	25
	K7	509	7.8	6.5	-80	shells+algae	20
	K8	511	7.7	5.5	75	shells+algae	30
	K9	503	7.7	5.1	143	shells+algae	20
	K10	475	7.6	5.8	45	algae	500

Ph values varied only slightly in both fjords with a minimum at station S8 of 7.4 and a maximum at station K1 of 8.0 (Table 2).

Sediment's temperature in both fjords was colder than in the outer basin and the lowest temperature was measured on the sill with 6.3°C. Temperature of the sediments changed only slightly in the rest of Saltfjorden. Average temperature in Skjerstadfjorden was about 1.5°C colder than in Saltfjorden (Table 2).

The sill station was characterized by the highest value of Eh with 446 mV. The Saltfjorden and the outer basin had negative Eh values ranged between -52 mV (station S5) and -140 mV (station S12). In Skjerstadfjorden most stations showed also negative or close to zero Eh values, while at the easternmost stations positive Eh values were measured (Table 2).

For all stations except of the sill the sediment mainly consisted of mud (grain size <63 µm). The most prevalent type of substrate after sieving was shell fragments. The sill was the most distinct from other station characterized by coarse sand. In addition algae fragments were found in the sediment of Skjerstadfjorden was almost constant, shells and algae. Algae were present in K10 station without any additional inclusion. In general, the content of other substrate types in the sample remains were almost negligible. Only two stations S9 and K10 had a relative large volume of sediment's inclusion (Table 2).

The bottom water showed considerable higher salinity, temperature and oxygen concentration in Saltfjorden compared with Skjerstadfjorden. Saltfjorden (include outer basin, S12) was characterized by constant salinity and temperature values in all stations (35.3 and 7ºC respectively). Oxygen concentration in Saltfjorden had a tendency to decrease toward the inner part of the fjord. Maximal oxygen concentration 94% was observed at the station S8; minimal value was found at station S5 (86.3%; Table 3).

Table 3. Bottom water salinity, temperature and oxygen saturation at the selected sampling stations.

Station №	Salinity (PSU)	t (ºC)	Oxygen concentration (%)
S5	35.3	7.0	86.3
S8	35.3	7.0	94.0
S12	35.3	7.0	92.7
K0	33.7	4.9	87.7
K5	33.7	4.9	84.9
K9	33.7	4.9	85.8

All three stations in Skjerstadfjorden had the same salinity and temperature values with 33.7‰ and 4.9ºC respectively. A maximal value of oxygen concentration was observed at K0 station contained 87.7%. A minimal oxygen concentration had K5 with 84.9%. The inner most station K9 had an oxygen concentration of 85.8% (Table 3).

3.2. General community composition

Overall, 5102 individuals were found in the 46 Van-Veen grab samples during this study in Saltfjorden and Skjerstadfjorden. The taxa belonged to 7 phyla comprising 69 families:

Annelida (28), Mollusca (14), Arthropoda (12), Echinodermata (6), Sipuncula (5), Cnidaria (3) and Nemertea (1). The list of taxa included in the analyses (without *Calanus* ssp., Ostracoda, planktonic larvae, fish eggs and fish *Myxine glutinosa*) is given in Table 4.

Table 4. List of taxa found in the study area.

Phylum	Class	Family
Cnidaria		
	Anthozoa	
		Cerianthidae
		Edwardsiidae
		Hormathiidae
	Hydrozoa	
Echinodermata		
	Holothuroidea	
		Synaptidae
	Echinoidea	
		Brissidae
	Ophiuroidea	
		Amphiuridae
		Ophiactidae
		Ophiuridae
	Asteroidea	
		Ctenodiscidae
Arthropoda		
	Malacostraca	
		Phoxocephalidae
		Oedicerotidae
		Melitidae
		Ampeliscidae
		Aoridae
		Lysianassidae
		Corophiidae
		Apseudidae
		Dyastylidae
		Leuconidae
		Nannastacidae
		Bodotriidae
Nemertea		
	Enopla	
Sipuncula		
	Sipunculidea	
		Golfingiidae
		Phascolionidae
		Aspidosiphonidae
		Phascolosomatidae
		Apseudidae
Annelida		
	Polychaeta	
		Ampharetidae
		Trichobranchidae

Table 4. Continued

Phylum	Class	Family
		Terebellidae
		Glyceridae
		Lumbrineridae
		Capitellidae
		Pholoidae
		Phyllodocidae
		Flabelligeridae
		Cirratulidae
		Onuphidae
		Spionidae
		Amphinomidae
		Nephtyidae
		Syllidae
		Maldanidae
		Orbiniidae
		Oweniidae
		Oenonidae
		Chaetopteridae
		Scalibregmatidae
		Nereididae
		Ophellidae
		Pectinariidae
		Sigalionidae
		Cossuridae
		Paraonidae
		Sabellidae
Mollusca		
	Caudofoveata	
		Chaetodermatidae
	Scaphopoda	
		Dentaliidae
	Gastropoda	
		Eulimidae
		Philinidae
		Naticidae
	Bivalvia	
		Thraciidae
		Semelidae
		Astartidae
		Yoldiidae
		Montacutidae
		Nuculanidae
		Pandoridae
		Tellinidae
		Montacutidae

Polychaetes were the most dominant group comprising 42% of the taxa and 62% of total abundance; the second largest group was mollusca with 20% of the taxa and 19% of total abundance. Echinodermata and arthropoda groups had 9 and 17% of taxa respectively, but only 2% of abundance. Cnidaria and sipuncula contributed both with 12% and 15% of the taxa and total abundance, respectively (Fig. 3).

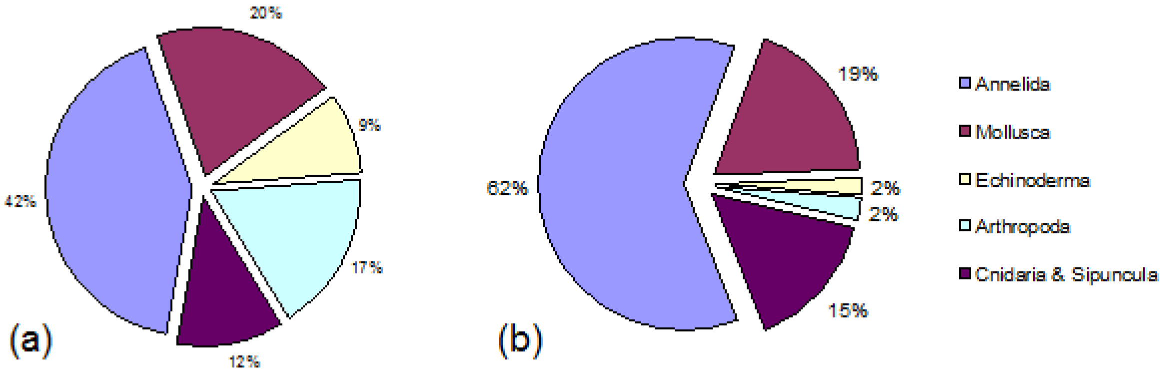

Figure 3. Percentage of a) taxa number and b) abundance (ind. $0.1m^{-2}$) of the different phyla in the entire study area.

3.2.1. Taxa numbers and total abundance

On the basis of bottom topography and geographical position the study area was subdivided in four areas: Skjerstadfjorden, Saltfjorden, the sill between open sea and Saltfjorden and the outer basin (Fig.2).

The highest total number of taxa was found at station S9 on the sill between Saltfjorden and the Atlantic with 39 taxa and a mean of 30 taxa (Fig. 4).

The Saltfjorden's deep basin area had the lowest taxa richness. Total number of taxa was varying from 8 to 17 taxa 0.2 m^{-2}; mean number of taxa was in the range from 6 to 13 taxa 0.1 m^{-2}. The outer basin was characterized by similar total taxa numbers of around 20 taxa 0.2 m^{-2}, whereas mean values were 15 taxa 0.1 m^{-2}. In Skjerstadfjorden two stations were clearly distinguished from all other stations in terms of taxa richness. The maximal taxa number was observed near Saltstraumen at K1 with 33 taxa 0.1 m^{-2}; also mean taxa richness was equal 23.5 taxa 0.1 m^{-2}. Number of taxa decreased toward to the inner part of Skjerstadfjorden, and generally wasn't exceeding 20 for total and 15 for average taxa (Fig.4).

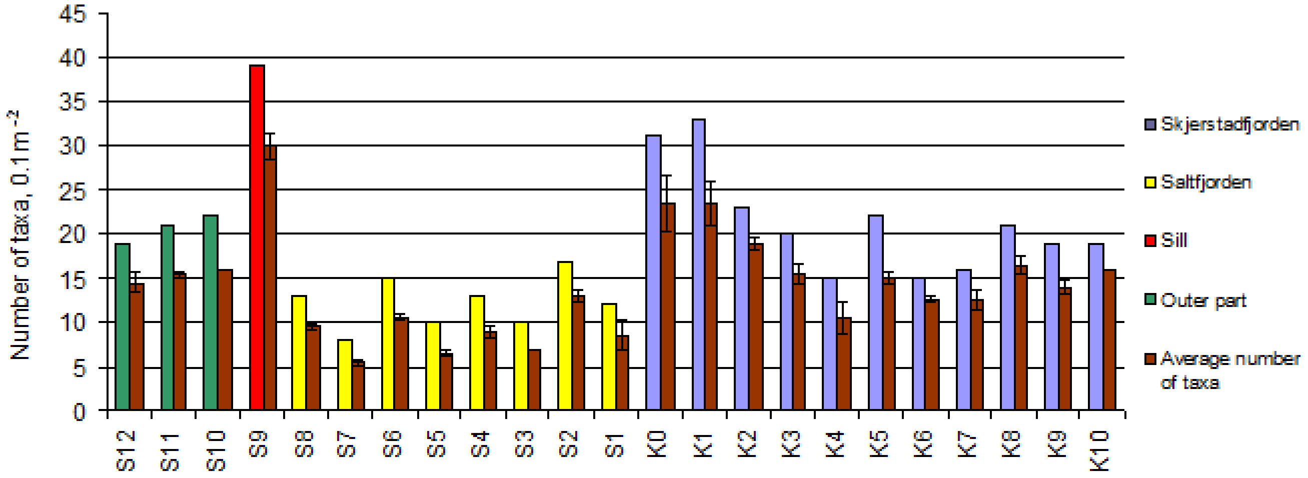

Figure 4. Total and mean number of taxa ($0.1m^{-2}$) in the study area (±SD).

The mean total abundance in Skjerstadfjorden varied from 62 to 253 ind. $0.1m^{-2}$. The lowest abundance was found in Saltfjorden deep basin with average value 36 ind. $0.1m^{-2}$. Here the mean abundance ranged from 16.5 ind. $0.1m^{-2}$ at station S7 to 66 ind. $0.1m^{-2}$ at station S2 (Fig.5).

The sill area had a relatively high mean total abundance of 178.5 ind. $0.1m^{-2}$ that was five times higher than in the deep basin of Saltfjorden (Fig.5).

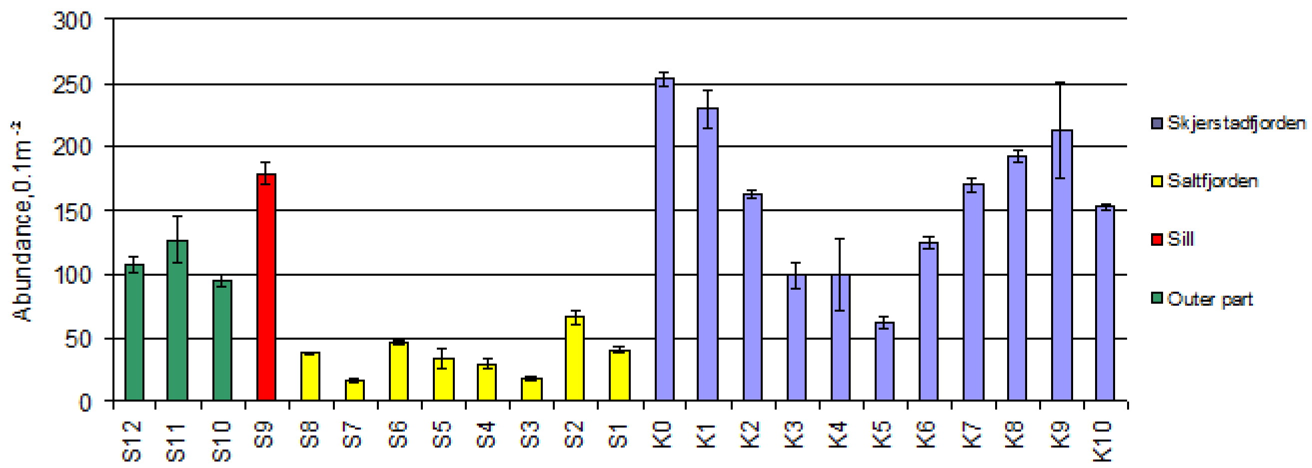

Figure 5. Mean total abundance (ind. $0.1m^{-2}$) for each station (±SD).

Mean abundance in outer basin was 111 ind. $0.1m^{-2}$; this abundance was approximately equal to mean abundance of entire fjord system. Mean abundance ranged from 94.5 to 127 ind. $0.1m^{-2}$. Despite the small number of samples this area was characterized by low variability in abundance.

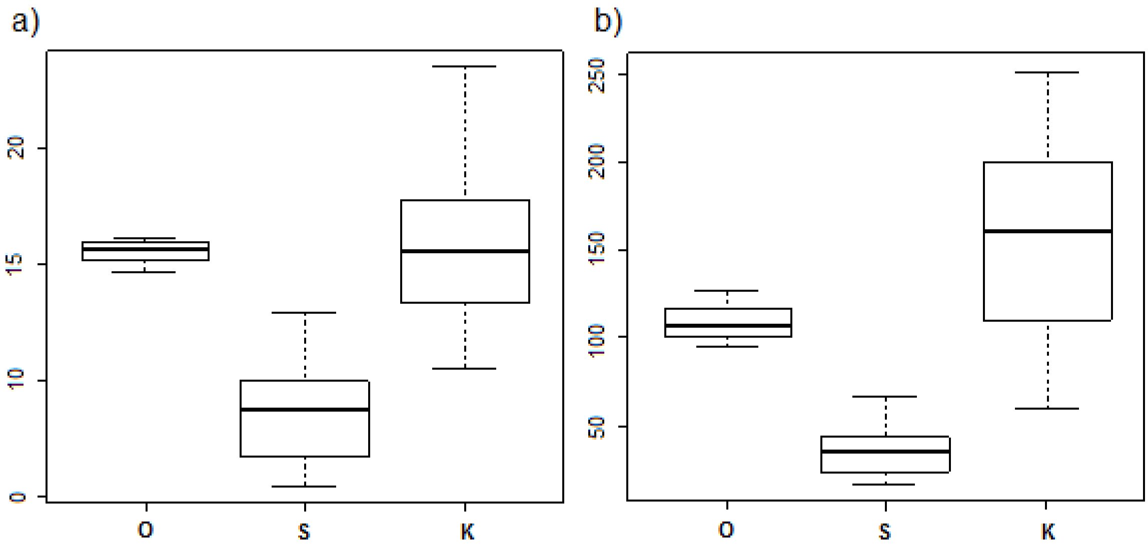

Figure 6. Difference in a) taxa richness and b) total abundance for each station between study sectors. Outer basin (**O**), Saltfjorden deep basin (**S**), Skjerstadfjorden (**K**).

The highest values of mean abundance and taxa numbers were indicated the for Skjerstadfjorden with high variability. Saltfjorden deep basin was characterized as area with minimal mean abundance and taxa number, whereas wider ranging was common for taxa richness. Outer basin took an intermediate position between other study areas with narrow data variability in the both parameters (Fig. 6).

The analysis of variance (ANOVA) applied on total abundance and taxa's richness revealed difference between study areas (Table 5).

Table 5. Significant ANOVA (F value 17.8; degrees of freedom 2; p-value 4.414e-05) for total abundance and taxon richness (statistically significant results are emboldened). Tukey's HSD test, confidence level is 95%.

Sectors	Abundance (p-value)	Taxon richness (p-value)
Skjerstadfjorden - Saltfjorden deep basin	**<0.0001**	**0.0004**
Skjerstadfjorden – outer basin	0.22	0.91
Saltfjorden deep basin - outer basin	0.062	**0.025**

By the Tukey test has been established that benthic community had significant differences between Skjerstadfjorden and deep basin of Saltfjorden. One more significant difference was observed in taxa richness between Saltfjorden deep basin and outer basin. Moreover, total abundance between these areas was very close to the confidence level and revealed p-value equal 0.062. Between Skjerstadfjorden and outer basin wasn't found significant differences in both parameters (Table 5).

3.2.2. Relative taxa numbers and abundance

The percentage of taxa per phylum was relatively constant throughout the entire fjord system. Majority of samples contained all five phyla: annelida, mollusca, echinoderma, arthropoda and cnidaria with sipuncula. Arthropoda were absent in the outer basin and half of Saltfjorden deep basin areas. Cnidaria and sipuncula were found at all stations except station K7 (Fig.7).

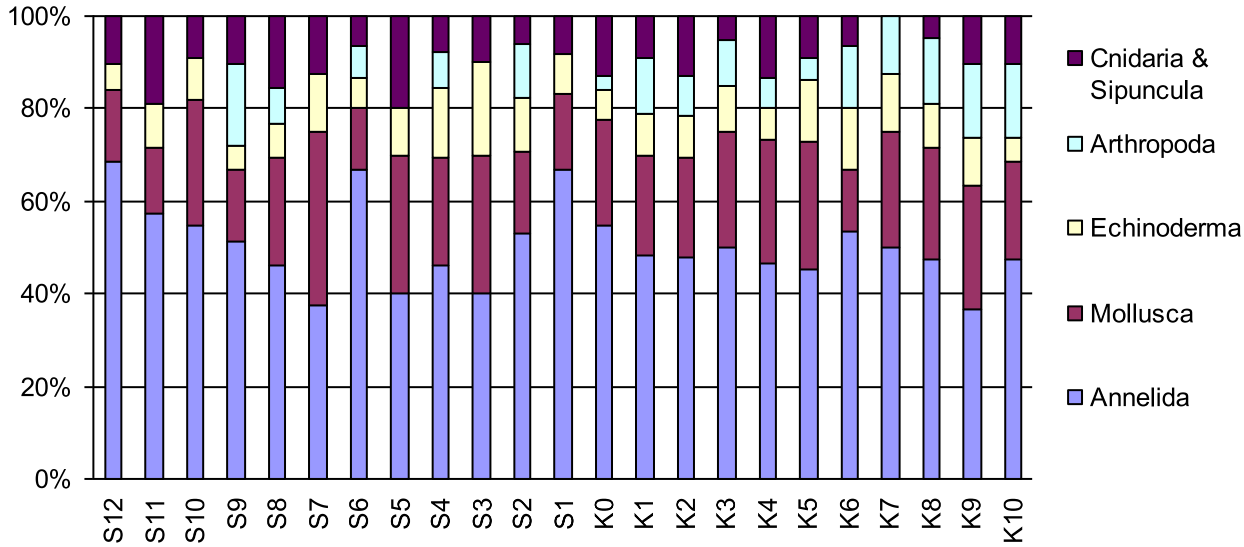

Figure 7. The percentage of number of taxa per phylum ($0.1m^{-2}$) at Saltfjorden and Skjerstadfjorden.

Annelida is the most numerous taxonomic group with relative taxa numbers ranged from 37 to 69%. Mollusca were the second largest group contributing 20 - 25% in Skjerstadfjorden and ranged from 13 to 40% in Saltfjorden. Cnidaria with Sipuncula was presented almost in every sample and reached maximum 20% in Saltfjorden deep basin and the outer basin. Other groups had relatively low taxa richness and distribution (Fig.7).

The most dominant phyla in Saltfjorden and Skjerstadfjorden in terms of relative abundance were cnidaria with sipuncula and annelida, respectively. The outer basin area was very homogeneous in relative abundance. Cnidaria with sipuncula was the dominant group in the outer basin area with about 50%, followed by annelida with 34-36%. Mollusca and echinoderma constituted a small fraction in the outer basin with average value equal 15 and 2% respectively (Fig.8).

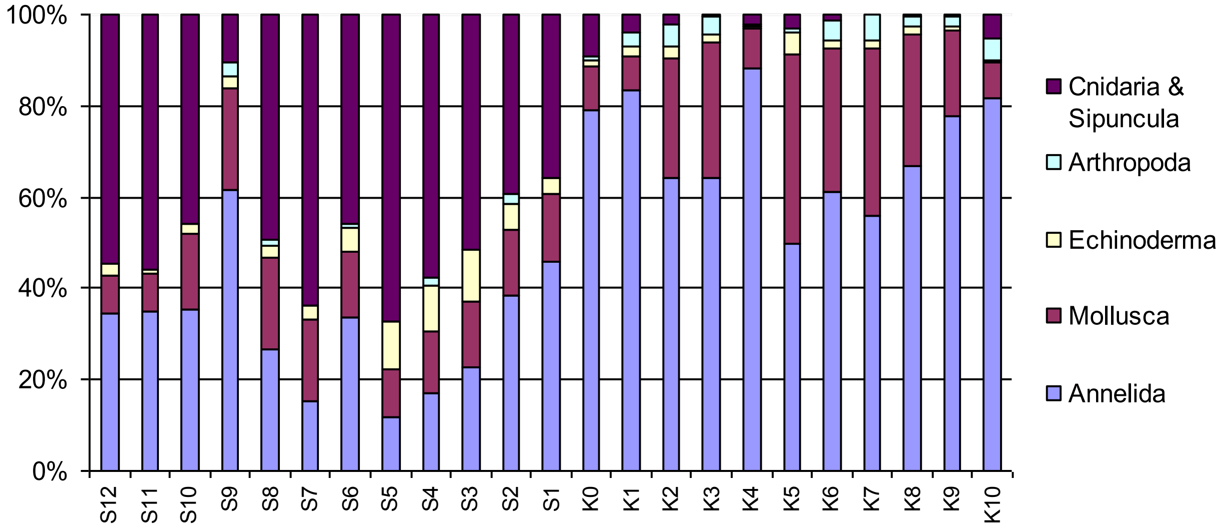

Figure 8. The relative abundance (%) of taxa ($0.1m^{-2}$) at Saltfjorden and Skjerstadfjorden.

The sill station was considerable dissimilar in abundance ratio with the rest of Saltfjorden: Annelida constituted 62%, whereas Cnidaria and Sipuncula made up only 10%. Saltfjorden deep basin and outer basin had approximately similar relative taxa abundance with Cnidaria and Sipuncula dominance (≥40 ind. $0.1m^{-2}$). Furthermore, relative Annelida abundance in deep basin had a tendency to increase toward the inner fjord part. Other phyla were presented not so substantial percentage, except Mollusca reached maximum 22% in the sill station. Annelida had apparent dominance in Skjerstadfjorden with varying from 50 to 88%. Distribution of annelida's abundance had a form of parabolas (except one extra station K4) with two maximums in the western and eastern part of Skjerstadfjorden. Mollusca were the second abundance group ranged from 8 to 43% with prevailing distribution in the middle of study area. Echinoderma, Arthropoda and Cnidaria with Sipuncula groups contributed maximum 12% altogether (Fig.8).

3.3. Relative abundance of feeding types

Saltfjorden and Skjerstadfjorden had different dominant feeding modes. Detritus feeders were the dominant group in Saltfjorden and constituted more than half the abundance, except the sill station. Predators were presented in every station of entire Saltfjorden and contributed 11%. For Skjerstadfjorden the deposit feeders were dominating with average proportion of 57%. Distribution of deposit feeder's abundance was characterized by gradual decline in the middle of Skjerstadfjorden and more sharp increase in the eastern part of study area (except station K4 with relatively high abundance). Minimal percentage (< 1% for entire Skjerstadfjorden) had scavenger and parasite modes which were found only at four stations (Fig.9).

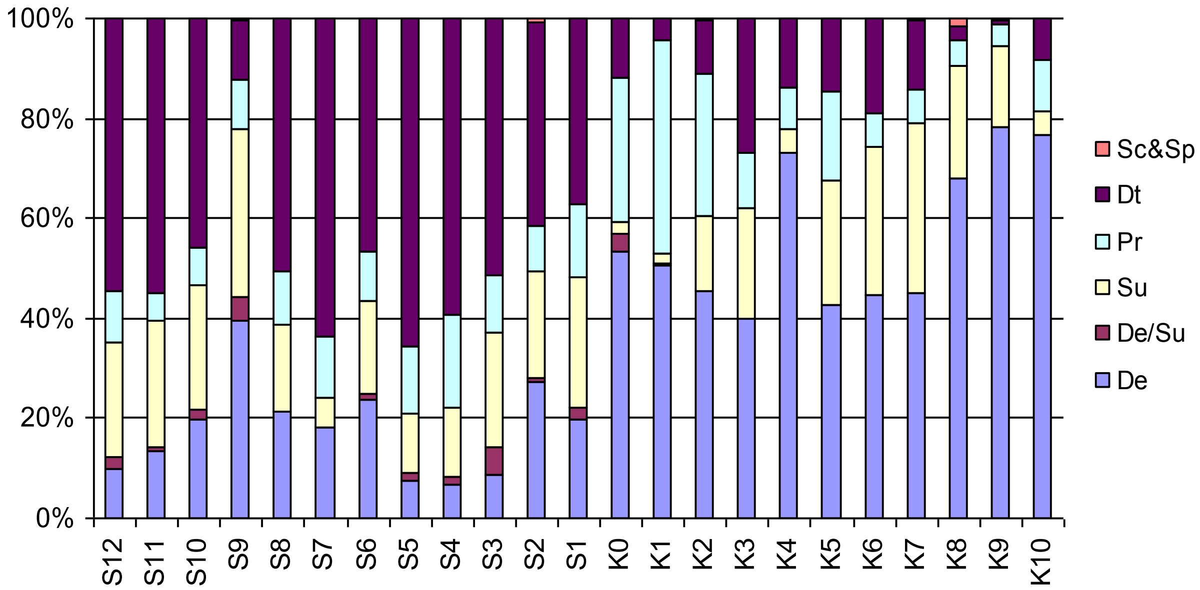

Figure 9. Feeding modes relative abundance at Saltfjorden and Skjerstadfjorden.

Deposit feeder (ingests sediment; **De**), detritus feeder (ingests particular matter only, without sediment; **Dt**), suspension/filter feeder (strains particles from the water, **Su**), predator (**Pr**), scavenger (carrion only; **Sc**), suctorial parasite (**Sp**) (Macdonald et.al. 2010).

Suspension feeders were found as the second numerous group in outer basin and contributed ≈ 25%. Deposit feeders range their abundance in outer basin area from 10 to 19%. The sill station was characterized by relatively small proportion of detritus feeders, and almost equal share between suspension and deposit feeder, 34 and 39% respectively (Fig.9).

Average percentage of detritus feeders for entire Saltfjorden deep basin was 51%. Moreover, abundance of detritivores deceased towards the inner part of the fjord. Deposit feeder's relative abundance ranged from 7 to 27%. Suspension feeding mode was typical for 5 to 27% of individuals in Saltfjorden deep basin stations (Fig.9).

In Skjerstadfjorden predator's feeding mode reach a distribution 30-45% only in the western part of study area (K0, K1 and K2) in the immediate proximity to Saltstraumen. In the rest of fjord predator's abundance was minor and varied from 5 to 17%. Suspension and detritus feeders had inverse dependence with predator feeding mode. Maximal distribution of these two groups was observed in the middle of study area. Abundance of suspension feeders ranged from 3 to 35% (Fig.9).

3.3.1. Relative abundance of reproductive modes

Saltfjorden and Skjerstadfjorden had different dominant reproductive modes. Taxa with Lecithotrophic development dominated in Saltfjorden, whereas taxa with planktotrophic development were dominant in Skjerstadfjorden (Fig.10).

For the both fjords a percentage of direct and unknown reproductive modes was insignificant and ranged from 1 to 10% maximum. The outer basin had similar proportion of reproductive modes within this area; abundance of taxa with lecithotrophy mode constituted ≈ 60%, whereas abundance of planktotrophic taxa was varied from 33 to 38% throughout study area. The sill station characterized by 50% contribution of individuals with planktotrophy mode at that abundance of lecithotrophic taxa constituted only 40%. The deep basin area was characterized by maximal distribution of lecithotrophic taxa abundance in whole Saltfjorden, where percentage was varying from 55 to 80%. Abundance of planktotrophic taxa ranged from 15 to 43%, moreover, increasing occurred from mouth toward the inner part of the fjord (Fig.10).

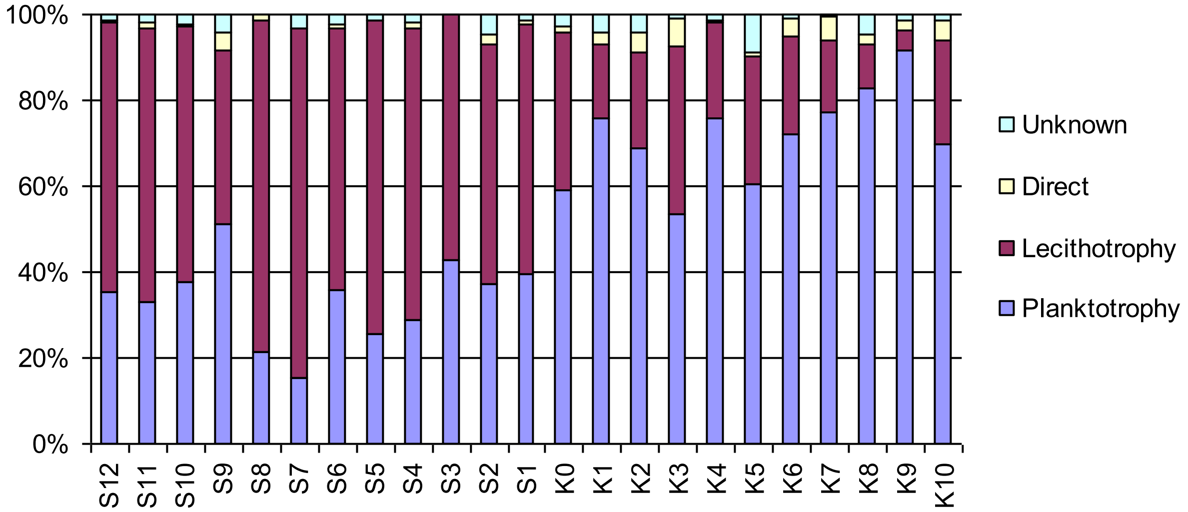

Figure 10. Reproductive mode's percentage of benthic fauna in Saltfjorden and Skjerstadfjorden.

Abundance of taxa with planktotrophic mode had sinewave form of distribution with constant increasing to the eastern part of Skjerstadfjorden. Minimal relative value of abundance planktotrophic taxa was found as 53%, whereas maximal value was constituted 92%. Abundance of taxa with lecithotrophic reproductive mode was varied from 5 to 39%, with maximal distribution in the western and middle parts of Skjerstadfjorden (Fig.10).

3.4. Multivariate analysis of community composition.

3.4.1. Hierarchical Cluster analysis

Using untransformed data for clustering analyses showed a clear separation between Saltfjorden and Skjerstadfjorden with a similarity of less than 15% (Fig. 11). Saltfjorden had three distinct study clusters, coinciding with geographical location. Outer basin was rather similar throughout the whole area with a similarity of more than 75%. The sill station has formed the same cluster with outer basin and constituted 40% similarity with Saltfjorden deep basin area. S4, S5, S6 and S8 were found as the most similar stations in deep basin area (Fig.11).

The majority of Skjerstadfjorden's samples were relatively similar to each other with more than 50%, but a cluster with stations K0 and K1 differed with only 40% similarity with the rest of study area (Fig.11).

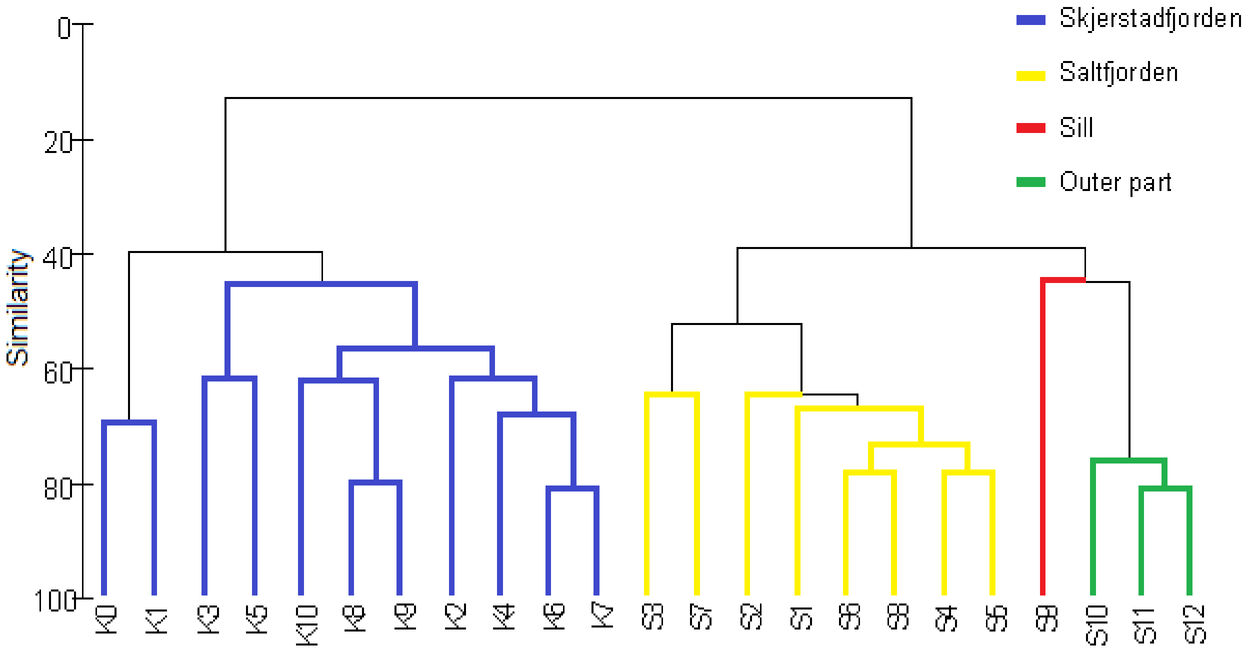

Figure 11. Hierarchical linkage between stations. Cluster analysis of untransformed abundance data.

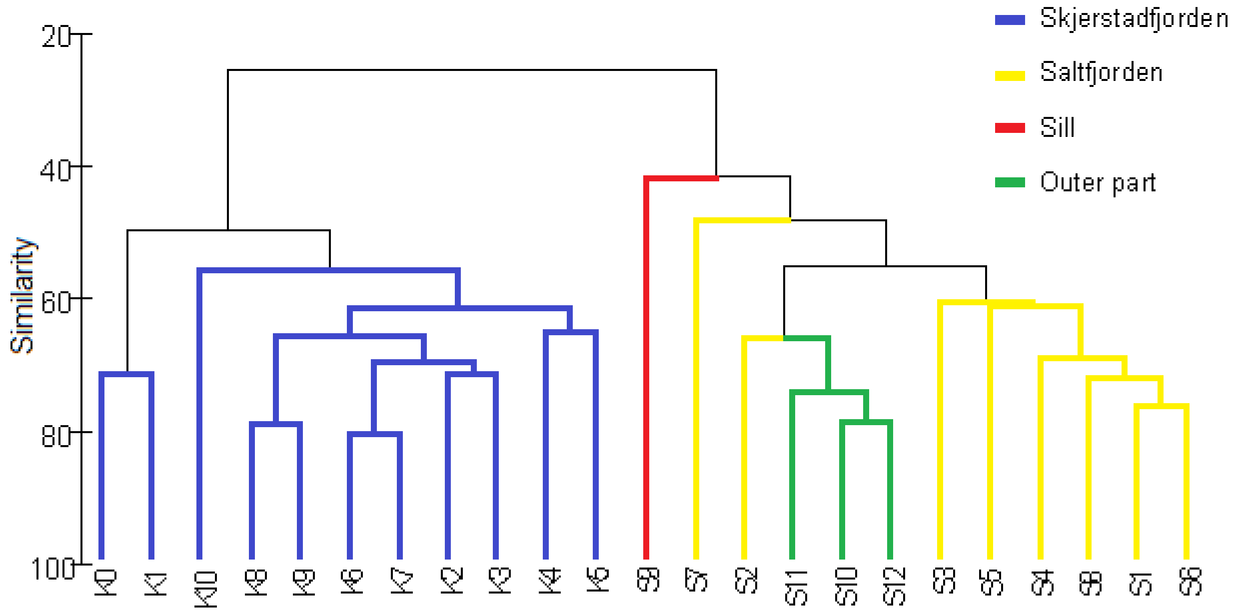

Figure 12. Hierarchical linkage between stations. Cluster analysis of square root transformed abundance data.

Square root transformation allowed reducing the impact of the most abundant taxa on the output. Cluster analyses with transformed data gave considerable different results in clustering. Similarity between Saltfjorden and Skjerstadfjorden increased to 25%. The outer basin area became more similar to the inner part of Saltfjorden (65% similarity). Two stations S2 and S7 in the deep basin were separated from the rest of the area with 55 and 48% of similarity. The sill station kept the same similarity proportion with entire Saltfjorden of 45% (Fig. 12).

Clustering after square root transformation was still corresponded to the geographical location of stations in Skjerstadfjorden. The cluster with K0 and K1 stations was separated from the main study area, but similarity increased to 50% with the rest of the fjord. The most eastern station K10 also showed relatively low similarity (55%) with majority of Skjerstadfjorden's stations (Fig. 12).

3.4.2. Non-metric Multidimensional scaling

Analysis of non-transformed data with multidimensional scaling also revealed a distinct separation between the benthic communities of Saltfjorden and Skjerstadfjorden, where intermediate point was S9 the sill station. The deep basin and outer basin were found as the most similar to each other, whereas the outer basin was more similar to the sill station. Furthermore, Saltfjorden and Skjerstadfjorden's benthic community was equidistant from the sill station on the MDS plot. The comparison of the entire Saltfjorden (include outer basin) with Skjerstadfjorden showed approximately the same variability within each fjord. Only stations K0 and K1, located near Saltstraumen trench, were separated from the main group of stations. The rest of the stations were arranged according to their geographical positions along the fjord (Fig.13).

The comparison of the MDS plots with untransformed and square root transformed data showed several minor changes in stations distribution. Study area's location also was remained together, only sill station became closer to K0 and K1 stations (area near Saltstraumen). Deep basin of Saltfjorden became more disjunctive with considerable separation between stations (Fig.14).

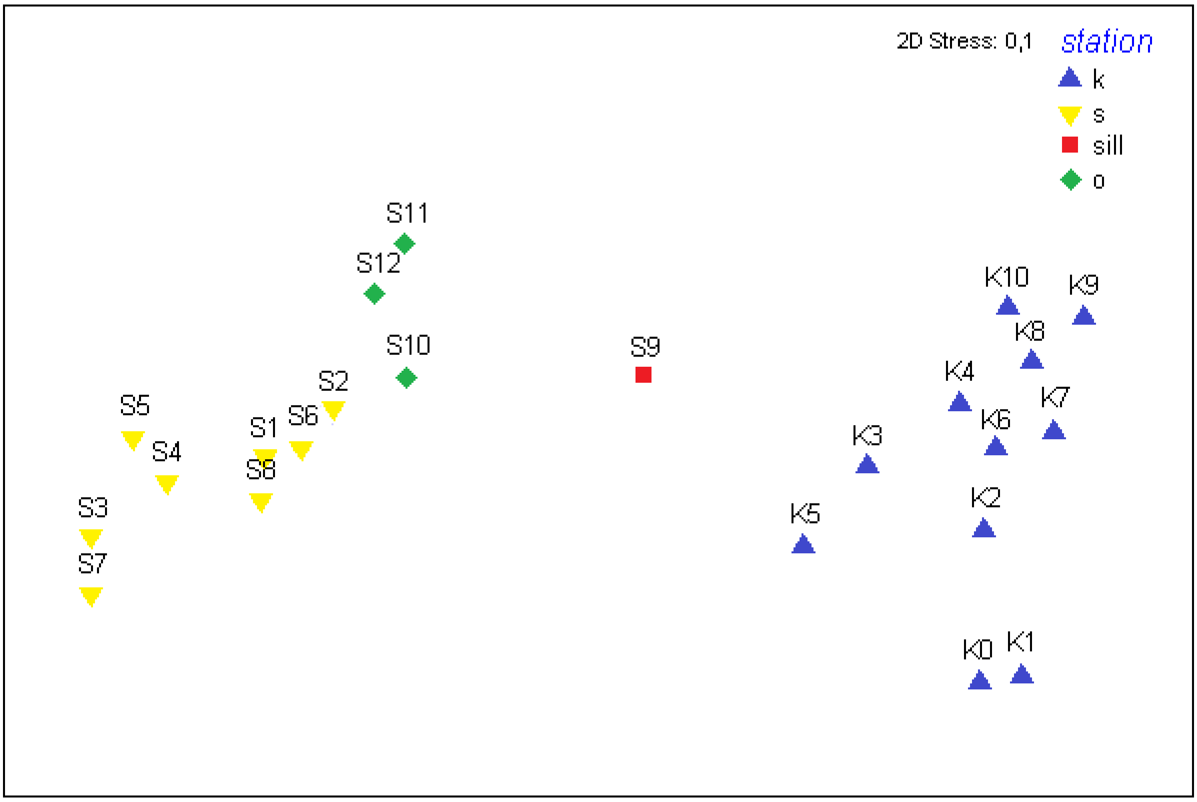

Figure 13. Multidimensional scaling plot of untransformed abundance data (Bray Curtis similarity).

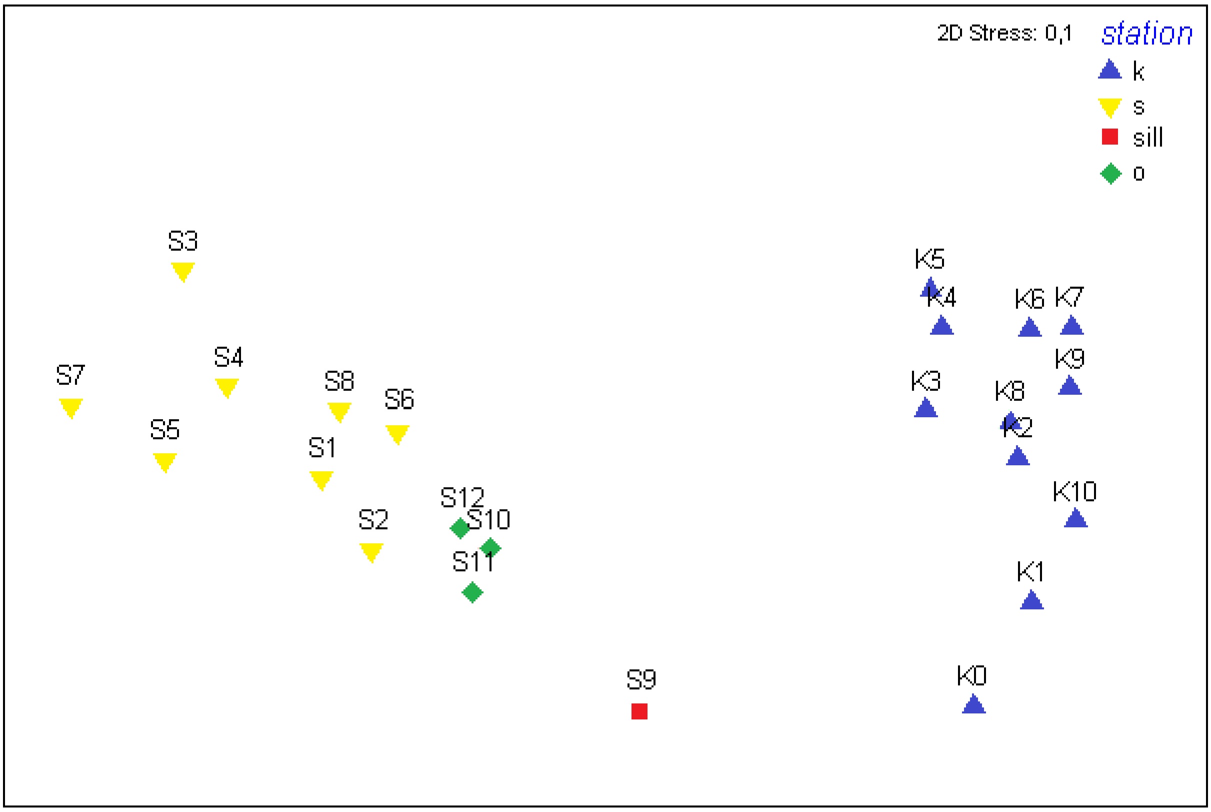

Figure 14. Multidimensional scaling plot of square root transformed abundance data (Bray Curtis similarity).

On the contrary, Skjerstadfjorden stations were closely grouped. Station K10 was displaced closer to the K0 and K1 stations. Furthermore, K0 and K1 became more distinct from each other but remained grouped together (Fig.11).

3.4.3. Benthic community similarity between study areas

A one-way analysis was performed for none transformed data for detecting significant differences between study areas.

Table 6. Results of ANOSIM test. Significance level of sample statistic is 5% (statistically significant results are emboldened).

Sectors	a-value	Significance level (%)
Skjerstadfjorden - Saltfjorden deep basin	**1**	0.1
Skjerstadfjorden - outer basin	**0.996**	0.3
Saltfjorden deep basin - outer basin	**0.737**	0.6

Analysis of similarities showed drastic differences in benthic community between Skjerstadfjorden and Saltfjorden deep basin (100%). In addition, comparing only these two areas gave the most statistically significant results. Skjerstadfjorden and outer basin also had significantly high differentiation in benthic community (99.6%). Saltfjorden deep basin and outer basin was found as the most similar areas to each other with 73.7% of dissimilarity (Table 6).

3.4.4. Characteristic families of the communities

Average dissimilarity between the study areas is shown in Table 7. The smallest dissimilarity was observed between Saltfjorden's areas. Outer basin had almost equal percent of dissimilarity with the sill and deep basin of Saltfjorden (55.1% and 57.5% respectively). Skjerstadfjorden and Saltfjorden deep basin had maximal percent of dissimilarity of 91%. Furthermore, Skjerstadfjorden had less dissimilar benthic community with sill area (67.7%). Compare Skjerstadfjorden with outer basin show intermediate value with 83.7% of dissimilarity (Table 7).

Table 7. Results of SIMPER test. Average dissimilarity (%) between study areas.

	Saltfjorden deep basin	Sill	Outer basin
Skjerstadfjorden	91	67.7	83.7
Saltfjorden deep basin	x	72	57.5
Sill	x	x	55.1

Skjerstadfjorden and Saltfjorden were characterized by common percent of similarity within each fjord 50.3 and 50.6% respectively. Annelida and bivalvia were found as the most dominant phyla characterizing the community in Skjerstadfjorden. Capitellidae dominated this community contributing with more than 50% to the similarity, followed by Thraciidae with 14.8%. Furthermore, Nereididae contributed almost 10% in Skjerstadfjorden. Other taxa had contribution less than 6% (Table 8).

Table 8. Results of SIMPER test (contribution to similarity of taxa, %) of the untransformed data of taxa abundance within Saltfjorden and Skjerstadfjorden.

Family	Average abundance (ind.)	Average similarity (%)	Contribution percentage
Skjerstadfjorden (average similarity 50.3)			
Capitellidae	64.4	25.9	51.5
Thraciidae	22.1	7.5	14.8
Nereididae	12.8	5.0	9.9
Amphinomidae	16.0	2.6	5.2
Chaetodermatidae	5.6	2.2	4.4
Phoxocephalidae	3.1	1.2	2.5
Maldanidae	4.9	1.2	2.4
Saltenfjorden (average similarity 50.6)			
Phascolionidae	26.8	29.1	57.5
Chaetopteridae	9.6	6.4	12.6
Chaetodermatidae	3.3	3.6	7.0
Thraciidae	5.5	3.2	6.3
Amphiuridae	2.0	2.5	5.0
Capitellidae	3.8	1.5	2.9

The community in Saltfjorden was mainly characterized by Phascolionidae with 57.5% (include outer basin). Chaetopteridae was found as second dominant group in Saltfjorden and constituted 12.6% of contribution. Others taxa contributed less or equal 7% (Table 8).

Outer basin had the highest average similarity of 77.6%, while Saltfjorden deep basin was more heterogeneous with 61.7% of average similarity. Phascolionidae was found as a characteristic taxon for both areas with more than 50% contribution followed by Chaetopteridae with 19.4% for the outer basin and 9.3% for the deep basin. The third dominant taxon for Saltfjorden deep basin was Chaetodermatidae with 7.9%, whereas Thraciidae was typical for the outer basin with contribution of 7.1% (Table 1 in appendix 2). Average dissimilarity between Saltfjorden and Skjerstadfjorden was 87.3%.

Table 9 shows the most common taxa contributing to the separation of the benthic communities of Saltfjorden and Skerstadfjorden. Capitellidae was found as the most dominant taxon for Skjerstadfjorden and simultaneously had relatively low abundance in Saltfjorden. On the contrary, Phascolionidae was the most abundant taxon in Saltfjorden, but practically absent in Skjerstadfjorden (average dissimilarity was 12.2%). Thraciidae was found in both fjords but obtained maximal distribution in Skjerstadfjorden with average abundance 22.1 ind. Furthermore, two polychaetes Nereididae and Amphinomidae had significant abundance only in Skjerstadfjorden constitute average dissimilarity more than 6%. Other taxa obtained contribution equal or less than 4.3% (Table 8). The contribution of taxa separating between the other areas was also calculated and can be found at Table 2 in appendix 2.

Table 9. Results of SIMPER test (contribution to dissimilarity of taxa %) of the untransformed data between Saltfjorden and Skjerstadfjorden.

	Skjerstadfjorden	Saltfjorden		
Family	Average abundance (ind.)	Average abundance (ind.)	Average dissimilarity (%)	Contribution percentage
Capitellidae	64.4	3.8	27.6	31.7
Phascolionidae	0.1	26.8	12.2	14.0
Thraciidae	22.1	5.5	9.6	11.0
Nereididae	12.8	0.0	6.6	7.6
Amphinomidae	16.0	0.8	6.1	7.0
Chaetopteridae	0.7	9.6	3.8	4.3
Oweniidae	7.0	0.0	2.5	2.9
Maldanidae	4.9	3.2	2.2	2.5
Chaetodermatidae	5.6	3.3	1.7	1.9
Phoxocephalidae	3.1	0.0	1.4	1.6
Nuculanidae	2.1	0.1	1.0	1.2
Edwardsiidae	2.6	0.0	1.0	1.1
Amphiuridae	0.0	2.0	1.0	1.1
Nemertea	2.1	1.6	0.9	1.0
Ampharetidae	0.8	2.0	0.8	0.9
Cirratulidae	2.1	0.3	0.8	0.9

Saltfjorden contains 21 unique taxa, whereas Skjerstadfjorden has 16 families specific only for this fjord. Taxa’s number of exclusive Polychaete, Mollusca, Arthropoda and Echinodermata was approximately the same. Taxa difference between fjords consist of Sipunculidae and Hydrozoa presence in Saltfjorden and total absence in Skjerstadfjorden and the opposite situation with Anthozoa and Sinaptine (Table 10).

Table 10. The list of taxa found exclusively in Saltfjorden (including the outer basin) and Skjerstadfjorden; the frequency of occurrence is given as percentage of stations for each fjord.

Family	Saltfjorden (%)	Skjerstadfjorden (%)
Amphiuridae	100	0
Nephtyidae	83.3	0
Lumbrineridae	58.3	0
Lysianassidae	16.7	0
Aspidosiphonidae	16.7	0
Onuphidae	16.7	0
Philinidae	16.7	0
Hydrozoa	8.3	0
Ophiuridae	8.3	0
Ampeliscidae	8.3	0
Bodotriidae	8.3	0
Aoridae	8.3	0
Corophiidae	8.3	0
Phascolosomatidae	8.3	0
Apseudidae	8.3	0
Paraonidae	8.3	0
Glyceridae	8.3	0
Pectinariidae	8.3	0
Montacutidae	8.3	0
Tellinidae	8.3	0
Pandoridae	8.3	0
Nereididae	0	81.8
Oweniidae	0	72.7
Dentaliidae	0	72.7
Leuconidae	0	63.6
Eulimidae	0	36.4
Cerianthidae	0	27.3
Synaptine	0	27.3
Astartidae	0	18.2
Naticidae	0	18.2
Hormathiidae	0	9.1
Ophiactidae	0	9.1
Nannastacidae	0	9.1
Oedicerotidae	0	9.1
Syllidae	0	9.1
Cossuridae	0	9.1
Oenonidae	0	9.1

Distribution of the most abundant taxa (Capitellidae, Phascolionidae, Thraciidae and Nereididae) was presented as four bubble plots, where circle diameter was corresponded to the taxa abundance (Fig. 1,2,3,4 in appendix 3).

4. Discussion

In this study the spatial patterns of taxa distribution, community composition, diversity, and composition of selected functional traits of the soft bottom benthic fauna in Saltfjorden and Skjerstadfjorden were investigated and related to the differences in the water exchange. Geophysical parameters have a strong direct influence on benthic taxa composition and abundance. Bottom current and sediments type determine feeding mode and motility of benthic organisms (Gray et.al. 2009; Fauchald 1979; Macdonald et.al. 2010). Furthermore, environmental processes play a significant role for primary production as a food base for higher trophic levels (Vance 1996).

The result revealed some differences in the physicochemical characteristics (e.g. salinity, temperature and Redox potential) between Saltfjorden and Skjerstadfjorden, with lower bottom water temperature and salinity as well as a slightly higher redox potential of the sediment in Skerstadfjorden. Significant differences between both fjords were found for total abundance, diversity and taxa composition of the benthos communities, with higher total abundance and diversity found in Skerstadfjorden. The multivariate analyses further revealed a subdivision into three distinct benthic communities in Saltfjorden: the outer basin, the sill and the deep basin of Saltfjorden. The only area that showed high difference from the rest of the Skerstadfjorden was the area near Saltstraumen (K0 and K1 stations).

Predominance of one or another mode of feeding depends on several conditions, e.g. type of substrate (clay, sand or rock), depth, type of water circulation, amount of suspended particles in water column (Levinton 2013; Fauchald 1979). The results indicate a difference in the composition of feeding modes between both fjords what can be attributed to difference in requirements of particular taxa to environmental conditions (e.g. water flow velocity, amount of suspended particles, level of organic enrichment) (Levinton 2013). The dominant feeding mode in Saltfjorden was detritus feeding (mainly Phascolionidae) and in Skjerstadfjorden deposit feeding (mainly Capitellidae). As mentioned above, Skjerstadfjorden is connected to Saltfjorden and the open sea through narrow and relatively shallow trenches only, possibly acting as a barrier of larval dispersal. Taxa with planktotrophic larvae were found to dominate in Skjerstadfjorden, in contrast to taxa with lecithotrophic larvae in Saltfjorden, indicating a barrier effect benefiting taxa with small, feeding larvae.

4.1. Environmental parameters

Various benthic organisms require specific environmental conditions, the content of dissolved oxygen in the water, type of substrate, temperature, salinity and etc. can determine habitat suitability for a species (Gray et.al. 2009). The sediment characteristics can have a strong influence on diversity and spatial distribution of benthic communities. The grain size of soft-sediment is depended on the hydrodynamic environment (Levinton 2013). The main component of all samples were related to the soft sediments with grain size <63 µm (Baeyens et.al. 1991). Other remains had a relatively low volume. Presence of large volume of muddy sediments in a sampling grab identify absent of strong bottom current (Li et.al. 2012). Thus, the sediment composition may not explain the differences in the community structure, taxa distribution and diversity. Only the sill between Saltfjorden and the open ocean was characterized by coarse sand and also showed a clearly distinct benthic community.

Consequently, value of physicochemical sediment indicator as Ph, Redox potential, salinity and temperature may have a direct connection with macrofaunal spatial differences. The Eh value gives an indication about the concentration of dissolved oxygen in the pore water of the sediment, with negative values indicating anoxic conditions. Thereby, Saltfjorden is more susceptible to anoxia development that Skjerstadfjorden. Prerequisites for hypoxia/anoxia development (according to the values of Redox potential) exist only in the eastern part of the Skjerstadfjorden. Moreover, Redox condition may indicate organic contamination and biological degradation (Vance 1996). In pursuance of a list with type of degradation according to Eh value, Saltfjorden suffer sulfate degradation except sill station with aerobic degradation. In Skjerstadfjorden positive values of redox potential where found in the eastern parts of the fjord indicating aerobic conditions. Thus differences in oxygen concentration might have caused the differences in benthic communities between the fjords.

Ph value is almost constant throughout the entire fjord system indicating the absence of influence on spatial structuring of macrofaunal communities. Temperature of deep water is relatively stable parameter independent from season (Saraswata et.al. 2011; Dethier 2005). Trend of sediment’s temperature is slightly decreasing from western to eastern parts of the fjord system. Furthermore, temperature doesn’t show legible relation with benthic structure and diversity, but maximal annelida’s distribution was found in areas with minimal temperature.

Depth is important parameter that is related to temperature, light transmission, oxygen concentration and etc. (Seitz et.al. 2009; Ansari et.al. 2012: Dauer 2008). Skjerstadfjorden and outer basin have the maximal depth compare with whole study area. After analysis depth influence on benthic community was testify that maximal taxa and abundance are correspond to minimal and maximal depth. Furthermore, depth has a great impact on food degradation, because suspended particles spend awhile in water column before subsidence on the bottom. Thereby, Skjerstadfjorden has a higher organic degradation because of the greater depth compared with Saltfjorden, what accordingly may affect differences in taxa composition between fjords. Reasonable to assume that colder and less oxygenated bottom layer in Skjerstadfjorden is connected with remoteness from open sea and relatively large depth (Eliassen 2001). Deep water is always more saline and denser than surface layer (Mann 2005). Halocline in Saltfjorden and Skjerstadfjorden was found at 125 meters depth. As was mentioned above, Skjerstadfjorden bottom water produced Saltfjorden water from depth 100 meters and deeper (Eliassen 2001). CTD samples of Saltfjorden water column identify salinity at 100 meters depth equal 34.4‰. In addition, Skjerstadfjorden have relatively more fresh water inflow than Saltfjorden that contributes water desalination. All these factors may explain greater salinity and consequently density reduction in Skjerstadfjorden compare with Saltfjorden.

4.2 Taxa richness and abundance

Differences in taxa composition and abundance were clearly detected between Saltfjorden and Skjerstadfjorden. Saltfjorden contained 52 taxa and Skjerstadfjorden 47 taxa of benthic macrofauna, while only 46 % of the taxa occurred in both fjords underpinning the great difference in taxa composition. Saltfjorden deep basin has the smallest differences in taxa richness between two replicates per one station that identify high homogeneity of this study area. Significant differences in taxa numbers and abundance were found between the two fjords and the outer basin. The sill station was the taxa richest area by reason of highest value of Redox potential, oxygen concentration and suitable location for new taxa introduction. Skjerstadfjorden also showed relatively high taxa richness, with maximum number of taxa in the vicinity of the trenches connecting the two fjords, Saltstraumen, Godøystraumen and Sundstraumen. This location seems to be influenced by the in- and out-streaming water providing highest oxygen concentration (87.7% at K0 station, maximal value in Skjerstadfjorden), suspended organic particles input and larvae. In contrast, Saltfjorden deep basin is characterized by the lowest taxa richness and abundance found in this study. Trend of taxa richness and diversity distribution along a fjord is specific for particular fjord. Benthic community distribution depends on several features unique for particular area, as geographic location, salinity (presence or absence of fresh water inflows), sediment characteristics, opportunity for larvae's entrance and etc. Several studies testify maximum of taxa richness and diversity in outer part and gradual regression toward inner fjord part (Renaud 2007; Włodarska-Kowalczuk 2012). An opposite benthic community distribution was found in northern Svalbard fjord (Norway) (Carroll 2012). Furthermore, taxa richness and diversity in Trondheimsfjord (Norway), Abyfjord and Stigfjord (Sweden) haven't particular trend throughout whole fjord and changed independently from location within fjord (Kuklinski 2013; Rosenberg 2005).

Saltfjorden - Skjerstadfjorden is a fjord system with relatively equal phyla ration per station. Annelida dominance in the entire fjord system is typical for many soft bottom communities and northern fjords (Renaud et.al. 2007; Fetzer 2004). In Skjerstadfjorden annelida is the most abundant phylum with dominance of the opportunistic Capitellidae which is relatively tolerant to organic enrichment and characteristic for muddy sediments (Pearson 1980; Holte 2005). In Saltfjorden the most abundant taxon is the sipunculida Phascolionidae. That's indicate complication Phascolionidae's entering in Skjerstadfjorden and possible lack of food recourses for detritus feeders (*Onchnesoma steenstrupii steenstrupii*) in Skjerstadfjorden.

Based on all above mentioned it is possible to clarify that only physiochemical measurements cannot assess whole differences between two fjords, whereas faunal analysis is more informative and precise in environmental factors determination (Weston 1990, Pearson 1992).

4.3. Feeding and reproductive modes in the study area

Several studies show that type of substrate, bottom current energy and abundance of prey have a fundamental influence on the composition of feeding modes (Fauchald 1979; Levinton 2013). Polychaete as the most 'taxa rich' group in Saltfjorden – Skjerstadfjorden is mainly represented by deposit feeders. Deposit feeders reach high abundance in fine-grained sediments, with increasing content of organic matter and microorganisms. Furthermore, deposit feeders are subdivided on two groups by their expose on the ground: surface and burrow-dwelling feeders (Gallagher 2008). Deposit feeder abundance in Skjerstadfjorden was dominated by capitellidae. Important to note that the sill station has a relatively high percentage of deposit feeders, mainly polychaete taxa, compared to the deep basin of Saltfjorden, reaching a similar percentage as in Skjerstadfjorden. Moreover, Redox potential is positive only in that station from whole Saltfjorden. Capitellidae is opportunistic taxa capable to occupy large territory in a short time (Pearson 1980), what may explain widespread in area with complicated entrance for new organisms such the Skjerstadfjorden.

In contrast to Skjerstadfjorden, Saltfjorden is dominated by detritus feeders. Detritus feeders take nutritious particles from the sediment surface. Majority of detritus feeders in

Saltfjorden were mainly Phascolionidae, whereas in Skjerstadfjorden this feeding mode was largely represented by the polychaete Nereididae. Constant water exchange between Saltfjorden and Norwegian Sea provide well organic particles supply.

Suspension feeders were found on every station and had approximately constant percentage throughout the whole fjord system (except western part of Skjerstadfjorden). By the reason of specific morphology filter feeders avoid clogging from large particles, consequently they can be rare or absent in locations where coarse particles fall. Most probably, that can explain the low abundance of suspension feeders near Saltstraumen trench in Skjerstadfjorden, while predators showed maximal abundance in this part of Skjerstadfjorden compared to the rest of the fjord system. Furthermore, locations with high taxa richness and abundance as a good food base, typically correspond high predator's diversity (Souza et.al. 2013). In this area predators are represented by Amphinomidae and Edwardsiidae as the most abundant taxa. Edwardsiidae are sessile Anthozoa feeding on hyperbenthic organisms and zooplankton. In that case, relatively strong currents may provide favorable condition for predators by means of prey delivery. Moreover, relatively high predator's abundance near Saltfjorden only from Skjerstadfjorden's side identifies bottom water transition through Saltstraumen only in one direction, from Saltfjorden to the Skjerstadfjorden. Station S5 has average for Saltfjorden percentage of individuals with carnivorous feeding mode, because water exchange from Skjerstadfjorden to Saltfjorden occur within layer 0-20 meters depth.

Two the most common types of larval development in Saltfjorden – Skjerstadfjorden study area were lecithotrophic larvae (in Saltfjorden) and planktotrophic larvae (in Skjerstadfjorden). The main distinction between these reproductions modes are differences in morphology (stock of nutrients), larval duration, dispersal range and amount of larvae (see Introduction). Cause by that distinctions lecithotrophic and planktotrophic larvae have a different time period for spatial distribution, diversity in water column and value for predators. Due to the ability to feed during the planktonic phase, planktotrophic larvae may disperse over relatively long distances and in combination with large amounts of larvae released the dispersal range may cover a larger area (Vance 1973).

In accordance with 'Thorson's rule' high latitude regions trend to have proportionally more individuals with direct and lecithotrophic development than planktotrophic (Fetzer 2004; Rohde 2009). This hypothesis is based on several factors: relatively short period of food availability in Polar Regions, predator's avoidance, aspiration to settle near parents in favorable environment, adaptation to the cold water and etc. Saltfjorden – Skjerstadfjorden study area have relative abundance of taxa with holobenthic and lecithotrophic development equal 64% that corresponds to 67º25’ of northern latitude.

In addition, number of taxa with direct larvae development equals 13, whereas 5 taxa are common for both fjords. Moreover, each fjord has 3 the most abundant taxa and only one taxon with direct development Trichobranchidae is dominant in Saltfjorden and Skjerstadfjorden. This distribution identifies complication of exchanging individuals with direct development between Saltfjorden and Skjerstadfjorden.

Important to note that ratio between the abundance of taxa with lecithotrophic and planktotrophic reproductive mode is approximately the same in both fjords, but with inverse values: 64% lecithotrophic and 36% planktotrophic in Saltfjorden and 38% and 62% in Skjerstadfjorden. A trend of decreasing abundance of taxa with lecithotrophic larvae was found from western to eastern part of the whole fjord system. This could be related to the transport of larvae with the prevailing currents and the duration of the planktonic larval phase, which is shorter for lecithotrophic larvae. As mentioned before, the entrance of Skjerstadfjorden consists of narrow and shallow trenches, which might act as a dispersal barrier. Moreover, a main part of newborn planktotrophic larvae in Skjerstadfjorden may remain in the fjord what can be attributed to complicated exit through Saltstraumen, Sundstraumen and Godøystraumen. Accordingly it can be assumed to increase abundance of organisms with planktotrophic mode in Skjerstadfjorden.

4.4. Benthic community characteristics in Saltfjorden and Skjerstadfjorden

Studying the spatial variation in the structure of benthic communities allows evaluating the ecological relationship between environmental processes and taxa distribution and diversity (Souza et.al. 2013). The multivariate analyses revealed significant differences in benthic community structure between Saltfjorden and Skjerstadfjorden. The main purpose of the multivariate analyses was comparing the stations based on the similarity in taxa composition. Merging in clusters occurred between stations in territorial proximity that testify about difference in benthic community composition between study areas.

The sill area is represented as a kind of ecotone by the reason of the highest taxa richness and its location with different hydrodynamic features on each side (Walker et.al. 2003). The sill station has 45 and 40% similarity with outer basin and Saltfjorden deep basin respectively that may detect about almost the same influence of adjacent areas on the sill benthic community. Saltfjorden is rather homogeneous area; only two stations S3 and S7 are separated from the main group caused by relatively low abundance of the dominant taxon Phascolionidae and overall low taxa richness. Skjerstadfjorden have relatively high similarity within whole study area with only one cluster (K0 and K1 stations) with 40% similarity with the rest of fjord. This similarity percentage is equal to similarity between the sill and outer basin with Saltfjorden deep basin. K0 and K1 cluster separation from whole Skjerstadfjorden. In addition, the stations K0 and K1 were located in proximity to Saltstraumen in location with strong water exchange and consequently great food delivery that connected with high abundance and taxa richness compared with the rest of the eastern Skjerstadfjorden. Moreover, K0 and K1 stations contain relatively high abundance of Edwardsiidae and low Mollusca abundance that's not typical for the rest of the fjord. After square root transformation and reducing the influence of the most abundant taxa, the communities of Saltfjorden and Skjerstadfjorden were still considerably different. Outer basin became closer to the most abundant and taxa rich station in Saltfjorden (S2) after data alignment, because of similar abundance of dominant taxa as Phascolionidae, Chaetopteridae, Capitellidae and Chaetodermatidae.

Multidimensional scaling has another way of data representation but the same output with hierarchical clustering. MDS plots with non- and square root transformed data also have clear separation between two fjords, whereas the sill station plays role of intermediate link in the benthic community structure of and Skjerstadfjorden. Thus, Skjerstadfjorden and Saltfjorden deep basin are the most dissimilar areas in our study region in terms of taxa composition. Average number of individuals in Saltfjorden and Skjerstadfjorden is 36 and 160 ind. $0.1m^{-2}$, whereas average taxa number is 12 and 21 families $0.1m^{-2}$, respectively. Furthermore, Phascolionidae is dominant group for Saltfjorden with relative abundance 18.7%; Capitellidae is dominating in Skjerstadfjorden with average abundance equal 19.3%. These considerable distinctions in benthic community composition testify about significant role of Saltstraumen and other two trenches as bottleneck for taxa distribution.

One more significant difference in benthic community was identified between Skjerstadfjorden and outer basin (only with multivariate analyses), but this results has to be interpreted with care because of the relatively small number of station within this areas. Considering the slight differences in physicochemical parameters between Saltfjorden and Skjerstadfjorden, the hydrodynamic conditions and the water exchange might have a stronger impact on forming two distinct benthic communities. In addition, difference in 1.6‰ salinity, 4% in oxygen concentration, 2°C in sediment's temperature, 128 meters in average depth and presence algae in Skjerstadfjorden's samples remaining couldn't shift distribution in benthic community so significant in relatively compact area (Blanchard 2013; Galeron 2009; Bandelj 2009).

5. Conclusion

The present study showed significant differences in benthic community structure between Saltfjorden and Skjerstadfjorden. The number of taxa exclusively occurring in one of the fjords only was relatively high for with 21 taxa for Saltfjorden and 16 taxa for Skjerstadfjorden. Distribution of taxa richness and abundance also showed difference between the fjords. Furthermore, differences in water depth, temperature and salinity not provide strong indication of a direct impact on abundance and taxa richness. Saltfjorden and Skjerstadfjorden have a predominance of detritus and deposit feeding modes that indicate difference in amount of food on the bottom surface and type of sediment exposure. Moreover, complicated water exchange through Saltstraumen into Skjerstadfjorden may affect larval transport indicated by a predominance of taxa with planktotrophic larvae in Skjerstadfjorden and lecithotrophic larvae in Saltfjorden. The contribution of the most abundant taxa was calculated for each fjord and outer basin. Capitellidae was the dominant taxon in Skjerstadfjorden and Phascolionidae in Saltfjorden. In addition, multivariate analyses revealed that Skjerstadfjorden and Saltfjorden deep basin had the highest dissimilarity between each other. Thereby, areas within Saltfjorden and outer basin possessed the highest similarity to each other ranged from 55.1 to 72%.

This Master Thesis represents initial study of Saltfjorden - Skjerstadfjorden benthic community and for a more clearly understanding of relations between ecological parameters and benthic structure further study is needed. The future research works may focus on samples number’s extension (especially in Saltfjorden areas), broader study of geophysical and sediment parameters (include Total Carbon Concentration), primary production and addition analysis of benthic biomass.

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Internet recourses:

1. www.marinespecies.org
2. www.species-identification.org
3. www.marlin.ac.uk (online Biological Traits Information Catalogue)

7. Appendices

Appendix 1

Results of MDS

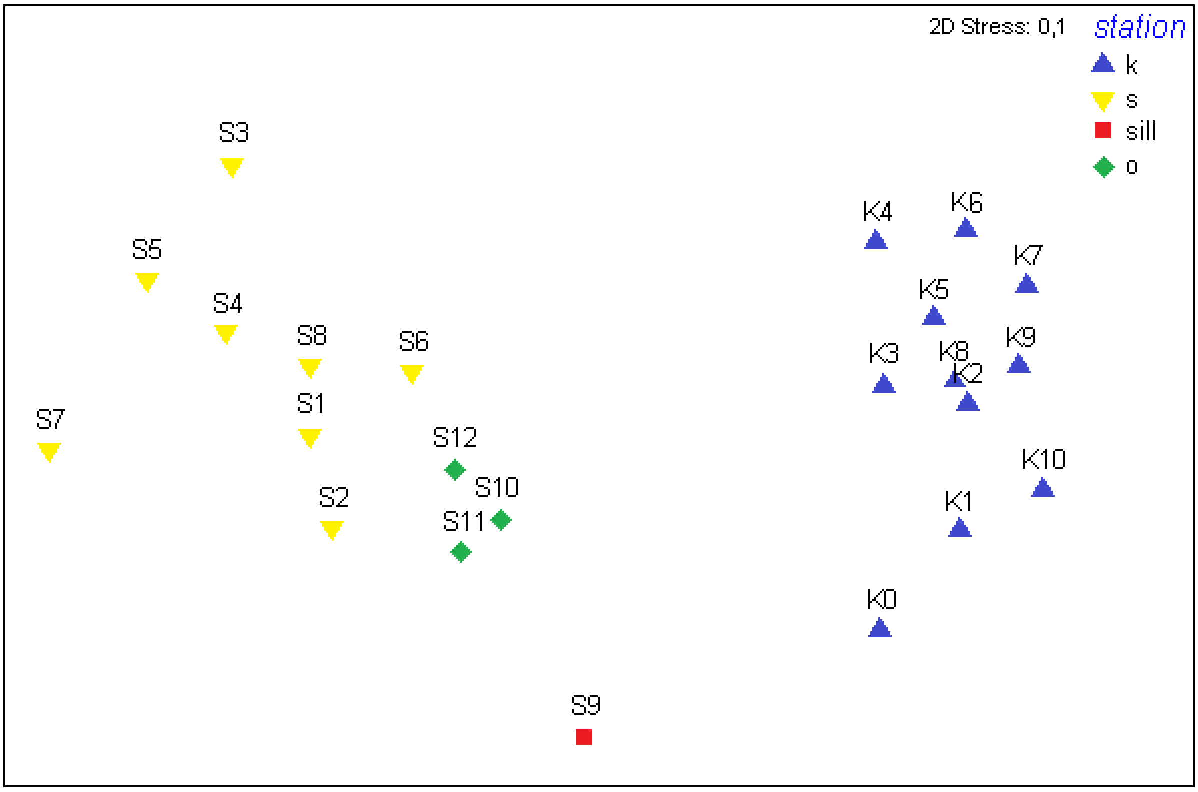

Figure 1. Multidimensional scaling plot of fourth root transformed abundance data (Bray Curtis similarity).

Appendix 2

Results of SIMPER test

Table 1. Results of SIMPER test (contribution to similarity of taxa, %) of the taxa abundance within two Saltfjorden's sampling areas.

Family	Average abundance	Average similarity	Contribution percentage
Saltfjorden deep basin (average similarity 61.7)			
Phascolionidae	17.3	38.9	63.1
Chaetopteridae	4.6	5.7	9.3
Chaetodermatidae	3.2	4.9	7.9
Thraciidae	1.7	3.9	6.4
Amphiuridae	2.0	3.8	6.2
Outer basin (average similarity 77.6)			
Phascolionidae	56.0	42.6	54.9
Chaetopteridae	19.0	15.1	19.4
Thraciidae	7.2	5.5	7.1
Capitellidae	4.8	3.5	4.5
Maldanidae	3.2	2.3	2.9
Chaetodermatidae	3.5	1.6	2.0

Table 2. Results of SIMPER test (contribution to dissimilarities of taxa, %) of the taxa abundance between sampling areas.

Family	Average abundance	Average abundance	Average dissimilarity	Contribution percentage
	Skjerstadfjorden	Saltfjorden deep basin		
Capitellidae	64.4	1.6	31.7	34.9
Thraciidae	22.1	1.7	11.2	12.3
Phascolionidae	0.1	17.3	9.6	10.5
Nereididae	12.8	0.0	7.5	8.2
Amphinomidae	16.0	0.1	6.9	7.6
Oweniidae	7.0	0.0	2.8	3.1
Chaetopteridae	0.7	4.6	2.2	2.4
Maldanidae	4.9	0.8	2.1	2.3
Chaetodermatidae	5.6	3.2	1.9	2.1
Phoxocephalidae	3.1	0.0	1.6	1.7
Nuculanidae	2.1	0.1	1.2	1.3
Amphiuridae	0.0	2.0	1.1	1.2
Edwardsiidae	2.6	0.1	1.1	1.2
Nemertea	2.1	1.1	1.0	1.1
Cirratulidae	2.1	0.1	0.8	0.9
	Skjerstadfjorden	Sill		
Capitellidae	64.4	19.0	13.2	19.5
Chaetopteridae	0.7	21.5	6.4	9.4
Ampharetidae	0.8	19.0	5.6	8.3
Maldanidae	4.9	22.5	5.5	8.1
Thraciidae	22.1	31.0	5.3	7.8
Phascolionidae	0.1	15.5	4.7	7.0

Table 2.Continued				
Family	Average abundance	Average abundance	Average dissimilarity	Contribution percentage
Nereididae	12.8	0.0	4.0	5.9
Amphinomidae	16.0	3.0	3.5	5.2
Spionidae	0.6	6.5	1.9	2.7
Oweniidae	7.0	0.0	1.8	2.6
Nemertea	2.1	5.5	1.1	1.6
Amphiuridae	0.0	3.0	0.9	1.4
Chaetodermatidae	5.6	4.0	0.8	1.2
Cirratulidae	2.1	1.5	0.8	1.1
Onuphidae	0.0	2.5	0.8	1.1
Phoxocephalidae	3.1	0.5	0.7	1.1
Edwardsiidae	2.6	0.0	0.7	1.0
Nuculanidae	2.1	0.0	0.7	1.0
Pandoridae	0.0	2.0	0.6	0.9
Lumbrineridae	0.0	2.0	0.6	0.9
Golfingiidae	1.4	1.5	0.5	0.8
Ophiuridae	0.0	1.5	0.5	0.7
Ampeliscidae	0.0	1.5	0.5	0.7
	Saltfjorden deep basin	Sill		
Thraciidae	1.7	31.0	13.8	19.2
Maldanidae	0.8	22.5	10.3	14.3
Ampharetidae	0.4	19.0	8.8	12.2
Capitellidae	1.6	19.0	8.3	11.5
Chaetopteridae	4.6	21.5	8.1	11.2
Spionidae	0.3	6.5	2.9	4.1
Phascolionidae	17.3	15.5	2.3	3.1
Nemertea	1.1	5.5	2.1	2.9
Amphinomidae	0.1	3.0	1.4	1.9
Onuphidae	0.1	2.5	1.2	1.6
Pandoridae	0.0	2.0	0.9	1.3
Chaetodermatidae	3.2	4.0	0.9	1.3
Lumbrineridae	0.3	2.0	0.8	1.2
Ophiuridae	0.0	1.5	0.7	1.0
Ampeliscidae	0.0	1.5	0.7	1.0
Bodotriidae	0.0	1.5	0.7	1.0
Golfingiidae	0.0	1.5	0.7	1.0
Phyllodocidae	0.0	1.5	0.7	1.0
	Skjerstadfjorden	outer basin		
Phascolionidae	0.1	56.0	21.6	25.8
Capitellidae	64.4	4.8	21.5	25.6
Chaetopteridae	0.7	19.0	7.1	8.5
Thraciidae	22.1	7.2	6.6	7.9
Nereididae	12.8	0.0	5.1	6.1
Amphinomidae	16.0	2.2	4.7	5.6
Oweniidae	7.0	0.0	2.1	2.5
Maldanidae	4.9	3.2	1.4	1.6
Chaetodermatidae	5.6	3.5	1.3	1.6
Phoxocephalidae	3.1	0.0	1.1	1.3
Edwardsiidae	2.6	0.0	0.8	1.0

Table 2.Continued				
Family	Average abundance	Average abundance	Average dissimilarity	Contribution percentage
Nuculanidae	2.1	0.2	0.8	0.9
Spionidae	0.6	1.7	0.7	0.9
Cirratulidae	2.1	0.5	0.7	0.8
	Saltfjorden deep basin	outer basin		
Phascolionidae	17.3	56.0	26.8	46.6
Chaetopteridae	4.6	19.0	10.1	17.6
Thraciidae	1.7	7.2	3.8	6.6
Capitellidae	1.6	4.8	2.5	4.4
Chaetodermatidae	3.2	3.5	1.8	3.2
Maldanidae	0.8	3.2	1.8	3.1
Amphinomidae	0.1	2.2	1.6	2.7
Spionidae	0.3	1.7	1.0	1.7
Nemertea	1.1	1.7	1.0	1.7
Lumbrineridae	0.3	1.5	0.9	1.5
Golfingiidae	0.0	1.2	0.9	1.5
	Sill	outer basin		
Phascolionidae	15.5	56.0	14.0	25.3
Thraciidae	31.0	7.2	8.3	15.1
Maldanidae	22.5	3.2	6.8	12.3
Ampharetidae	19.0	0.7	6.4	11.6
Capitellidae	19.0	4.8	5.0	9.0
Spionidae	6.5	1.7	1.7	3.1
Nemertea	5.5	1.7	1.4	2.5
Chaetopteridae	21.5	19.0	1.3	2.3
Onuphidae	2.5	0.0	0.9	1.6
Chaetodermatidae	4.0	3.5	0.8	1.4
Pandoridae	2.0	0.0	0.7	1.3
Amphinomidae	3.0	2.2	0.6	1.1
Ophiuridae	1.5	0.0	0.5	1.0
Ampeliscidae	1.5	0.0	0.5	1.0
Bodotriidae	1.5	0.0	0.5	1.0
Phyllodocidae	1.5	0.0	0.5	1.0

Appendix 3

Results of MDS, bubble plots of the most contributive taxa

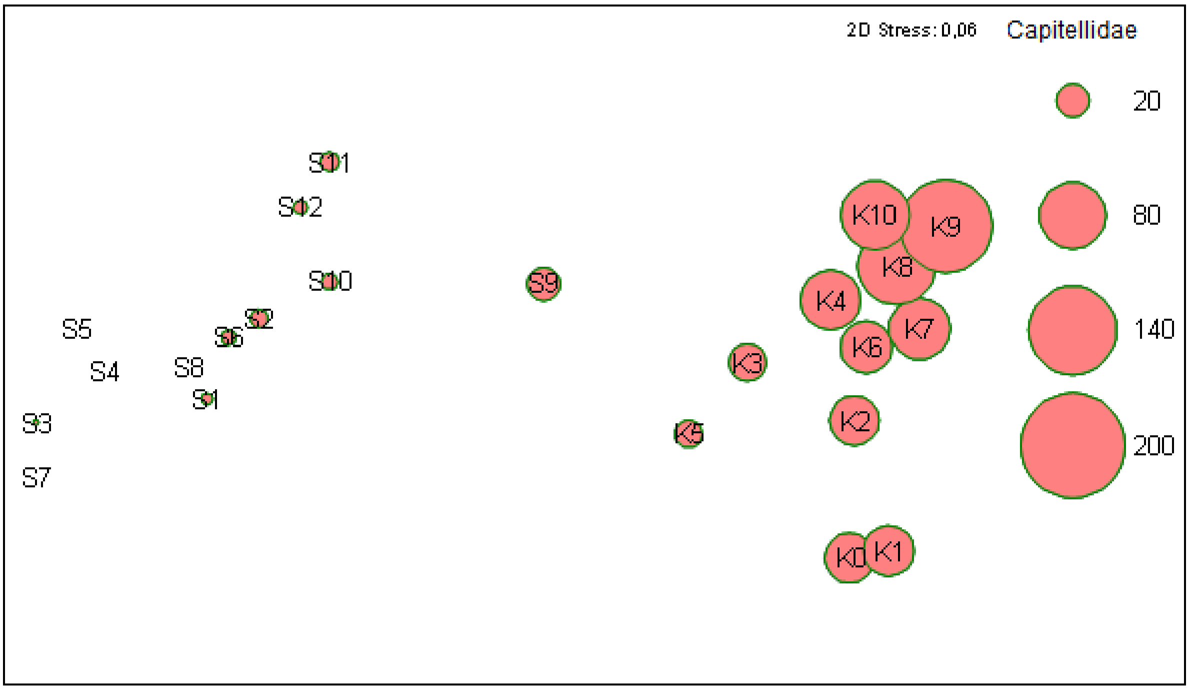

Figure 1. Capitellidae abundance distribution in Saltfjorden and Skjerstadfjorden.

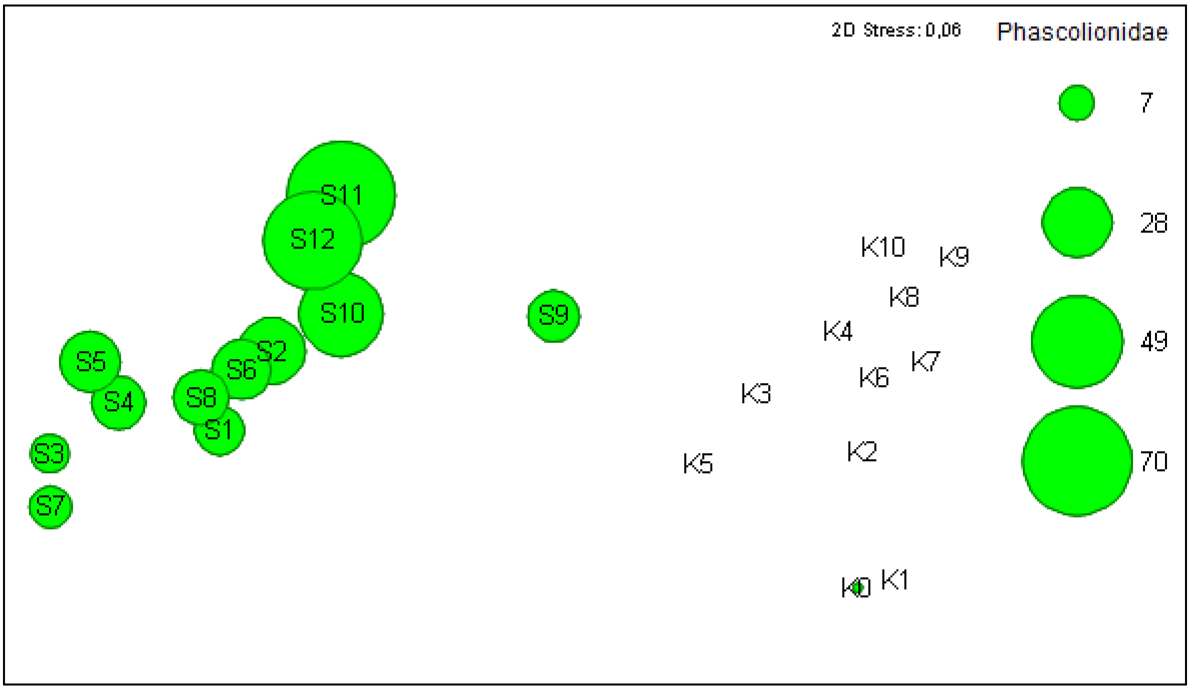

Figure 2. Phascolionidae abundance distribution in Saltfjorden and Skjerstadfjorden.

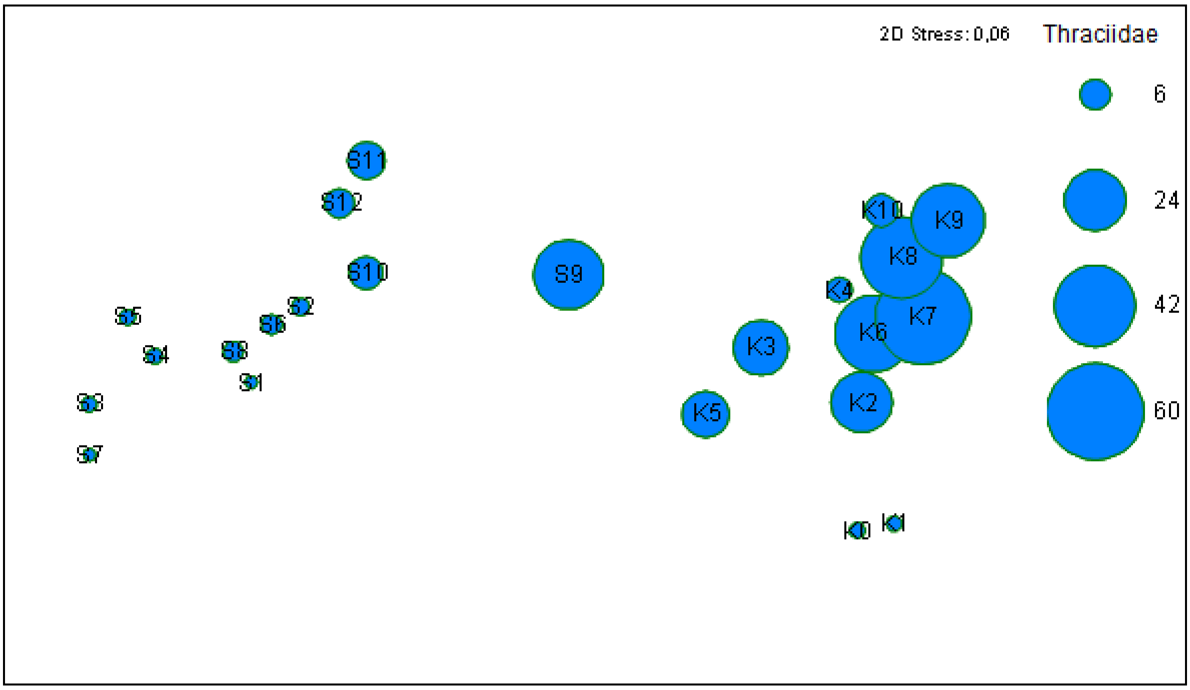

Figure 3. Thraciidae abundance distribution in Saltfjorden and Skjerstadfjorden

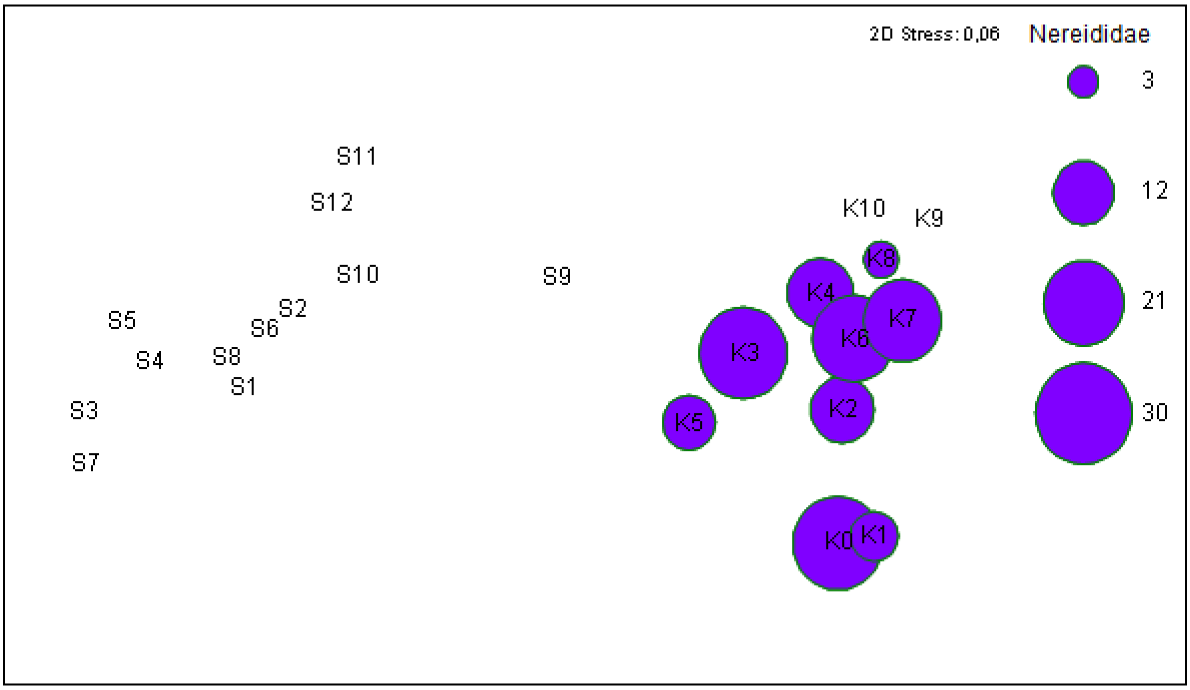

Figure 4. Nereididae abundance distribution in Saltfjorden and Skjerstadfjorden