

# MASTER THESIS

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MSc in Biology and Aquaculture

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## Diversity and species composition of the soft-bottom benthic communities of Tysfjord – Northern Norway's deepest fjord

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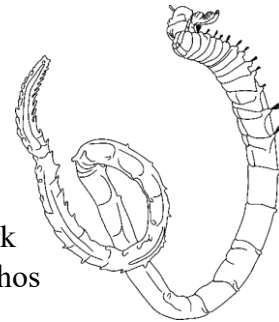
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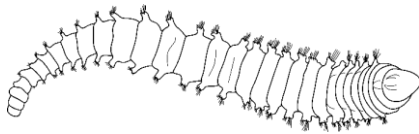
# Acknowledgements

After two intense years studying the Master of Science in Biology and Aquaculture at Nord University, the present thesis is the final result out of it.

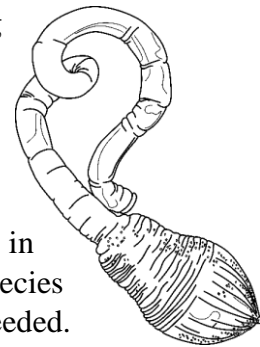
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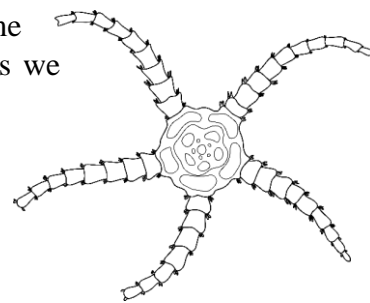


Thank you Katrin Reiss for the nice time spent in the lab, for sharing our struggles with species identification and for all your support when I needed.

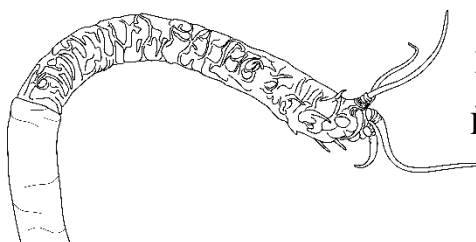
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**Bodø, May 2018**

Èric Jordà Molina

## Abstract

Acquiring basic understanding of the main benthic community composition patterns together with the environmental drivers that structure them is an essential step prior to any monitoring program that uses macrofauna as proxy for the biological status of a system. The soft-benthic communities of North Norwegian fjords have been poorly studied in the last decades despite increasing human activities such as fish farming. A first assessment of the soft-bottom macrobenthic species composition patterns of Tysfjord is given in the present study together with the prevailing environmental drivers that potentially structure the communities along a “mouth” to “head” transect. Tysfjord is a sub-arctic fjord with 3 basins and 3 sills, being the deepest fjord of Northern Norway with a maximum depth of 725 m. Our results showed low species diversity in the main basins and each basin had distinct macrofauna assemblages. The faunal composition in the deepest basin resembled other deep fjords from Southern Norway, being mainly dominated by the suspension feeding bivalve *Kelliella miliaris* and the tube-building polychaetes *Paradiopatra fiordica* and *Spiochetopterus typicus*. The inner-most basin (450 m), which is delimited by a shallow sill (60 m), presented oxygen deficient conditions at the sampling time which was reflected by the presence of low-oxygen tolerant species such as the thyasirid bivalve *Thyasira cf. rotunda* and the siboglinid polychaete *Siboglinum cf. ekmani*. The percentage of organic matter in the sediments together with the oxygen conditions of the bottom water were identified as the environmental factors that explained most of the variance observed in the fauna dataset. Given the importance of these two environmental drivers, the potential addition of organic waste from the surrounding fish-farms or other sources as well as potential effects on the benthic fauna should be carefully monitored and a precautionary approach should be taken, especially, when evaluating future uses of the oxygen depleted inner-most region of Tysfjord.

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# 1. Introduction

Since the first ecological study in Norwegian fjords, dating from the 18<sup>th</sup> century and carried out by the Danish naturalist O. F. Müller, several studies have been conducted in these estuarine formations along the Norwegian coast (Brattegard et al., 2011). The first studies had a naturalistic motivation, since fjords were regarded as accessible places where the main human settlements tended to aggregate and where the main academic institutions were located (Bergen, Trondheim and Oslo). However, by the 20<sup>th</sup> century, a significant shift took place from the more descriptive studies towards investigating the effects of anthropogenic impacts from industrial areas and other sources. Those studies made evident that marine communities in fjords and their ecological functioning were threatened by human activities (Brattegard et al., 2011).

Fjords are important both to humans and marine life. Fjords provide on their coasts suitable locations for human settlements and sheltered waters for safe navigation, while they also support unique communities of marine flora and fauna. For instance, they give room to nursery grounds for marine fish species and provide feeding areas for migratory birds (McLusky and Elliott 2004). It is due to all these ecosystem services that humans have been using these estuarine environments and, although being considered as highly resilient systems, significant changes in response to anthropogenic impacts can be detected (McLusky and Elliott, 2004).

In response to anthropogenic impacts on coastal systems, the European Water Framework Directive (WFD, 2000/60/EC) was established as a framework to monitor and protect groundwater, inland surface waters, estuarine waters and coastal waters (Borja, 2005). In Norway, the WFD is incorporated into the Norwegian Water Management Regulations that set an objective of reaching at least a “good quality status” for all Norwegian waters by 2021 (Husa et al., 2014). The ecological quality of the coastal waters is assessed by a combination of both biological and physical-chemical parameters (Borja, 2005; Husa et al., 2014).

One of the biological components regarded as good indicator for such assessments are macrobenthic communities (Borja et al., 2000), which have been shown to respond to man-induced or natural stressors (Pearson and Rosenberg, 1978; Dauer, 1993). In Norway, for instance, soft-bottom macro-fauna is assessed in the monitoring program MOM (Modelling-Ongrowing fish farms\_Monitoring) which evaluates the environmental impacts of aquaculture facilities.

However, most benthic species in estuarine environments are relatively more tolerant to environmental variations than those from other marine ecosystems (in contrast to the open ocean, where conditions remain almost the same throughout time). Therefore, it is more difficult to detect man-induced impacts in the biota of fjords and discern them from natural drivers and environmental variability (Alden et al., 1997; Veríssimo et al., 2013).

The structuring drivers of benthic communities, as mentioned before, may consist both of natural and anthropogenic factors and processes (Son et al., 2016). It is important that prior to any environmental monitoring program the spatial structure of the main benthic components and their dynamics are known. By doing so, researchers lend an increased ecological insight that serves as a basis for identification and understanding of compositional change over time (Olsgard et al., 1998; Økland and Eilertsen, 1996; Son et al., 2016).

Soft-bottom community studies in north Norwegian fjords have been scarce in the last decades and most efforts have been focused on researching the off-shore waters for monitoring and management under the MAREANO programme (Buhl-Mortensen et al., 2015).

Some of the deepest southern Norwegian fjords such as Hardangerfjord (max. depth 890 m) have been investigated (Buhl-Mortensen and Buhl-Mortensen, 2014; Husa et al., 2014), revealing that deep basins of silled fjords have relatively low species diversity (Fauchald, 1972; 1974). In this deep sub-euphotic environment, the benthic fauna seems to be controlled mainly by the import-export of carbon, the oxygen levels inside the basin and the sedimentation rate of particles (Burrell, 1988). The sub-euphotic benthic communities of fjords might play an important role in the recycling of organic matter since the deep basins may be important carbon sinks (Burrell, 1988).

So far, however, there is no well-grounded knowledge on the soft-bottom benthic communities inhabiting the third deepest fjord of the country: Tysfjord, the deepest fjord of Northern Norway with a maximum depth of 725 m.

Tysfjord is regarded as an important spawning and overwintering region for pelagic clupeoids like herring that migrate to the sheltered waters of the fjord every year. Wintering herring enter the fjord in October following the copepod *Calanus finmarchicus* and then descend to deep waters, where they hardly eat, enter in a state of energy conservation and try to avoid predator encounters until the end of January (Nøttestad and Axelsen, 1999). Killer whales follow the migrating herring and predate on them. Big concentrations of these marine mammals provide a highly profitable touristic economical income for the region (Kuningas et al., 2013).

Several studies have confirmed the presence of genetically isolated population of the European lobster (*Homarus gammarus*) in the eastern parts of Tysfjord which are adapted to the extreme light climatic conditions of Northern Norway, with 24h light during summer and permanent darkness in winter (Jørstad and Farestveit, 1999; Agnalt et al., 2009).

Since a high number of human activities are developing in Tysfjord (fish farming, industry, tourism, fisheries, etc.) it is important to provide a first description of the seafloor communities



to provide a baseline for future monitoring programs studying the ecological quality status of this inlet.

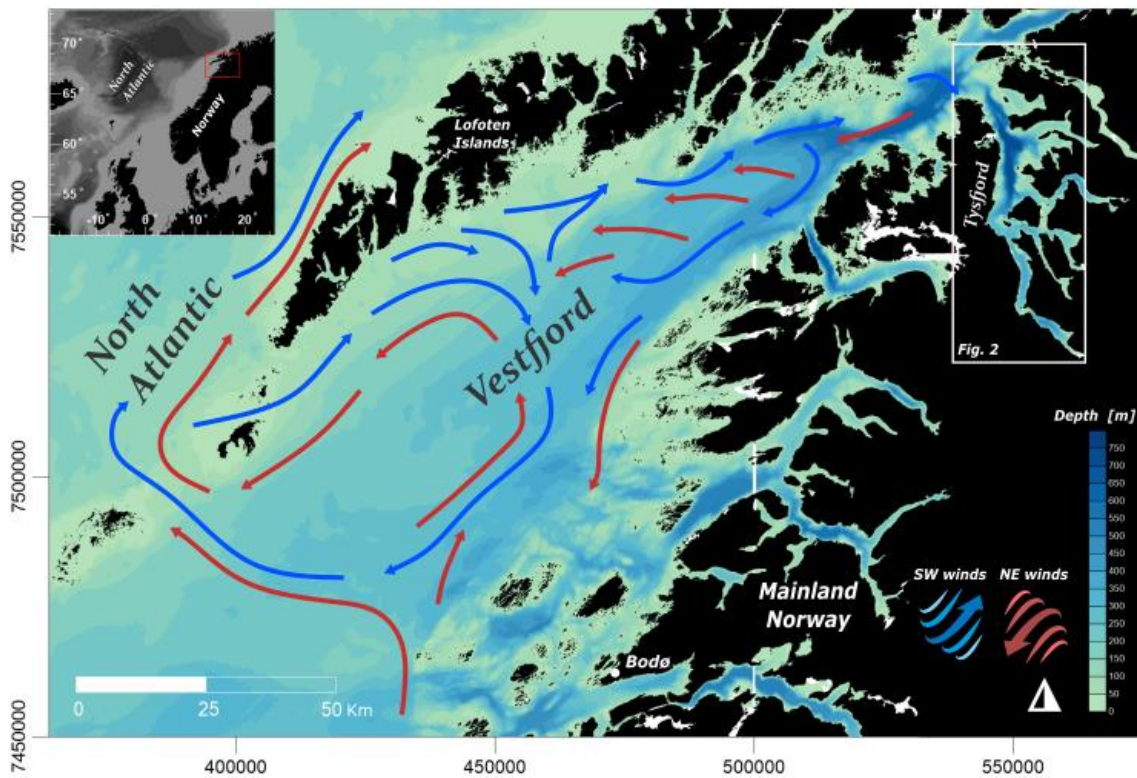
The present study investigates the soft-bottom communities of Tysfjord, a multibasin subarctic fjord. The main objectives are to: **1) provide a first assessment of the benthic communities along an outer-inner transect of the fjord, 2) describe the patterns of taxonomic diversity within the fjord, and 3) relate the patterns in species composition and ecological functioning to the prevailing environmental conditions.**

## 2. Material and Methods

### 2.1. Study area

**Tysfjord** is the deepest fjord in Northern Norway (Fig. 1). Located in Nordland county, it has a maximum depth of 725 m. It is approximately 55 km in length and 4-5 km across at its widest part and 1-2 km at its narrowest section. The east margin of the fjord presents several connections to other secondary fjords that run into Tysfjord (Fig. 2).

Tysfjorden is connected on its outermost part with Vestfjorden. **Vestfjorden** is an unusual fjord as it is wider than most typical fjords (Mitchelson-Jacob and Sundby, 2001). The mouth, around 70 km wide, extends from Bodø to Røst, narrowing down along the Lofoten archipelago to around 20 km in the inner most part.



**Figure 1:** Map of Vestfjorden with Tysfjord (indicated with a white box (Fig. 2)) with the bathymetric data. The blue arrows represent the main circulation pattern when SW winds prevail, while the red arrows represent the predominant circulation when NE winds dominate. **Bathymetry data source:** The Norwegian Mapping Authority Hydrographic Service

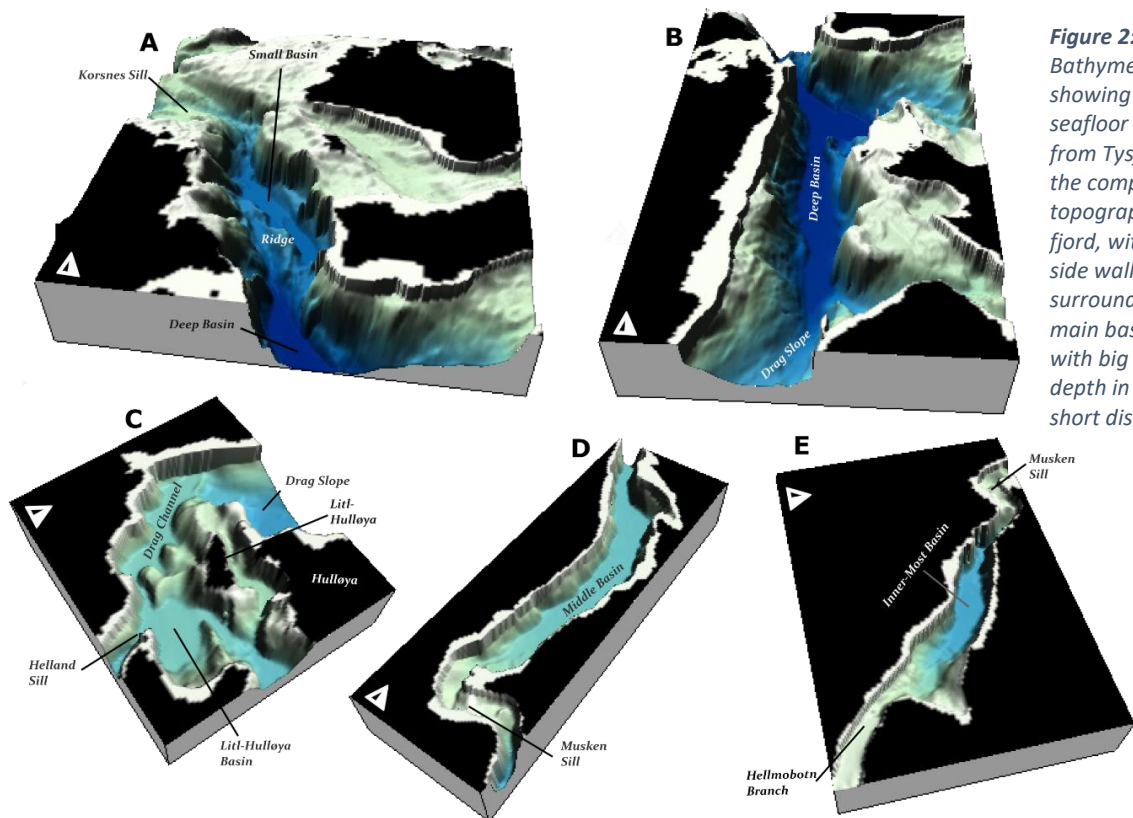
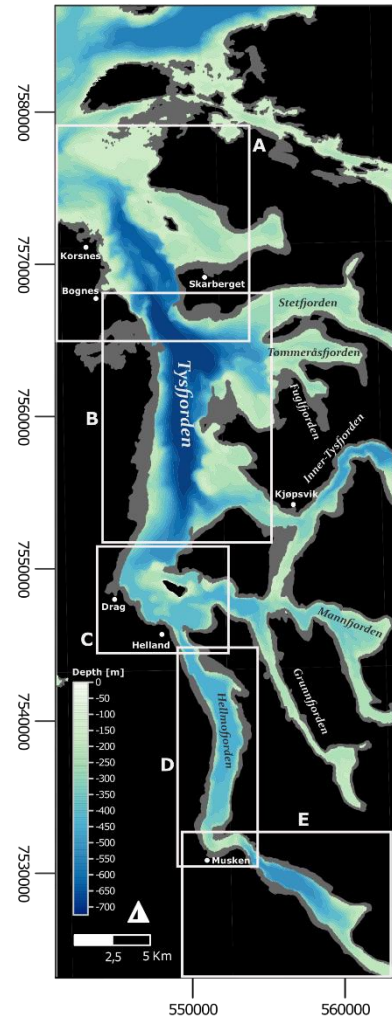
**Tysfjorden** is a multibasin type fjord with 3 main sills and 3 main basins (Fig. 3). The outermost sill of Tysfjord is called Korsnes sill and its upper part is relatively flat with a deepened section, reaching up to 280 m depth. Right after the Korsnes sill, a small basin at around 600 m depth takes place being separated from the main deepest basin by a prominent structure resembling a seamount or submarine ridge approximately 100 m high from the seafloor (Fig. 2 and 3).

The deepest basin of the fjord has a depth between 700 and 725 m (Fig. 2 and 3). The walls of the submarine cliffs surrounding the basins are almost vertical and provide hard substrate habitats for a wide range of sponges, anemones and cold-water corals such as the reef-forming species *Lophelia pertusa* (MAREANO, 2018 and ROV observations by David Cothran\_Lindblad Expeditions, LLC).

Following towards the head of the fjord, the deep basin ends with a relatively pronounced slope (here named Drag Slope) that leads to a narrow channel (Drag Channel) at 330 m depth close to the settlement of Drag (Fig. 2 and 3).

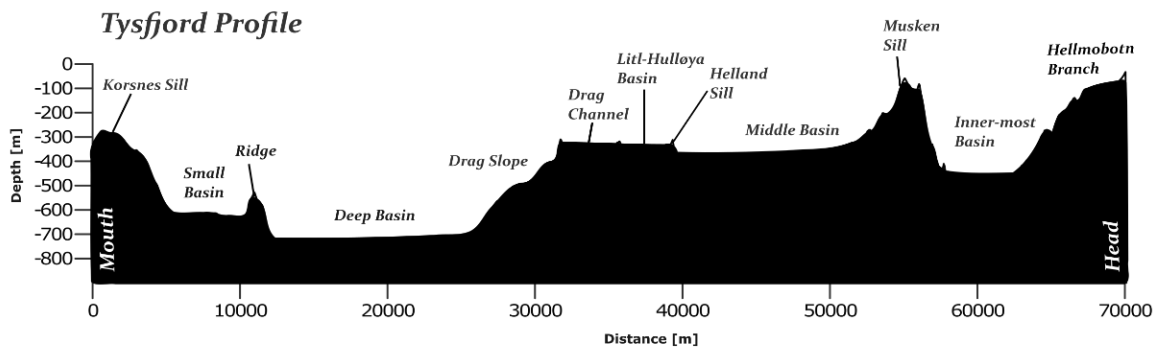
The Helland sill separates Tysfjord from Hellmofjorden. This sill is small, with 303 m deep at its shallowest point. The mouth of Hellmofjorden is relatively narrow (about 1 km), with depths between 370 and 350 m.

Finally, a very pronounced sill called Musken sill, separates the middle basin from the inner-most part of the fjord. This sill rises from 350 m up to 60 m at its shallowest point and drops again down to 450 m where the last basin



**Figure 2:** Bathymetric map showing the main seafloor accidents from Tysfjord. Notice the complex topography of the fjord, with very steep side walls surrounding the main basins and with big changes in depth in relatively short distances.

starts. The inner-most basin ends with a narrow branch that leads to the head of the fjord, where the small settlement of Hellmobottn is located (Fig. 2 and 3).



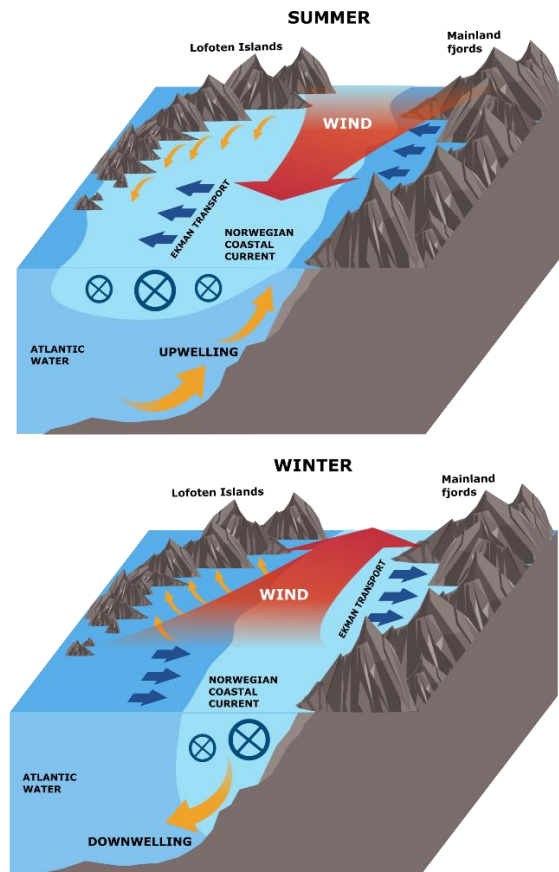
**Figure 3:** Profile showing the seafloor characteristics along the Tysfjord transect (including the Hellmofjord section). Notice the 3 main sill (Korsnes, Helland and Musken) and the 3 main basins (Deep, Middle and Inner-most). The horizontal axis represents distance [m] along the profile and the vertical axis represents depth [m]. The profile starts from the “mouth” of the fjord and ends in the “head” section (from left to right)

## 2.2. Environmental setting

In a local scale, the oceanography of Tysfjord is driven by wind patterns (Faust et al., 2017). However, the tide fluctuations and the dynamics of the North Atlantic and Norwegian Coastal Current systems flowing northwards along the Vestfjord have an impact on the hydrography at a regional level (Furnes and Sundby, 1981; Mitchelson-Jacob and Sundby, 2001).

Mitchelson-Jacob and Sundby (2001) described a general circulation pattern in the Vestfjord system consisting of an inflow of Atlantic water along the mainland side and an outflow current along the Lofoten archipelago producing a cyclonic pattern.

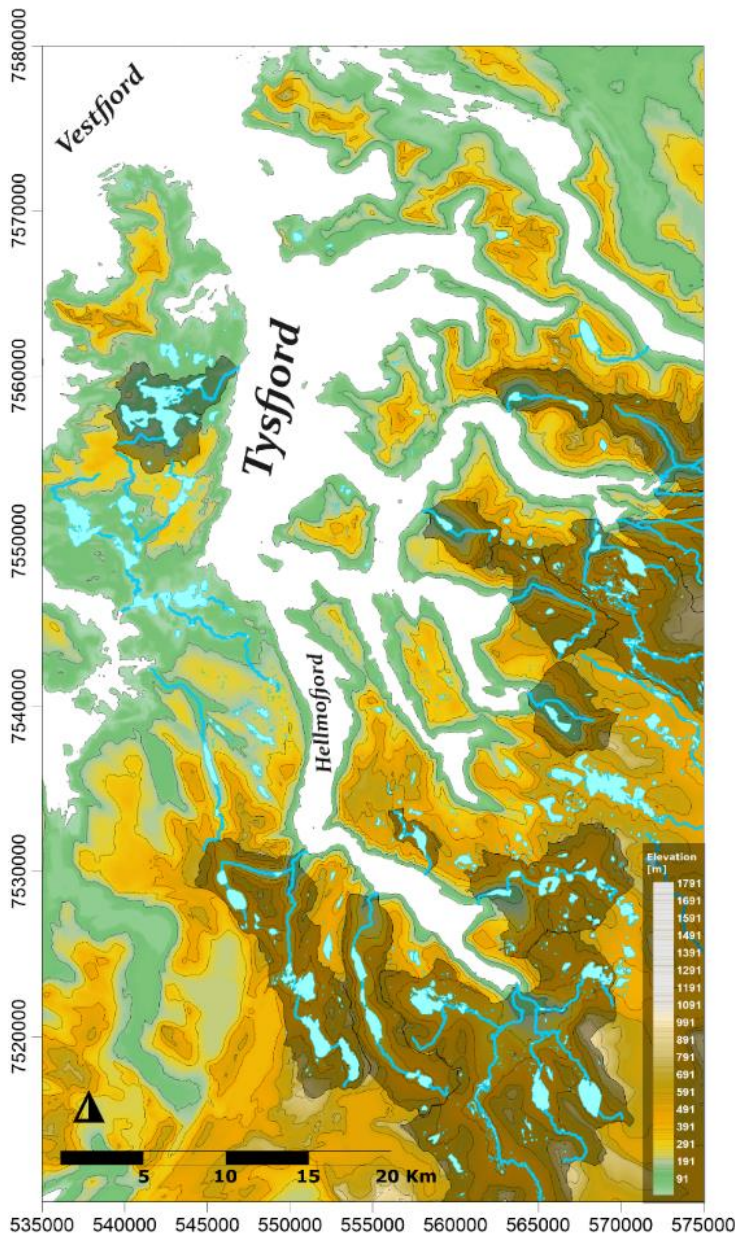
However, this general trend is often modified by changes in the wind direction. Upwelling episodes in the Lofoten side may take place when south-westerly winds prevail in the area (usually in winter), pushing the coastal waters into the



**Figure 4:** Schematic representation of the monsoon effect in the Vestfjord region. In summer, when winds from the Vestfjord region, in the Lofoten side may take place when south-westerly winds prevail in the area (usually in winter), pushing the coastal waters into the

fjords of the mainland side (Fig. 1). However, when the prevailing winds blow from the north-east, the effects are the opposite and upwelling is produced in the mainland side while surface waters are being flushed out from the fjords towards Vestfjord (Furnes and Sundby, 1981). These variations in wind direction are mainly induced by the so-called monsoon effect that affects the Norwegian coast on a seasonal basis (Sætre, 2007) (Fig. 4).

The region presents a complex physiographic setting marked by an alpine landscape with mountains sometimes higher than 1000 m and sparse vegetation (Faust et al., 2017). Due to the irregular topography, precipitation is greatly variable within short distances (500-2000 mm/a).



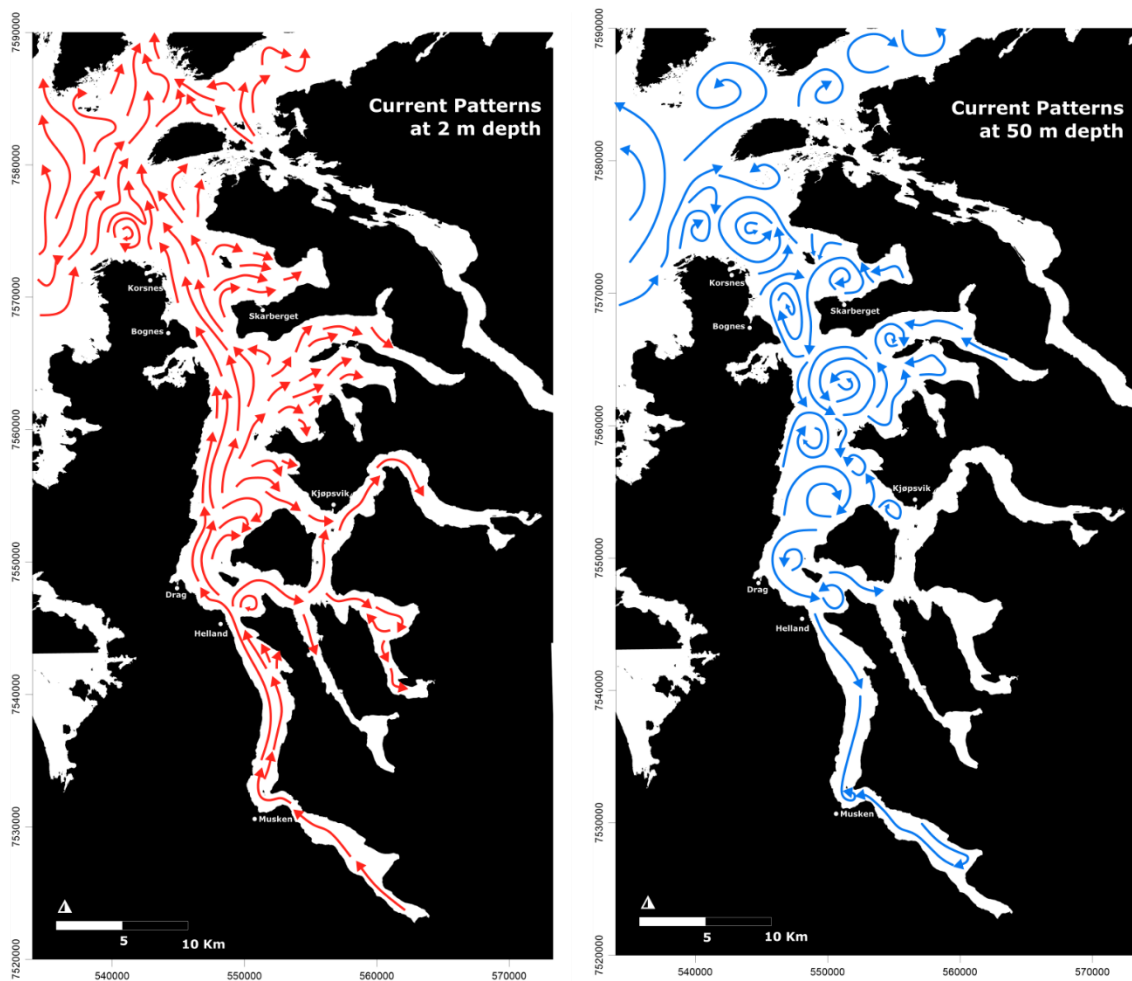
**Figure 5:** Topographic map of the area surrounding Tysfjord. The main rivers are in light blue and the main catchment areas are indicated in dark colour. **Topographic data and river data source:** Kartverket.no and The Norwegian Water Resources and Energy Directorate (NVE).

The rivers running into Tysfjord are generally small (Faust et al., 2017). The total catchment area that drains into Tysfjord is approximately 1147 km<sup>2</sup> (data from The Norwegian Water Resources and Energy Directorate (NVE)) and 51,62 % of this area is represented by 14 sub-fluvial systems with their respective catchment areas (Fig. 5). Due to the small size of the catchment area and the small riverine system in the area, the freshwater inflow is rather diffuse.

Faust et al. (2017) found a complex pattern of mineral and grain size distribution in the surface sediments of the Tysfjord basins which is most likely explained by the irregular erosion and the inhomogeneous sediment supply from each drainage area. This produces strong patchiness in the seafloor sediment composition over short distances.

Current direction models from SINMOD, SINTEF suggest an average annual pattern of water flushing out of Tysfjord through the upper layer of the water column (2 m depth), mostly brackish water (Fig. 6). However, the annual average for the layer at 50 m depth suggest a complex circulation marked by eddies over the whole fjord.

The water column of Tysfjord presents seasonal variations in temperature and salinity (Brkljajac et al., 2016). The temperature of the surface waters at the deep basin area during 2015 varied between 3.5 – 5.5°C in winter to a maximum temperature of 14.4 – 15.1°C in July. The salinity of the surface water ranged from 33.0-33.1 in winter and dropped down to 24.5-25.5°C between June and July. During summer and winter, the thermocline lies down as deep as 50 m (Brkljajac et al., 2016).



**Figure 6:** Simplified representation of the current direction models from MODS Nordland by SINTEF. In the upper water column (2m depth in red arrows) the annual pattern consists mainly in water being flushed from Tysfjord out to Vestfjord. In contrast, at 50m depth (in blue arrows) am complex series of eddies predominate throughout Tysfjord. **Source:** <http://nordland.sinmod.com/>.

Twelve aquaculture farms operate in Tysfjord, the majority of them dedicated to the cultivation of Atlantic Salmon. Moreover, a concrete factory in Kjøpsvik and a quarz plant in Drag operate in the region.

### 2.3. Sampling strategy

The sampling campaign was conducted between the 22<sup>nd</sup> and the 26<sup>th</sup> of May 2017 on board RV Tanteven. A Van Veen grab of 0.1 m<sup>2</sup> was deployed to retrieve a total of 36 samples along a transect from the innermost to the outermost part of Tysfjord, including the Hellmofjorden branch and two stations outside the Korsnes sill in Vestfjorden (see Table 1 and Fig. 7)

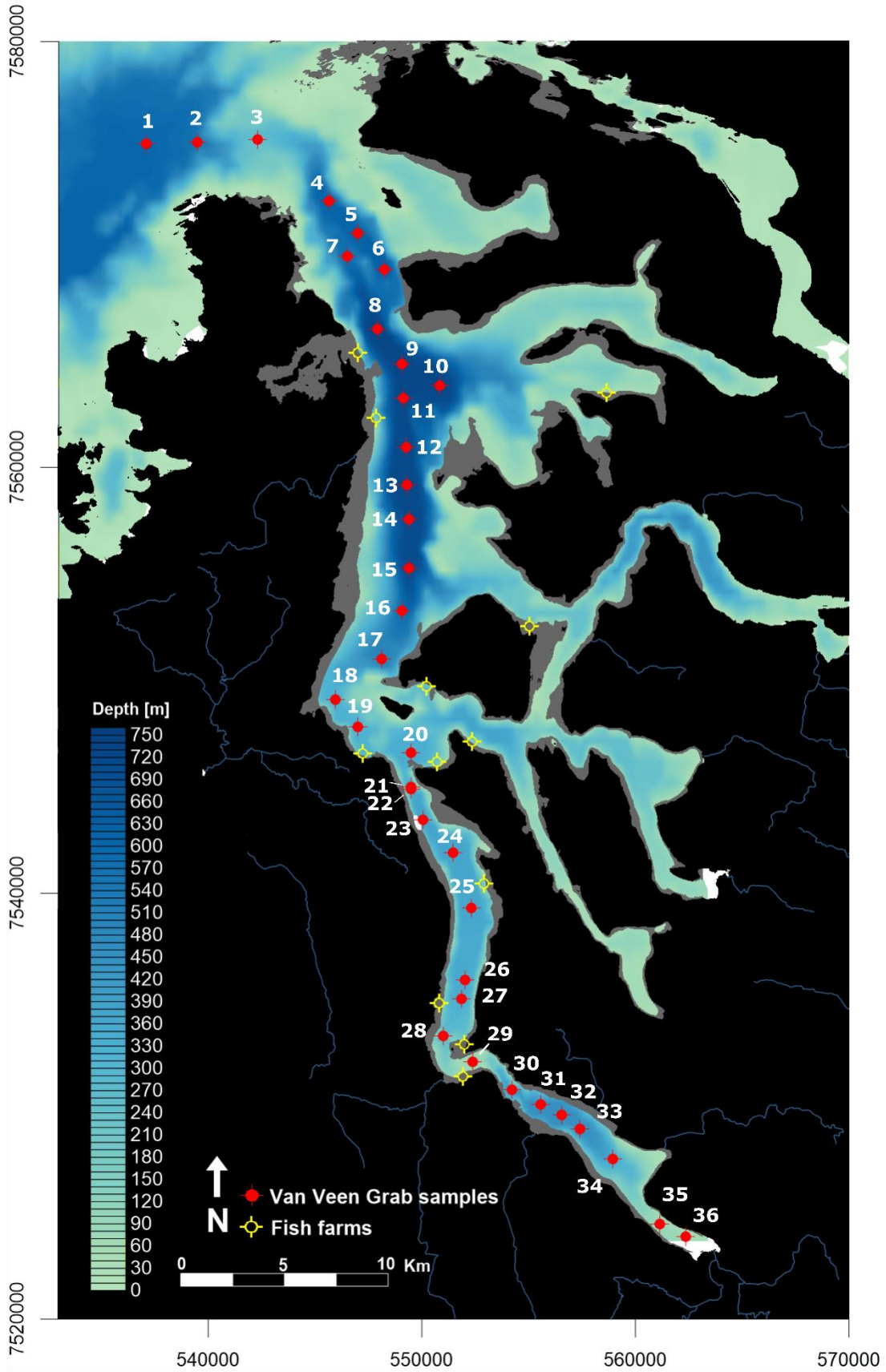
For each grab, measurements of temperature (°C), pH and Redox potential (mV) were recorded from the surface layer of the sediments using electronic probes (EcoSense® ORP15A ORP Temperature Pen Tester 11 and EcoSense® pH10A Pen Tester). The upper 5 cm and 2 cm of the sediment were sampled with a 50 mL syringe for granulometric analysis and total organic content, respectively. All sediment subsamples were filled in plastic bags and immediately frozen at -20°C.

The remaining content of the grabs was sieved on board using a 1 mm mesh size sieve and preserved with 4% formaldehyde seawater buffered with Borax.

**Table 1: Stations sampled during the Tysfjord campaign in May 2017**

Station	Latitude	Longitud	Depth [m]	Station	Latitude	Longitud	Depth [m]
1	68°17,262	15°53,897	596	19	68°02,428	16°07,607	325
2	68°17,321	16°01,487	284	20	68°01,753	16°11,135	334
3	68°17,278	15°57,406	548	21	68°00,894	16°11,093	375
4	68°15,735	16°06,299	630	22	68°00,833	16°11,104	350
5	68°14,901	16°08,180	620	23	68°00,050	16°11,863	374
6	68°13,974	16°09,974	630	24	67°59,204	16°13,821	367
7	68°14,332	16°07,467	580	25	67°57,800	16°14,979	360
8	68°12,483	16°09,428	716	26	67°55,984	16°14,452	346
9	68°11,580	16°11,014	719	27	67°55,505	16°14,200	333
10	68°11,017	16°13,550	714	28	67°54,588	16°12,932	278
11	68°10,712	16°11,078	715	29	67°53,913	16°14,848	110
12	68°09,486	16°11,200	713	30	67°53,184	16°17,466	438
13	68°09,529	16°11,218	710	31	67°52,799	16°19,329	452
14	68°07,653	16°11,305	708	32	67°52,526	16°20,730	455
15	68°06,418	16°11,227	703	33	67°52,153	16°21,932	450
16	68°05,346	16°10,712	575	34	67°51,379	16°24,081	354
17	68°04,143	16°09,280	486	35	67°49,708	16°27,099	100
18	68°03,136	16°06,116	325	36	67°49,381	16°28,845	88,7

The environmental conditions of the water column were measured with 23 CTD casts deployed along the transect (see Fig. 8). For all casts, temperature [°C], salinity, dissolved oxygen [mg/L], fluorescence [µg/L] and density [Kg/L] were measured every second while the CTD was ascending at an approximate speed of 1 m/s. Only the up-cast records were processed and analysed.



*Figure 7: Map of the study region with the sampling locations indicated in red and aquaculture farms indicated in yellow. Depth is indicated by the colour scale.*



A good sampling strategy is crucial in order to retrieve successfully the underlying gradients in species composition. Both the environmental variation and the species composition of each site have to be properly represented (Son et al., 2016). Traditionally this has been achieved by a strategy of “many-samples, one-site” where replication allows for robust statistical analysis in a rather experimentally methodological approach (Schweiger, 2016). However, limited resources (money, time, etc.) force researches to find a balance between the number of sites visited and the number of samples per site. As a consequence, a strategy of “many-sites, one-sample” may be beneficial since it allows to visit more sites in the study area, optimizing this way the coverage of spatial variability in species composition (Son et al., 2016). Aarnio et al. (2011) pointed out that although this last strategy may recover fewer species per site, a higher number of species will be recovered in total since species missed at one site will most likely appear at other sites. In the present study, the strategy “many-sites, one-sample” was chosen.

#### **2.4. Fauna processing**

The formaldehyde fixed grab samples were rinsed with freshwater for at least 30 minutes and macrofauna was sorted under a stereomicroscope. Prior to the sorting, a picture was taken of each sample for posterior visual examination of the general appearance of the seafloor material.

All benthic macrofauna was identified to the lowest taxonomic level possible. Foraminifera were discarded during the sorting together with planktonic organisms like copepods.

For each sampling station, taxon abundance (ind./0.1 m<sup>2</sup>) was assessed.

#### **2.5. Grain-size analysis**

The frozen samples for grain size analysis were defrosted and steered in a beaker with water to homogenize its content. Any large organisms were removed. The content was washed through a set of sieves (mesh sizes: 2mm-1mm-500µm-250µm-125µm-63µm). The effluent (<63 µm) was collected into a bucket. Each sediment grain size fraction was transferred into a pre-weighed aluminium container. The effluent collected in the buckets was left to settle for at least 48 hours and up to 1 week. Once the water was clear from particles, the excess of water was decanted without disturbing the sediment. Finally, the content left in the bottom of the buckets was transferred into a pre-weighed aluminium container. All containers were placed in an oven at 90°C for approximately 24 hours until all water content evaporated. All containers were weighed again and the weight of the individual size fractions was calculated by deduction of the container weight.

The weights of each size fraction for each grab sample were introduced in the software GRADISTAT (Blott and Pye, 2001) in order to calculate the mud content [%] and the textural

group for each sample based on the Folk and Ward (1957) ternary classification in terms of Mud, Sand and Gravel.

## **2.6. Percentage of organic matter in sediments**

The organic matter content (in%) of the sediment samples was quantified through the method of loss on ignition (LOI). LOI is a widely used method to estimate both the organic and the carbonate content of sediments by burning sequentially the sediment samples at different temperatures in a muffle oven to achieve different degrees of oxidization of carbon (Heiri et al., 2001).

For the present study, only the organic fraction was assessed.

For the LOI procedure, porcelain crucibles were dried in an oven at 105°C for 20 minutes to remove any traces of humidity, then transferred to a desiccator and each crucible was weighted on a fine scale with 0,0001g precision. The frozen sediment samples were transferred into the crucible and steered to defrost the sediments. Large animals or other large inorganic particles (e.g. shells, wood, etc.) were removed from the sample. Finally, the crucibles with the samples were dried in an oven: first at 90°C for ca. 3 hours and then at 105°C for ca. 20 hours. At first, the temperature was set to be lower than 100°C to avoid spilling the samples when reaching the boiling point too violently. Therefore, the temperature was increased to 105°C when most of the water already evaporated.

Thereafter, the crucibles were transferred into the desiccator and, after cooling down for 10 to 20 minutes, the weight was measured.

Once the dry weight for each crucible was recorded, the samples were transferred in a muffle oven *Heraeus D-6450* and burned at 520°C for 5 hours. After this time, the muffle oven was switched off and the door was opened to cool it down. With protecting gloves and with the aid of a pair of oven pincers, the crucibles were transferred once more into the desiccator. After 10 to 20 minutes, the weight of the crucibles was once more recorded.

The TOC content was then calculated as:

$$\text{Dry Weight} = \text{Dried sediment in crucible} - \text{Crucible weight empty}$$

$$\text{LOI} = \text{Dried sediment in crucible} - \text{Burned sediment in crucible}$$

$$\% \text{ of organic matter} = \frac{\text{LOI} * 100}{\text{Dry Weight}}$$

## **2.7. Hydrography**

The CTD data of the up-cast for all CTD stations was cleaned and plotted in Golden Surfer © to obtain a profile plot along the fjord for each variable using a krigging method to interpolate the data from the measurement points.

The values for the bottom water of each CTD were assigned to the closest grab to represent the prevailing environmental parameters.

## **2.8. Statistical Analysis**

Today, unconstrained and constrained analysis are the method of choice to identify spatial patterns of benthic community structure and environmental gradients that might play a role in shaping these patterns (Legendre and Legendre, 2012).

For long, the chi squared distance was considered to be the suitable metric for species data with unimodal distribution along an environmental gradient. However, severe drawbacks with this metric have led to a frequent choice to work with Euclidean distances (Legendre and Legendre, 2012). For this metric, PCA (principal-component analysis; for unconstrained ordination) and RDA (redundancy analysis; for constrained ordination) are used. The problem when working in Euclidean distances with raw species data along long gradients is that at some point some species for one site will be mostly replaced by others in other distant sites. This generates a large number of zeros in the dataset and ecologists have been arguing for long time that Euclidean distances are not suited for species abundance data with null abundances (Clarke and Warwick, 2001).

Legendre and Gallagher (2001), proposed to transform the abundance species data with the Hellinger transformation in order to work with Euclidean distances employing PCA or RDA analysis. This transformation allows to preserve the chosen distance among objects, avoiding this way the problem with many zeros in the dataset. Hellinger transformed data is also recommended for clustering analysis with species abundance data. Legendre and Legendre (2012) also suggested a better compromise between linearity and resolution after running simulations with Hellinger transformed data.

In this study, all statistical analyses were performed using the computing software R©, Version 1.1.383.

For all statistical tests involving the biological community data, the Hellinger transformation was applied using the “vegan” package (Oksanen et al., 2010).

The present study falls into the category of being an exploratory investigation since it is the first time that a thorough assessment of soft-bottom communities is conducted in Tysfjord. Clarke

et al. (2008) suggested that in studies with a null-hypothesis backbone hierarchical cluster analysis is a good approach to identify statistically significant groupings of *a priori* unstructured samples of assemblage data. This method tests for the null-hypothesis among the distances (Euclidean, in our case) of randomly selected samples to define which are the significant groupings among all samples. For that, a **clustering analysis** with a **SIMPROF test** was performed with 999 permutations and an alpha of 0.05 using the package “clustsig” (Whitaker 2014).

Following, the 5 most abundant species in each cluster group were determined.

For the ordination analysis, a **variation partitioning analysis** was performed. In variation partitioning, in contrast to the simple redundancy analysis, groups of independent variables are defined to create sets or variables representing broad factors (in our case environmental variables) in order to infer the common and unique contributions into the model of the different sets (Mood, 1969, Peres-Neto et al., 2006) through multiple redundancy analysis. In this study, the environmental factors recovered after the sampling were grouped in 4 sets according to their belonging into biochemical properties, physical properties, sediment properties and depth (see Table 2).

When too many factors are included as explanatory variables to an already fitted model the model tends to lose predictive power. This happens as a violation of the parsimony principle, which postulates that the less explanatory variables needed to explain the model, the better (Blanchet et al., 2008). For this reason, Forward Selection (FwS) was applied to the sets of environmental variables presented in Table 2 prior to the variation partitioning to determine which of them contributed significantly to the explanation of the model. The FwS uses two stopping criteria: the alpha significance level (0.05) and the adjusted coefficient of multiple determination ( $R^2_{adj}$ ) calculated using all explanatory variables (Blanchet et al., 2008). Only the significant variables in each set were included in the model for the variation partitioning analysis.

The forward selection was performed with the packages “adespatial” (Dray et al., 2018) for the numerical factors and “ade4” (Dray, 2018) for the categorical factors (for the sediment properties). For the variation partitioning analysis, the package “vegan” was employed.

The Shannon index ( $H' \log e$ ) (Shannon, 1948) and Pielou's evenness ( $J'$ ) (Pielou, 1977) diversity indices were calculated for the fauna dataset using the package “vegan”. In addition, the species richness ( $S$ ) was calculated for each phylum subset (Mollusca, Polychaeta, Echinodermata and Arthropoda)

For all analysis mentioned above, the species of Porifera from all samples were removed.

**Table 2: Sets of the explanatory environmental variables for the constrained analysis**

<b><u>Set of environmental variables</u></b>	<b><u>Environmental variables</u></b>
<b>Biochemical properties</b>	<ul style="list-style-type: none"><li>- Organic matter % in the sediment</li><li>- O<sub>2</sub> % in bottom water</li><li>- O<sub>2</sub> mg/L in bottom water</li></ul>
<b>Physical properties</b>	<ul style="list-style-type: none"><li>- Salinity of the bottom water</li><li>- Temperature of the bottom water</li><li>- Temperature of the sediments</li></ul>
<b>Sediment properties</b>	<ul style="list-style-type: none"><li>- Mud %</li><li>- Sand %</li><li>- Textural Group</li></ul>
<b>Depth</b>	<ul style="list-style-type: none"><li>- Depth</li></ul>

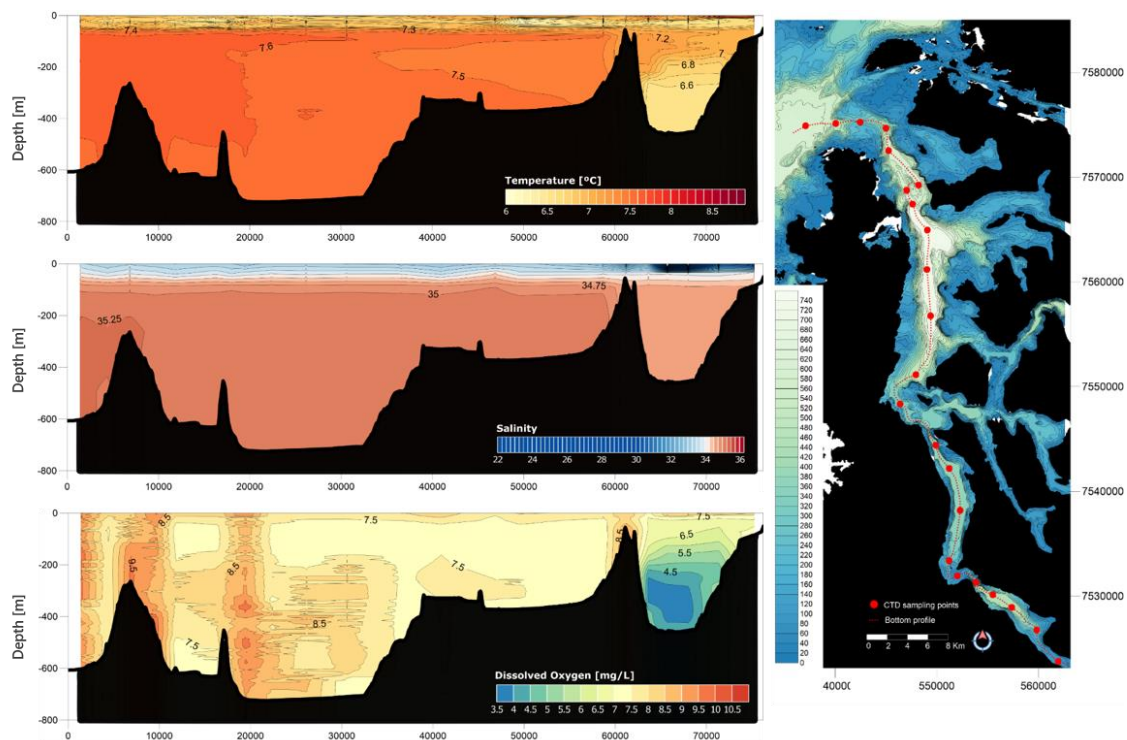
### 3. Results

#### 3.1. Environmental conditions

The temperature profile of the CTD revealed a colder layer of water from the surface down to around 100 m depth throughout the whole fjord (Fig. 8). Beneath this upper layer, a gradient of temperature from warmer to colder appears in the direction from outer to inner Tysfjord. The water temperature at the Korsnes sill was 7.6 °C, decreasing towards the Middle basin with values between 7.5 and 7.4 °C. The Inner-most basin presented the lowest temperatures at the bottom water, with 6.6 °C (Fig. 8).

The salinity measurements showed a similar pattern to the temperature profile. While the salinity at the outer-most part of the fjord was 35.25 at the Korsnes sill, it decreased slightly towards the Helland sill with 35 and was around 34.75 in the Inner-most basin. In the upper-most water layer values ranged from as low as 22 to 34.5 within the upper 100 m with the lowest values at the inner-most basin (Fig. 8).

Oxygen values ranged between 9.5 to 7.5 mg/L in the outer region and the deep and middle basins of Tysfjord (Fig. 8). However, at the Inner-most basin, dissolved oxygen levels between 4 and 6 mg/L were recorded, with the lowest values at the deepest parts of this basin.



**Figure 8:** CTD profiles for Temperature [°C], Salinity and Dissolved Oxygen [mg/L] for Tysfjord. The map shows the points where measurements were taken with the CTD that later on were interpolated to create the profiles.

Regarding the pH in the sediments (Fig. 9) the lowest values were found at station 5, with values of 6.73. The highest pH values were recorded at station 14, with 8.2. A gradient to more alkaline values was found from station 6 all the way to station 13, at the deep basin. At the middle basin, pH values were between 8.04 and 7.96. Relatively low values of pH were recorded in the shallowest and inner-most station, while they were a bit higher in the central part of the Inner-most basin, with 7.88 at station 31.

The highest temperatures at the sediment surface (Fig. 9) were recorded along the middle basin, and were highest at station 23, with 8.5 °C. The lowest temperature was recorded at the inner-most basin, with values between 7 and 7.2 °C (stations 30 to 33). The part of the deep basin closer to Drag seems to have higher sediment temperatures than the part closer to the Korsnes sill. The Redox potential at the sediments was highest at stations 5 with 285 mV and stations 18 and 19 with 276 and 273 mV, while the lowest values were recorded at station 3, at the Korsnes sill, with 60 mV. All Redox potential values were above 0.

Regarding the mud % in the sediment composition (Fig. 9), the lowest values were found at the Musken sill (stn. 29) with 3.8%. The highest mud % was recorded at station 8 with 92.8%. The stations of the deep basin closer to the Drag slope had relatively lower % in mud content than the stations closer to Korsnes, although it seems that the values in this basin are quite heterogeneous. At the stations closer to the Helland sill less % in mud was found, while it was higher at the central parts of the middle basin. In general, a pattern of high mud content in basins and low mud content in sills was found.

In terms of organic matter % in the sediments (Fig. 9), the highest % was recorded at station 1, outside Tysfjord, with 7.9%. The highest values in the Deep basin were found closer to the Drag slope, at stations 13 and 14 with 7.13 and 7.20% respectively. The lowest values were found at station 19 (Helland sill) and 29 (Musken sill) with values of 1.75 and 0.74% respectively. At the Middle basin, the % values in organic matter were relatively lower than in the inner-most basin. However, it is clear that, in general, values of organic matter were higher before the Helland sill and lower after, towards the head of the fjord. In general, a pattern of high organic content in basins and low organic content in sills was observed.

## **3.2. Infauna community**

### **3.2.1. Community composition**

A total of 206 taxa and 5378 individuals were identified belonging to 115 different families.

The overall highest abundances were recorded in stations 19, 20 and 22 (in the region of the Helland sill) with 302, 275 and 280 individuals respectively and in station 36, (at the inner-most station) with 280 individuals (Fig. 9). In general terms, the abundance of individuals tended to

decrease from the beginning of the deep basin towards the Drag slope. The maximum abundance in the deep basin was in station 8, with values of 234 individuals. The average abundances in the middle basin (119 ind./0.1 m<sup>2</sup>) and in the inner-most basin (115 ind./0.1 m<sup>2</sup>) were lower than in the deep basin (152 ind./0.1 m<sup>2</sup>). The lowest abundance in this study was recorded at station 10 of the deepest basin, with 54 individuals.

The phyla Polychaeta (1801 ind.) and Mollusca (2905 ind.) dominated along the whole fjord, followed by Echinodermata (238 ind.), Arthropoda (172 ind.), Sipuncula (165 ind.) and Cnidaria (71 ind.). Mollusca, however, were very poorly represented in the shallowest stations (29, 35 and 36). The number of Mollusca decreased progressively, especially in the middle basin towards the head of the fjord (Fig. 9). Polychaeta abundances, in contrast were more or less constant until the Musken sill, where afterwards they were higher. Echinodermata were only found in high abundances close to the Helland sill (Stations 18-23), while they were only found in low abundances within the basins. Cnidaria were almost exclusively recorded at the shallowest stations 29, 35 and 36. Arthropoda were relatively low in abundance in all fjord, with slightly higher abundances around the Helland sill and in the shallowest and inner-most stations. The phylum Sipuncula was practically anecdotic, with highest abundances at stations 21, 22 and 33. In general polychaetes and molluscs were dominating the basins while other taxa were more important at the sills and shallowest stations.

The Shannon index showed highest values in diversity at stations 19 and 28 with H' values of 3.46 and 3.32 respectively (Fig. 9). The lowest values in H' index were found at station 2 (1.70). While the shallowest stations, together with the middle basin stations had relatively high values in H' index, the deep basin and the outer-most regions of Tysfjord presented lower values. Accordingly, samples can be divided in two groups: shallow (depth<400m; H'>2.5) and deep stations (Depth>400m; H'<2.5). Also, the inner-most basin had low values in H'. In terms of Pielou's Evenness index (J'), the values were higher from the Helland sill and towards the inner parts. However, in general, they are lower going towards the outer parts.

The species richness (S) was high in the sills and the shallowest inner stations (Fig. 9). However, low values for S were recorded for the three main basins of the fjords. The species richness for polychaetes was lower in the basin stations than in the sills and for molluscs a tendency of decreasing towards the head after the Helland sill. Arthropoda and Echinodermata presented a comparatively lower species richness than the other two phyla mentioned above, with more or less stable values along the whole transect.

- Polychaeta:

In the outer stations and the Deep basin, the polychaetes from the families Chaetopteridae, Onuphidae and Siboglinidae were the dominating ones (Fig. 11). However, after the Helland sill,



a shift occurred and polychaetes from the families Capitellidae, Spionidae, Siboglinidae, Trichobranchidae and Amphinomidae became dominant. It is quite noticeable the large amount of

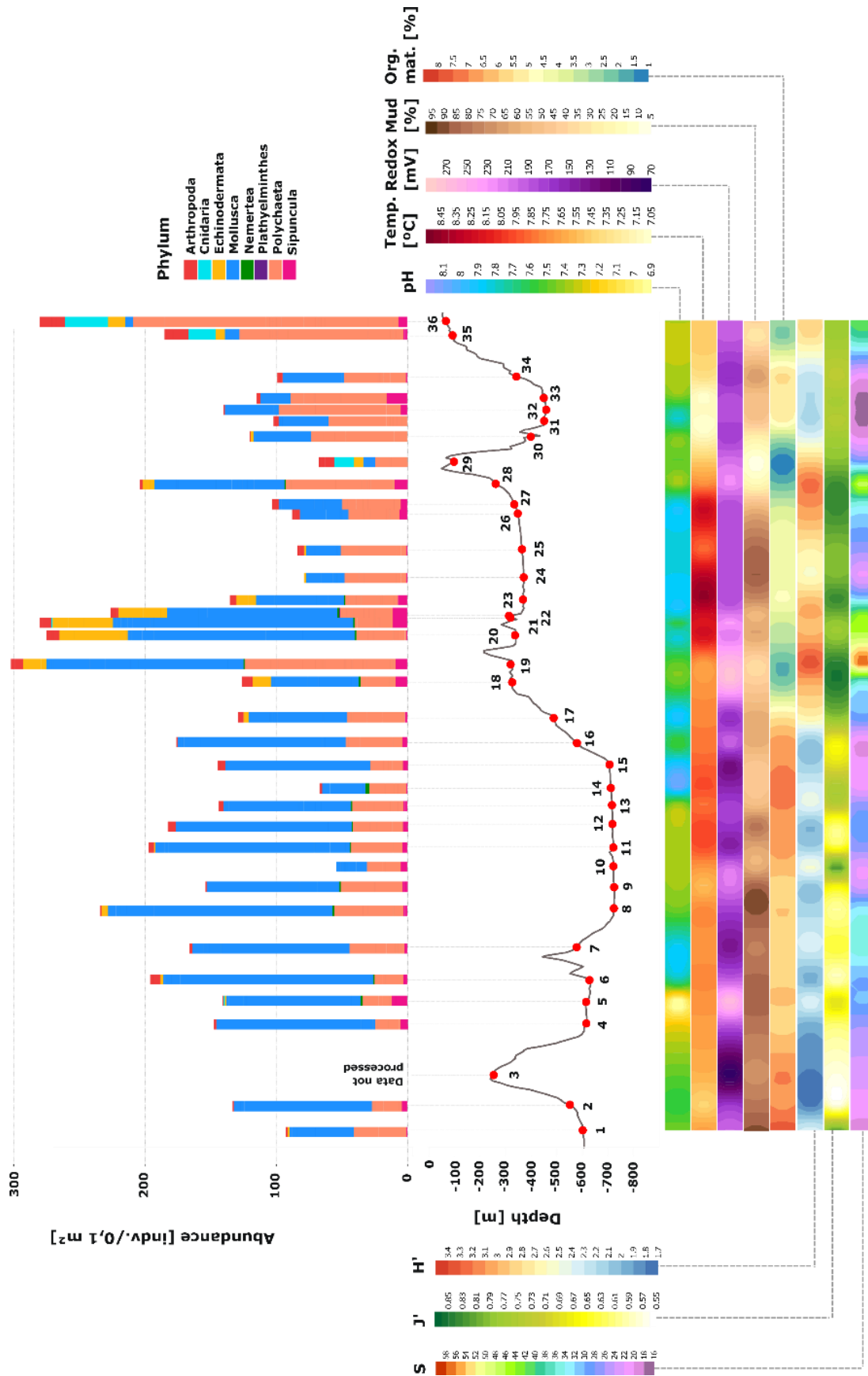


Figure 9: Profile of Tysfjord showing the sampling depths for each station. On top, abundance of individuals/0.1m<sup>2</sup> for each phylum. Colour scales at the rights show the values for the sediment environmental conditions, while the colour scales on the left show the diversity measurements for the community

different families at the stations from the Helland sill towards the inner-fjord in comparison with the deeper and outer parts (Fig. 11).

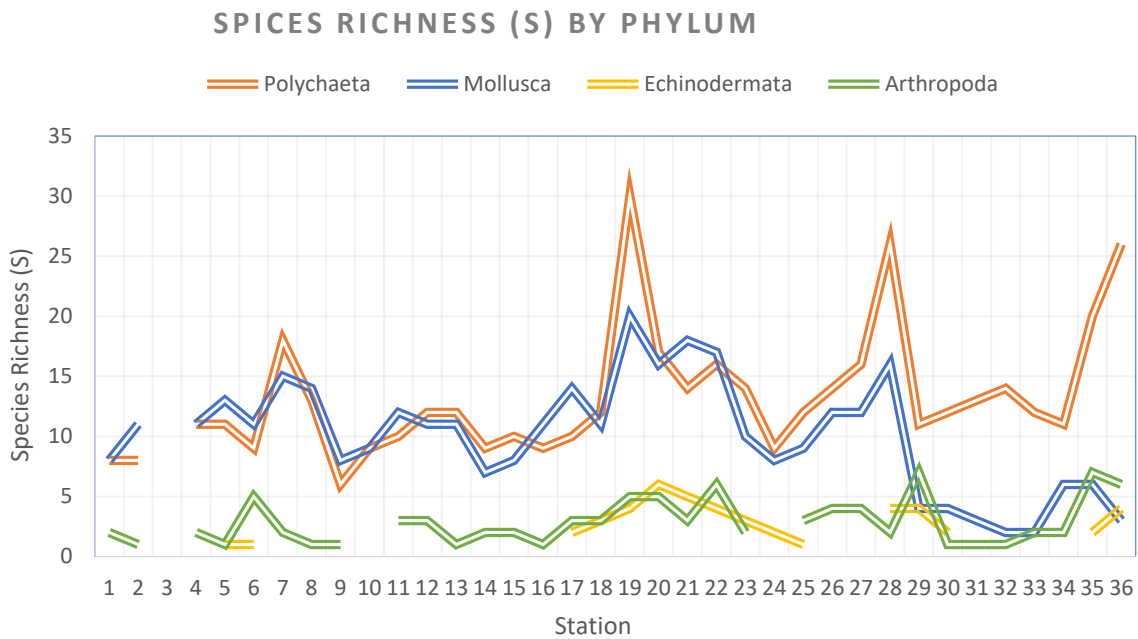


Figure 10: Species richness (S) for each phylum (Polychaeta, Mollusca, Echinodermata and Arthropoda) at each station.

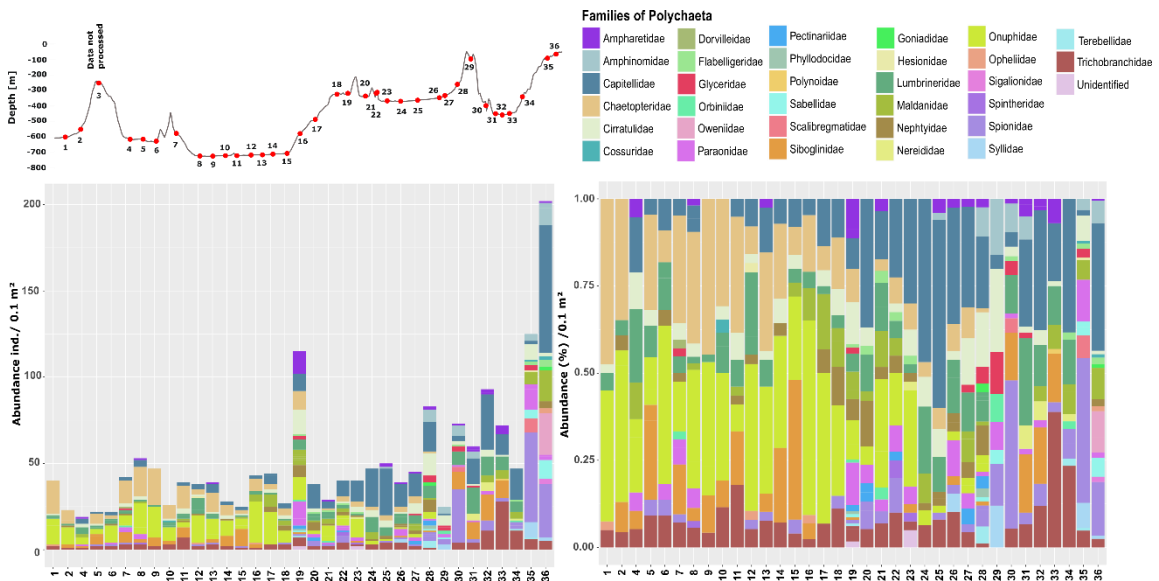


Figure 11: Abundance of individual/0.1m<sup>2</sup> (left) and relative abundance in % (right) for the families of Polychaeta in Tysfjord. Missing stations had no abundances.

By looking at the species level, the pattern for polychaetes looked quite similar to the one for families. In the deepest parts, from stations 1 to 17, the most abundant species were *Spiochaetopterus typicus*, *Paradiopatra fiordica* and *P. quadricuspis* (Fig. 12). After the Helland sill there was a noticeable increase in *Heteromastus filiformis* with the exception of stations 29, 30 and 35. At the extreme sides of the inner-most basins (stations 30, 35 and 36) there was a high abundance in *Prionospio cirrifera*. *S.typicus* was found in high abundances in the deep basin, had

intermediate abundances in the middle basin and it was completely absent from the inner-most basin. *Terebellides stroemi* was quite abundant at the inner-most basin, specially at the centre of the basin, together with *Siboglinum cf. ekmani* (Fig. 12). This last species was also found in most of the stations of the deep basin.

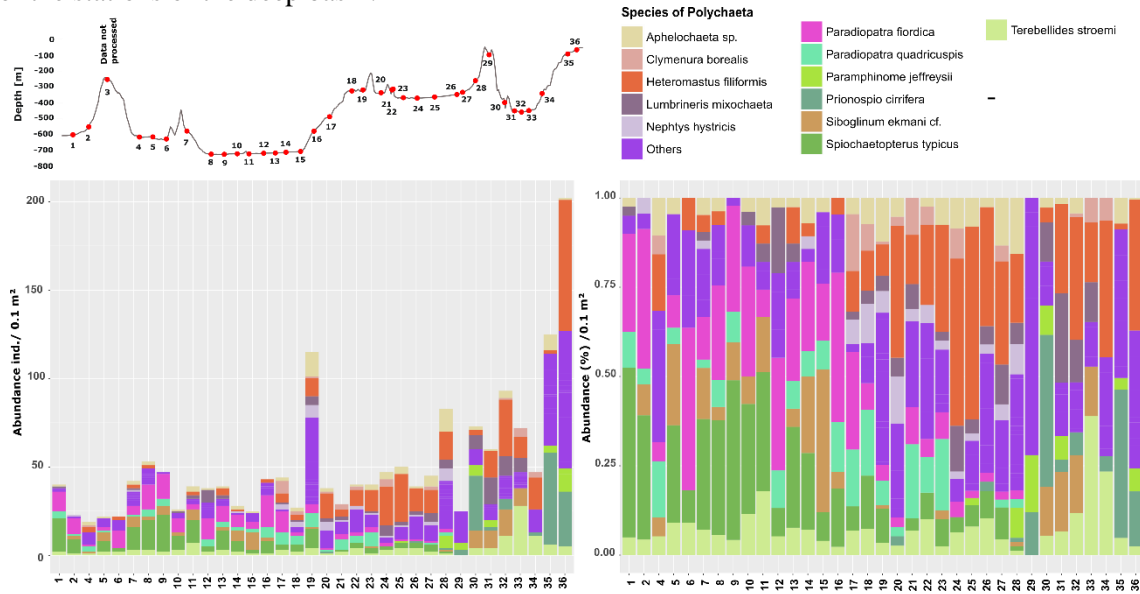


Figure 10: Abundance of individual/0.1m<sup>2</sup> (left) and relative abundance in % (right) for the most-abundant species of Polychaeta in Tysfjord. Missing stations had no abundances.

- Mollusca:

The family *Kelliellidae* was the most abundant from the Mollusca at the deepest basin and parts of the Middle basin (Fig. 13). However, from the station 24 until the head of the fjord, *Kelliellidae* was almost absent. The family *Thyasiridae* was the second one in abundance in all stations but was relatively low in the deep basin. This family was most abundant at stations 19 and 20 (Helland sill) and was almost the only one present in the inner-most basin (Fig. 13). *Nuculidae* were also present in all stations to some extent but were almost completely absent in

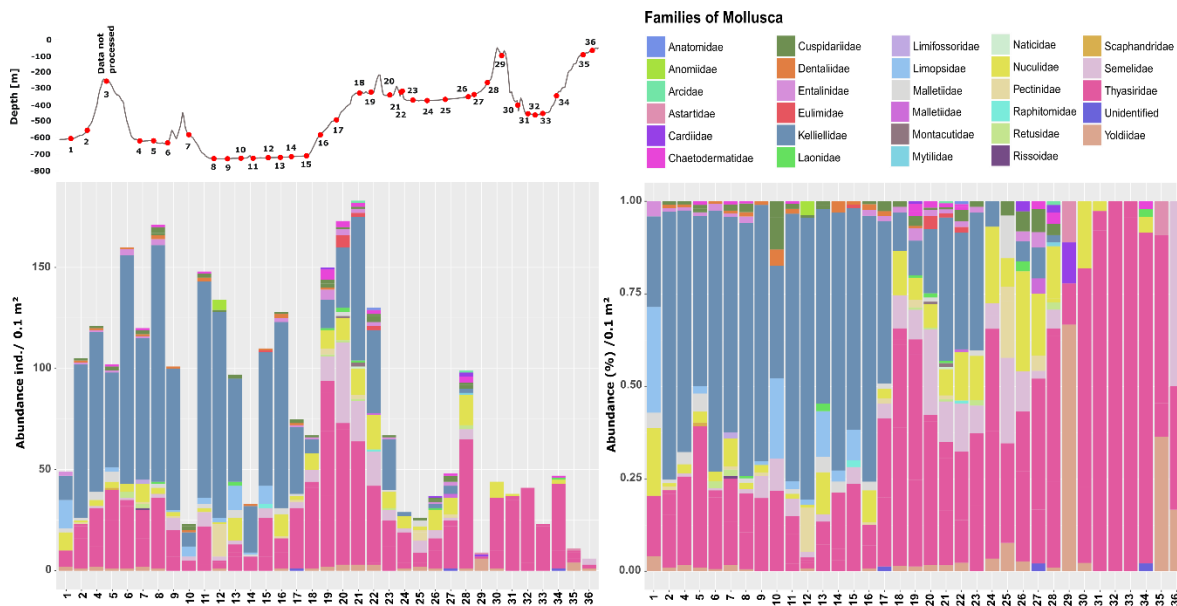


Figure 11: Abundance of individual/0.1m<sup>2</sup> (left) and relative abundance in % (right) for the families of Mollusca in Tysfjord. Missing stations had no abundances.

the inner-most basin (Fig. 13). Most of the molluscs observed in Tysfjord belonged to the class Bivalvia.

For the family *Thyassiridae* the species *Thyassira cf. rotunda* and *Thyassira obsoleta* were the most common (Fig. 14). *T. obsoleta* was the most common species of *Thyassiridae* outside of the inner-most basin, while in that basin, *T. cf. rotunda* was the most common and almost unique species present (Fig. 14). The species *Genaxinus eumyarius* was also a species of *Thyassiridae* mostly present in all stations from the Helland sill stations (from station 24) towards the outer parts of the fjord. However, this species was completely absent in the Inner-most basin (Fig. 14). The species *Aspalima cristata* was also somehow present in stations 1, 10, 13 and 15. *Abra nitida* was abundant in the stations adjacent to Helland (19, 20, 21 and 22) (Fig. 14).

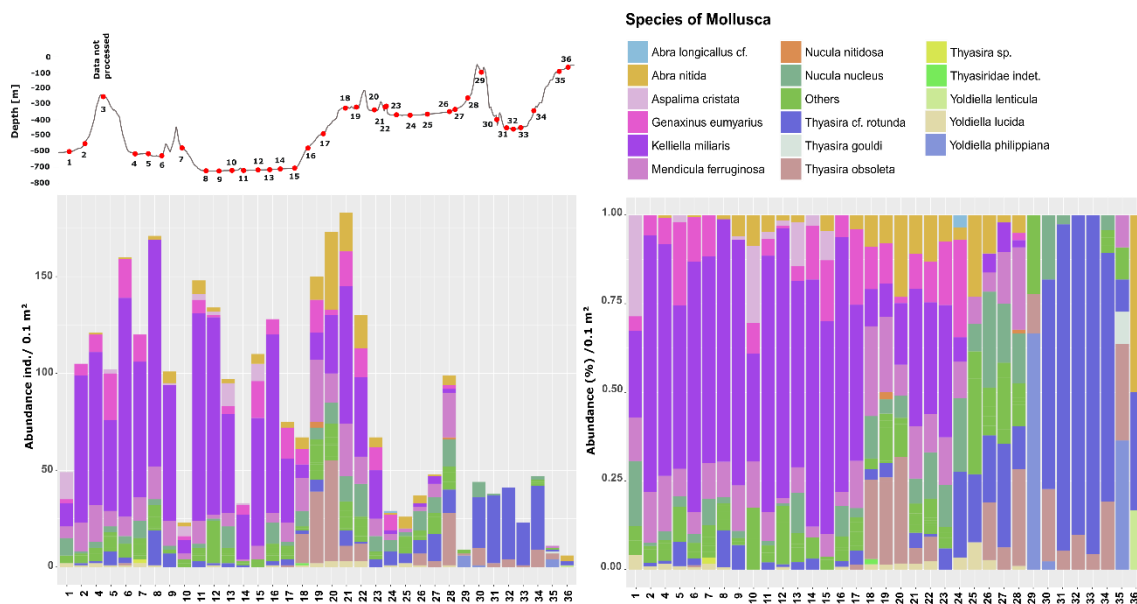


Figure 12: Abundance of individual/0.1m<sup>2</sup> (left) and relative abundance in % (right) for the most-abundant species of Mollusca in Tysfjord. Missing stations had no abundances.

- Echinodermata:

Regarding the families of Echinodermata, the brittle stars of the family *Ophiuridae* dominated in station 18, 19, 20, 21, 22, 23, 28, 29, 35 and 36 (Fig. 15). The family *Spatangidae*, which are irregular sea urchins, also dominated most of these stations. These two families appeared to be abundant in the sill and the shallowest stations but were almost absent at the basins (Fig. 15). In some of the deepest stations, together with stations close to the Helland sill and part of the Middle basin the *Amphilepididae* representatives were also present (Fig. 15).

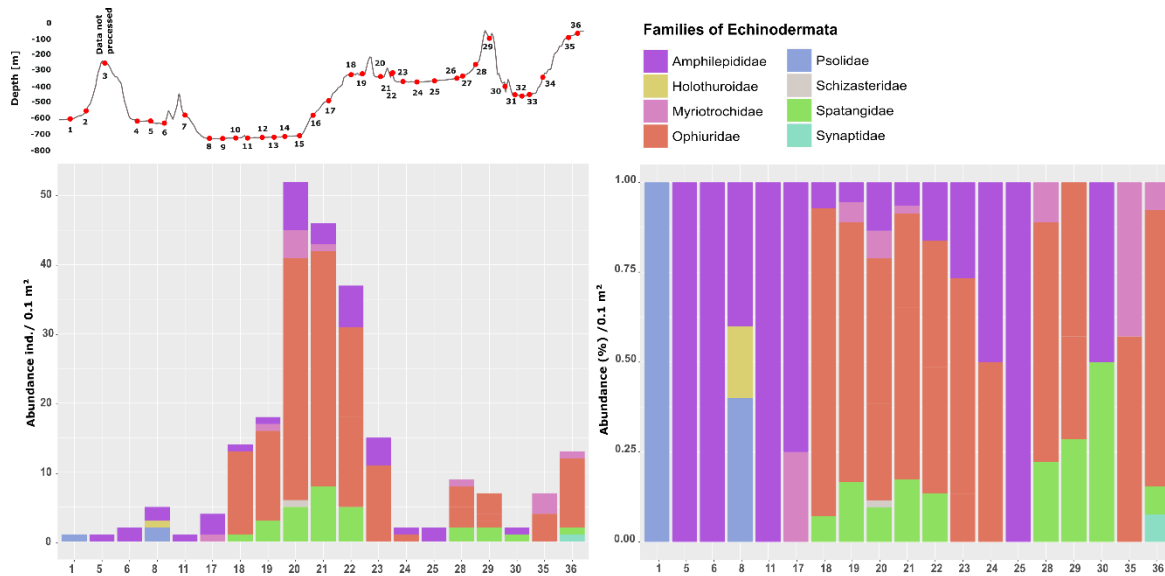


Figure 13: Abundance of individual/0.1m<sup>2</sup> (left) and relative abundance in % (right) for the families of Echinodermata in Tysfjord. Missing stations had no abundances.

Most of the families of Echinodermata were represented by only 1 species. Only in station 20, 21 and 22, the family *Ophiuridae* was split between *Ophiura carnea cf.* and *Ophiuridae juveniles* (Fig. 16).

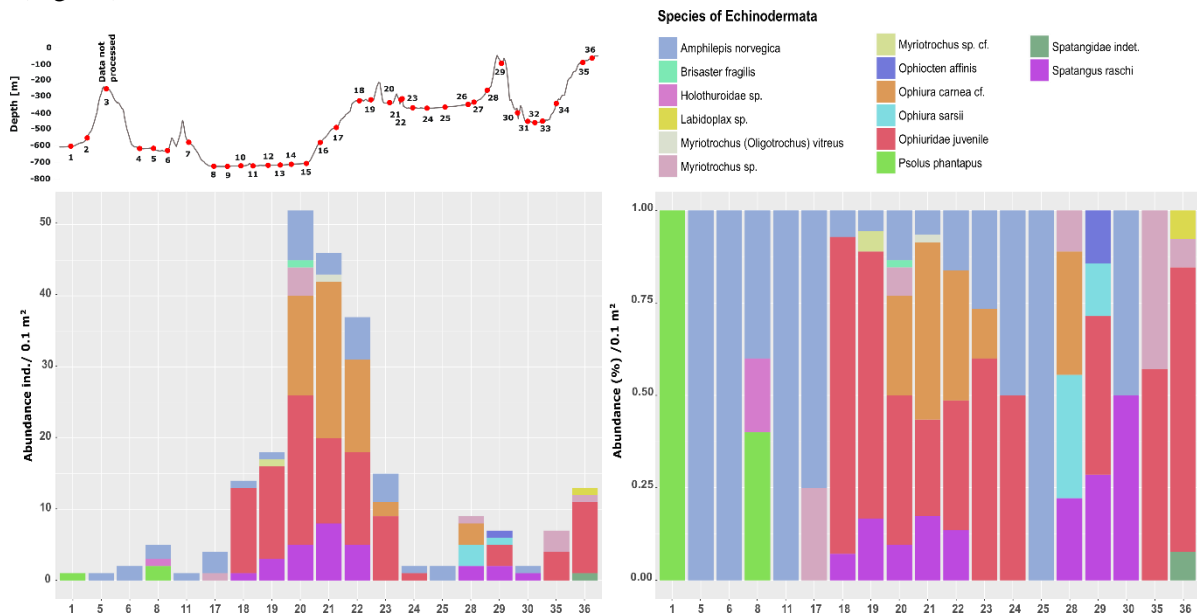


Figure 14: Abundance of individual/0.1m<sup>2</sup> (left) and relative abundance in % (right) for the most-abundant species of Echinodermata in Tysfjord. Missing stations had no abundances.

- Arthropoda:

The most abundant arthropoda families were the amphipoda *Eriopisidae* mainly at the Helland sill and inner-most basin and the ostracods *Cyprididae* at the sills and station 24 (Fig. 17). The

cummacea family Diastylidae was also quite abundant at the stations after the Helland sill towards the inner parts.

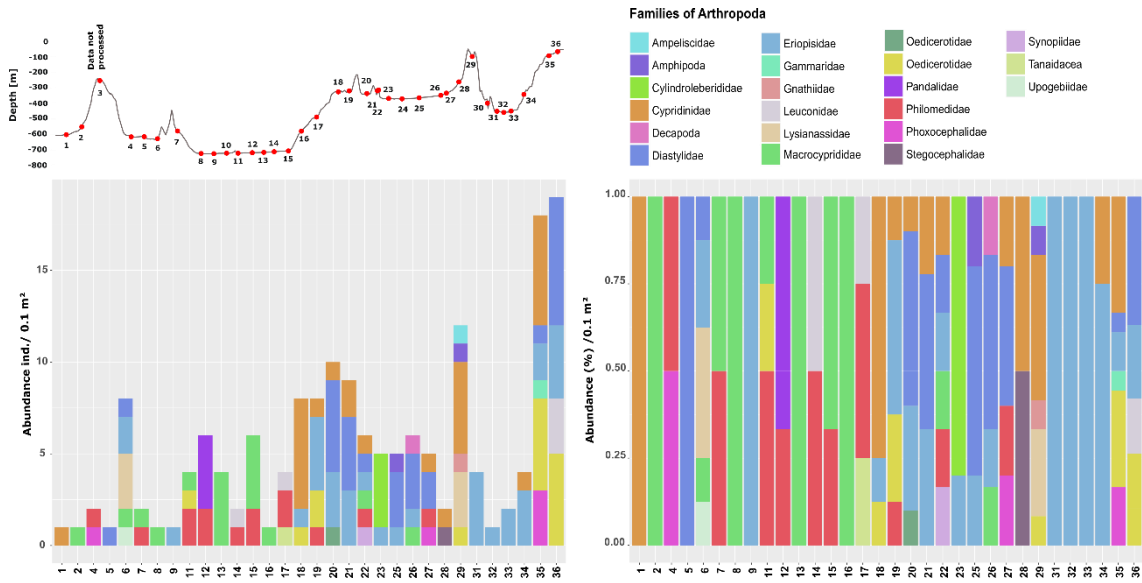


Figure 15: Abundance of individual/0.1m<sup>2</sup> (left) and relative abundance in % (right) for the families of Arthropoda in Tysfjord. Missing stations had no abundances.

The ostracod *Vargula norvegica* was the dominant species around the Helland sill and the Musken sill and was also abundant at stations 34 and 35 (Fig 18). The cumacean *Diastylis lucifera* was mainly present in the Helland sill and Middle basin, and also abundant at station 36. The amphipod *Eriopisa elongata* was the only arthropod species that was repeatedly found in the inner-most basin (Fig. 18).

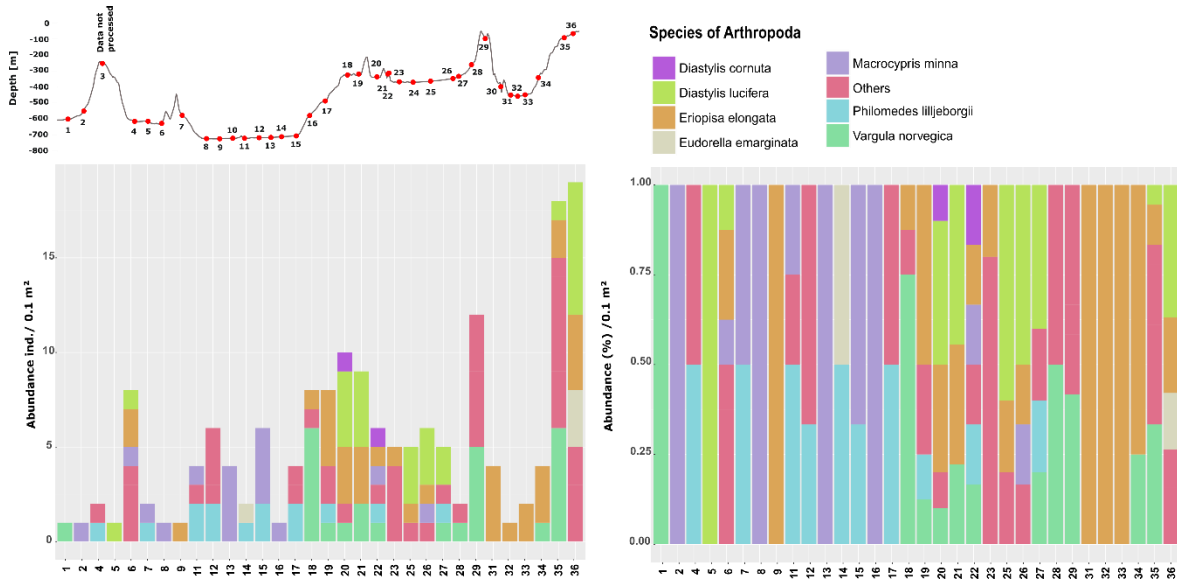


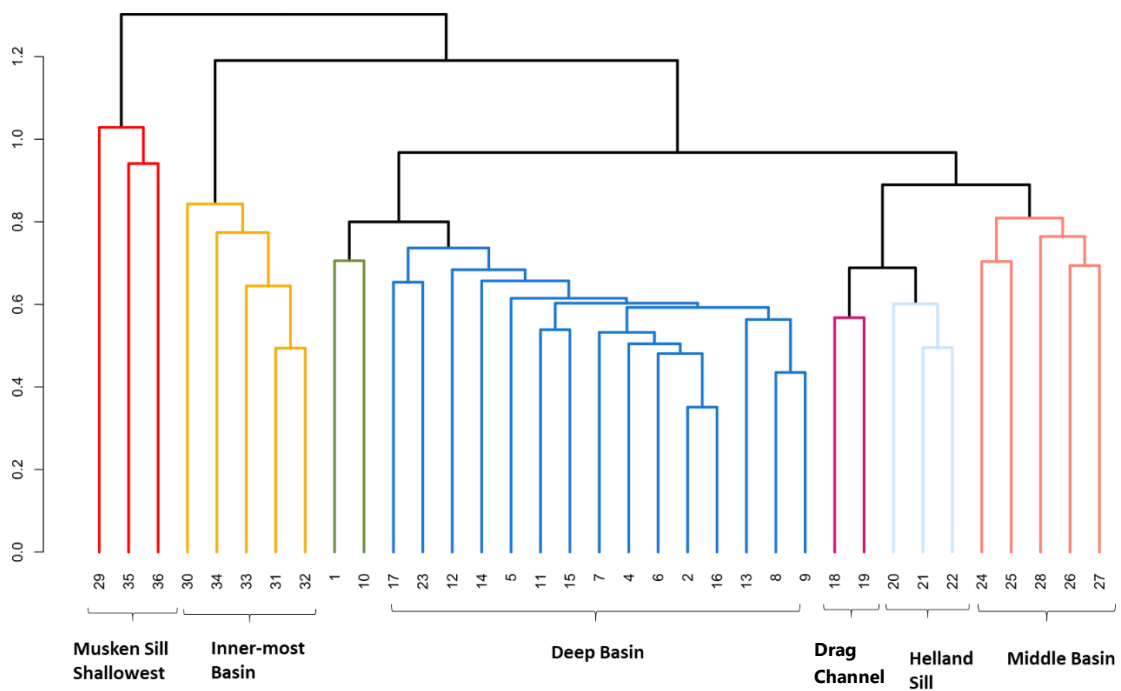
Figure 16: Abundance of individual/0.1m<sup>2</sup> (left) and relative abundance in % (right) for the most-abundant species of Arthropoda in Tysfjord. Missing stations had no abundances.

### 3.2.2. Spatial patterns

The cluster analysis showed 4 main branches based on the distances between samples which reflected the similarity based on the community species composition (Fig. 19). The outer stations

and the deep basin stations were grouped in one branch. This branch had some degree of similarity with the branch grouping the Helland sill stations and the middle basin. However, the stations of the inner-most basins were more different from those two branches mentioned, and the stations of the Musken sill and the shallowest inner-most stations appeared to be the more distinct ones from the rest.

The SIMPROF analysis applied to the Hellinger transformed data identified 7 significantly different groups (Fig. 19). The first group included the station from the Musken sill and the two inner-most stations of the transect, which correspond to the shallowest stations in the study. Another group was formed by the stations of the inner-most basin. The deepest stations (from the small basin and the deep basin (station 2 to 17 excluding 10 and including 23)) formed a consistent significant group. the Drag Channel stations clustered together, while the Helland sill (20, 21 and 22) formed another group. The stations from the Middle basin (24, 25, 26, 27 and 28) were significantly different from all the others and finally, station 1 and 10 formed a last single group.



**Figure 17:** Cluster analysis for the Hellinger transformed data. The vertical axis is the Euclidean distance. Different colours indicate the statistically significant groups obtained after the SIMPROF test (with 999 permutations and  $\alpha=0.05$ ).

The mean average of each species for the samples of the different cluster groups identified the 5 most abundant species which corresponded as well with the patterns observed for each station mentioned in the community species composition section (Fig. 20). Polychaetes and Molluscs were the most abundant for each cluster group.

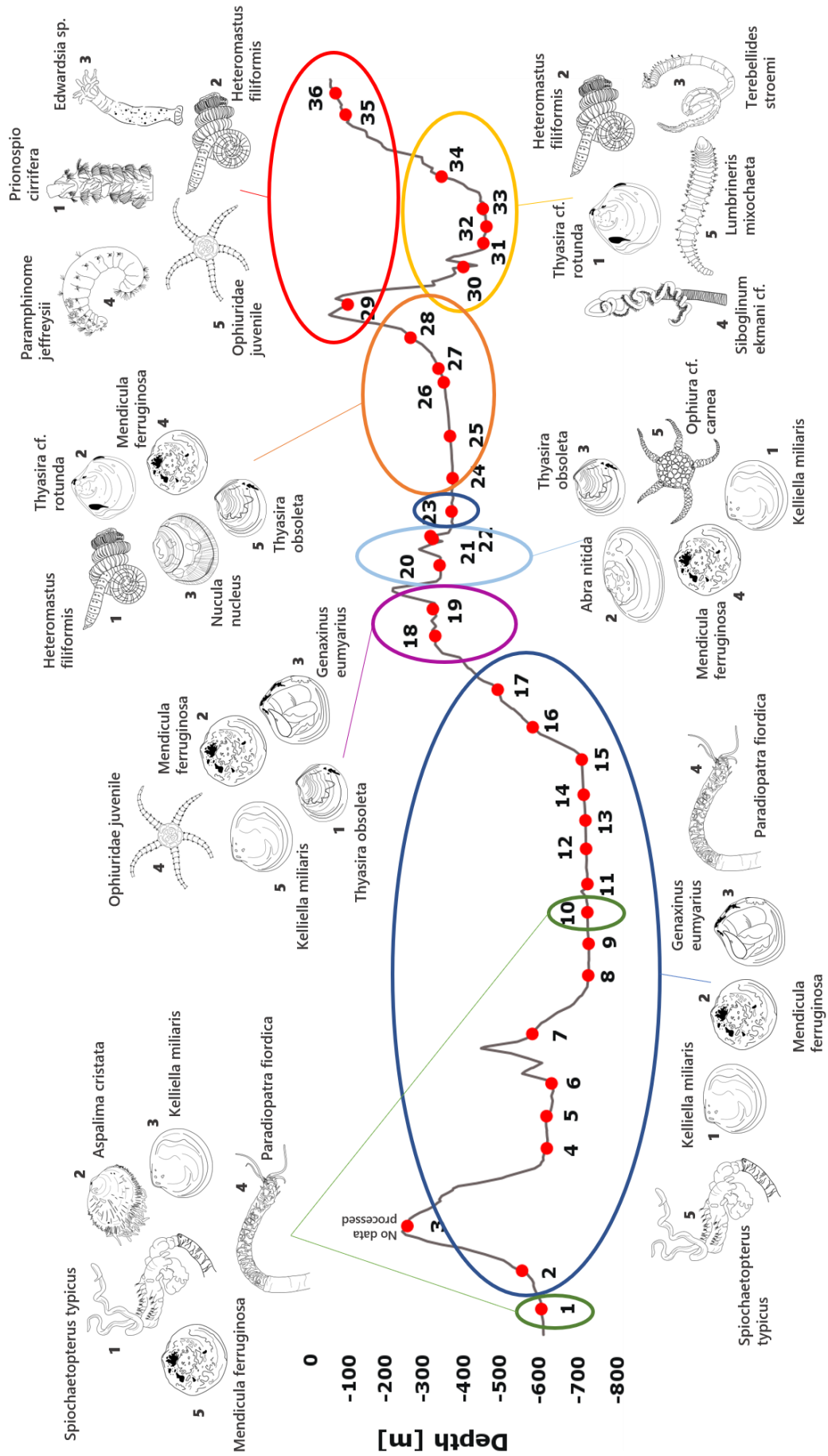


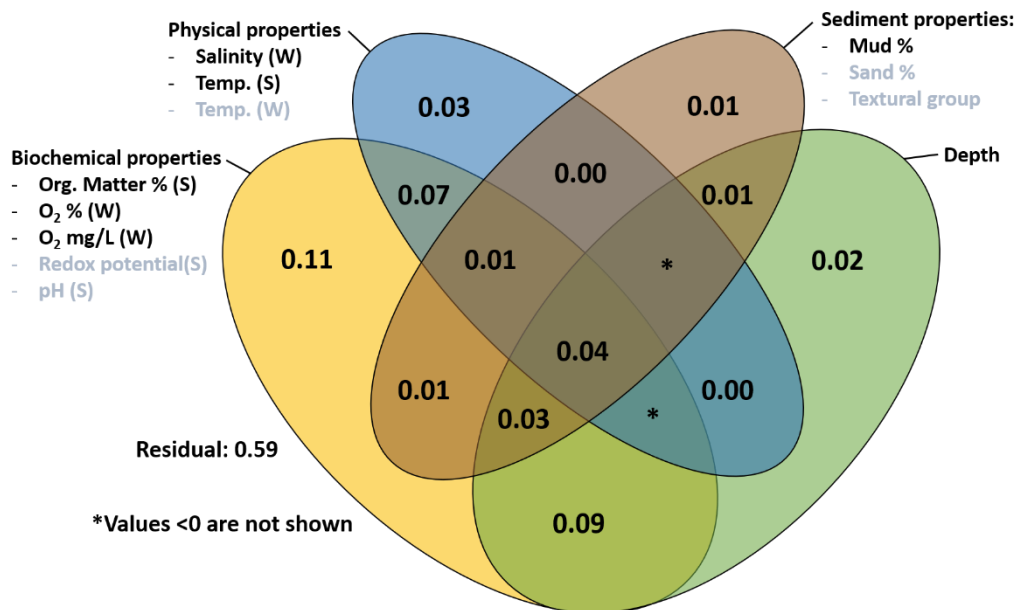
Figure 18: 5 top most abundant species for each cluster group. The values are calculated as the average mean for each species for each cluster group. The number next to each species indicates the order in abundance.



### 3.2.3. Environmental drivers

After applying the Forward Selection only some variables for each set of environmental factors were selected (Fig. 21). For the biochemical properties the organic matter % in the sediments the oxygen percentage (%) and dissolved oxygen (mg/L) of the bottom water were selected. The temperature of the bottom water was excluded from the physical properties set and for the sediment properties, the mud content (%) was the only one preserved. The depth factor was maintained as a single variable for its set.

The variation partitioning results (Fig. 21) showed that the biochemical parameters such as organic matter in the sediments and oxygen (dissolved % and mg/L) of the bottom water reflected a big part of the variance of the faunal patterns (36%) together with the physical parameters (3%) of salinity of the water column and temperature of the sediments and depth (2%). All together they explained 32% of the variance in the community composition. The mud % reflected a total 11% of the total variation when included together with all the other variables but was the one contributing the less by its own adding only to 1% of the variation. Altogether, the environmental data explained a total of 41% of the variance, while 59% of the variation remained unexplained.



**Figure 19:** Diagram showing the variation partitioning results for the environmental drivers. Each circle represents a set of environmental variables. When the circles overlap it means that both sets explain part of the variance of the community patterns. The number in each part of the circles indicate how much of the variance (in %) is explained. The residual value indicates that a 59% of the total variance for the community data is not explain by any of the environmental sets presented in this study.

## 4. Discussion

The results obtained after the analysis of the soft-bottom benthic communities revealed different patterns in the assemblages between basin and sill regions but also indicated that the macrofauna communities in each basin seem to be distinct. Molluscs and Polychaetes seemed to dominate the Tysfjord system and two main environmental drivers were suggested as the main structuring factors for the fauna dataset: the organic matter content in the sediment (%) and the oxygen conditions of the bottom water.

### 4.1. Faunal patterns - abundance, diversity and evenness

All basins in Tysfjord, independently of location along the outer/inner gradient, showed relatively low diversity measures (Shannon Wiener diversity ( $H' \log e$ ) ranging from 1.7 to 3.46) (Fig. 9).

Generally, the highest species richness was found at the shallowest stations (Helland and Musken sills and the two inner-most stations) (Fig. 9) which seems in contradiction with the findings of Holte et al. (2004) that suggested an increased infauna species richness with increasing depth in three north Norwegian fjords. However, Holte et al. (2004) only sampled to a maximum depth of 90 m in all fjords while the shallowest station sampled in our study was 88.7 m deep, indicating that this pattern may not be applicable to the deep environments of north Norwegian fjords. In fact, it is known that the basins of deep fjords such as Hardangerfjord and Sognefjord are generally poorer in species than other off-shore regions with similar depths (Fauchald, 1972; 1974). The deep basin of Tysfjord generally presented a higher abundance of individuals than the middle and the inner-most basins and the low evenness index ( $J'$ ) indicates that a few species were dominant (Fig. 9), especially the suspension feeder bivalve *Kelliella miliaris*, the thyasirid bivalves *Mendicula ferruginosa* and *Genaxinus eumyrius* and the tube-building polychaetes *Paradiopatra fiordica* and *Spiochaetopterus typicus*. (Fig. 20).

The changes in benthic diversity along the sampling transect in Tysfjord, with low values of  $H'$  (around 2.5) in stations deeper than ca. 400 m depth, together with low values in species richness (Fig.9), suggests that the environmental gradients associated with changes of depth or with the inner/outergradient of the fjord were influencing the fauna. Similarly, Rosenberg et al. (1996), identified a deep faunal assemblage of species characteristic of deep communities (>400 m) in the deep part of the Skagerrak, in the Norwegian Trench (with maximum depths of 700 m). They suggested that the main structuring factors for the communities in the deep Skagerrak were the sediment characteristics, sediment transport and accumulation rates. Since depth is a variable that co-varies with other environmental factors we could expect different environmental conditions for the deep basins of Tysfjord than for the shallow parts of the fjord. However,

together with depth, different drivers structuring the communities at each one of the three main basins could play a role, which will be discussed further below. Buhl-Mortensen and Høisæter (1993) reported a decrease in the richness of mollusca species along an outer to head gradient in a fjordic system in south-western Norway adjacent to the Norwegian trench. A similar trend is seen for the mollusca species in Tysfjord, with a species richness decline towards the inner-most basin (lowest value at the inner-most station) (Fig. 10). Spatial patterns and the according environmental drivers can differ between epifauna and infauna (Silberberger et al., in press), and it has to be kept in mind for the comparisons of this study with Buhl-Mortensen and Høisæter (1993), who conducted their study with epibenthic sleds.

Kędra et al. (2013) described a higher abundance and species richness in polychaeta species at the opening and central regions of Hornsund, an arctic fjord in the south of Svalbard, with lower values at the head of the fjord. In Tysfjord, however the *S* values for polychaeta species at the head were quite high (26 species at Stn. 36) (Fig. 10) and total polychaete abundance (Fig. 9, 11 and 12) seemed to increase from the mouth towards the head of the fjord. This does not seem to be in line with the patterns described by Kędra et al. (2013). However, fjords in the archipelago of Svalbard are relatively shallow (in the case of Hornsund the maximum depth is 260 m), which again raises the question whether the differences in the patterns observed for polychaetes, and other benthic taxa, are highly influenced by depth variations in Tysfjord, or if other abiotic factors are the ones really inducing these patterns. At the same time, it is worth mentioning that Hornsund is a fjord with a glacier in its head which could be causing the patterns described by Kędra et al. (2013), where they found that the polychaete assemblages were mainly determined by bottom temperature, sediment characteristics (grain size), and distance to the glacier.

#### **4.2. Linking the faunal patterns with the environment**

One of the main forcing drivers of fjordic ecological processes is the seafloor topography of the fjord (Burrell, 1988) which ultimately influences many other variables (hydrography, sedimentation rates, etc.) and to which benthic communities may respond accordingly. Since each fjord has unique topographic characteristics it is difficult to infer a general and universal theory to describe their ecological parameters. Even fjords belonging to the same geographical region, expecting similar environmental conditions, present marked differences in their benthic species composition (Larsen, 1997).

In Tysfjord, significantly different benthic communities suggest distinct environmental conditions between the three main basins and also for the shallowest parts of the fjord. The variation partitioning analysis indicates that these variations are mainly driven by the organic matter content in the sediments and by the oxygen conditions of the bottom waters (Fig. 21). Together with those variables, depth, salinity of the bottom water and sediment temperature are

also relatively important explanatory variables for the faunal patterns observed. The sediment grain size, in contrast, seems to be less important to structure the benthic communities in Tysfjord.

#### 4.2.1. The deep basin and the outer stations

The deep basin group was dominated by the subsurface suspension feeder (Holte, 1998) bivalve *Kelliella miliaris* (Fig. 20). This species is very common in Norwegian fjords below depths of 100m (Warén, 1989) and is susceptible to high rates of sediment deposition (Holte, 1998). *K. miliaris*, among other benthic species, is a typical representative of the Lusitanian-boreal species (Buhl-Mortensen and Høisaeter, 1993) and it is believed that this faunistic group migrated north following Atlantic water masses flowing into Norwegian fjords, replacing more arctic species, after the last glacial maximum (around 7800 yr BP). The fact that this species is especially common in deep water fjords indicates that silled fjords could act as a refugium for this bivalve. However, this species is also commonly found along the Norwegian shelf (MAREANO 2018). *K. miliaris* was also dominating at the group of the Litl-Hulloya basin and the Helland sill stations (stns. 20, 21 and 22) and was relatively abundant in the groups of stations 1 and 10 and the Drag Channel group. The 4 cluster groups mentioned above, therefore, seem to present a rather low sedimentation rate, which fits well with the rather little presence of rivers at the outer parts of Tysfjord and the low energy environment of the deep basin. This is also supported by the quite high abundance of the thyasirid bivalves *Genaxinus eumyarius* and *Mendicula ferruginosa* (Fig. 20). These deep-water species are suspension feeders and prefer well oxygenated sediments and do not tolerate H<sub>2</sub>S since they lack symbiotic bacteria in their gills (Dufor, 2005). The bivalve *Aspalima cristata*, which also dominated at the group of stations 1 and 10 (Fig. 20), may indicate a more heterogeneous composition of the seafloor sediments since this byssate species attaches to larger sediment particles and partly burrows into the sediment, reflecting a semi-infaunal mode of life (Oliver and Allen, 1980). This species was also found for the outer stations in the western Norwegian fjords studied by Buhl-Mortensen and Høisaeter (1993). This, might be reflecting a high patchiness in sediment composition due to the sediment supply from the fluvial system of Tysfjord.

Regarding the polychaetes, the deepest parts of Tysfjord were dominated by the omnivorous (Kucheruk, 1975; 1978) polychaete *Paradiopatra fiordica* (Fig. 20), which also appeared to dominate the deepest parts of Hardangerfjord (Husa et al., 2013). *Spiochetopterus typicus*, which was the most dominant species at stations 1 and 10, was found to dominate the deepest parts of Hardangerfjord in 1996 but was mostly eliminated during periods of anoxia, resulting in *P. fiordica* dominated communities years after (Husa et al., 2013). This indicates, nevertheless, that *S. typicus* and *P. fiordica* most likely characterises the polychaete assemblages in deep basin fjords (like in Tysfjord), but that they seem to have different tolerance to oxygen conditions. The

presence of *S. typicus* at the deepest basin of Tysfjord indicates that this basin might be well flushed year-round.

The relatively high domination of suspension feeders suggests that the fauna of the deep basin of Tysfjord is potentially exploiting readily available high quality marine organic matter transported from off-shore waters into the fjord deep basin and, potentially, also to some extent lower amounts of local primary production. The CTD results (Fig. 8) indicate a high entrainment of intermediary water above sill depth from the adjacent coastal waters of Vestfjord. Indeed, the import and export of carbon is highly influenced by the circulation patterns of the intermediary waters above sill depth in deep silled fjords (Burrell, 1988). The community of this basin also indicates a rather low turbid environment, since the suspension feeders dominate. The two cluster groups from the Drag Channel and the Helland sill (see below) also seem to fall into this environmental description.

#### **4.2.2. The Drag Channel and the Helland sill**

The Drag Channel stations, which were dominated by *Thyasira obsoleta*, seem to present a rather low polluted sediment despite of being close to the main settlement of Drag, where a quartz factory is located. This suspension feeder does not tolerate highly enriched environments and anoxic conditions (Dufour, 2005). However, the high abundance of the semelid *Abra nitida* (Fig. 20) of the adjacent cluster group from the Helland sill, especially in station 20, might be suggesting a relative high deposition of organic waste from the surrounding fish farms. This species is known to be a surface deposit feeder (Wikander, 1980) and may benefit of such a source of organic matter. Kutti et al. (2008) found a high productivity of this deposit feeding bivalves close to fish farms in western Norwegian fjords. This hypothetical fish-farm waste, however, does not seem to be reflected in the sediment organic matter results (Fig. 9).

#### **4.2.3. The middle basin**

The high presence of the capitellid *Heteromastus filiformis* in the middle basin group (Fig. 20) suggests, maybe, a disturbed environment. The high abundance of the bivalve *Nucula nucleus* indicates that a high sedimentation rate might prevail in this basin. These highly efficient detritus-feeding bivalves feed both at the surface and sub-surface of sediments collecting organic matter with their long palp proboscis (Morton, 1983). At the same time, they can easily remove mineral particles from the mantel, preventing the clogging of their respiratory system (Rhoads, 1974). *H. filiformis* has been reported to be a head-down deep subsurface feeding polychaete being very efficient in exploiting the organic matter from the deepest sediments, depositing their pellets at the surface which are richer in nutrients than the original sediments and, thus, making them readily available for deposit feeders (Holte, 1998) such as *N. nucleus*. In this cluster group, the suspensivore bivalves *K. milliaris* and *G. eumyrius* seem to be almost absent, while the still high

presence of *M. ferruginosa* and *T. obsoleta* suggests that these species might be somehow more adapted to high sedimentation. *Thyasira cf. rotunda*, which was also abundant in the middle basin, seems to prefer homogeneous sediments with rather low organic content (Keuning et al., 2011). In fact, this basin had the lowest content of organic matter from all three main basins, possibly due to a high accumulation rate of inorganic material (Fig. 9). Despite of being deeper than the middle basin and having more rivers running directly into it the Tysfjord inner-most basin presents coarser sediments (Fig. 9). This could only be explained if the fine size material discharged at the inner-most basin is transported to the middle basin along the highly stratified surface waters (see salinity CTD profile Fig. 8)). It is quite likely this stratification prevents the imminent deposition of the finest material entered in fjordic waters, transporting it over long distances with the freshwater plume (Burrell, 1988). Once at the middle basin, the salinity at the surface increases and this mixing of river and marine water triggers flocculating processes that enhance the settlement of sediment particles (Burrell, 1988). The high-sedimentation tolerant community (like *Nucula nucleus*) found in the middle basin supports the theory of large amounts of fine sediment being transported into this basin. The models from SINTEF for the upper 2 m layer of Tysfjord suggest a mean annual velocity of around 10 cm/s at the middle and inner-most parts flowing towards the mouth of the fjord with highest velocities (up to 20 cm/s) at the Helland sill. This means that the water runoff from the rivers of the inner-most part of Hellmofjord could flow into the middle basin in only 2 days and could enter the region of the deepest basin of Tysfjord in a bit more than 4 days. Therefore, the horizontal distribution and transportation of the riverine material discharged into Tysfjord must be highly impacted by this rather fast flow.

#### **4.2.4. The inner-most basin**

From the cluster analysis, it is clear that the inner-most basin group and the Musken sill/shallowest stations were very different from the rest of the fjord and also very heterogeneous in terms of fauna (Fig. 19). The colder temperature at the inner-most basin of about 6.5 observed in the CTD results suggests that its water could be retained by the shallow Musken sill, preventing the entrainment of warmer Atlantic intermediary water coming from offshore (Fig. 8). The low temperatures might be the result of vertical cooling during winter. Therefore, water stagnation may be an important factor structuring the fauna inhabiting this basin, which is supported by the lowest oxygen concentration found in the fjord (Fig. 8).

Below sill depth, water can be isolated in the basin of the fjord for a short period of time or longer periods. The biochemical consequences of water stagnation in fjord basins can include a reduction in dissolved oxygen and hypereutrophication of the basin (Inall and Gillibrand, 2010). This can lead to anoxic conditions in the sediment interface of the basin. In the most extreme, anoxia can lead to defaunation of the seafloor. Values lower than 1-2 mg/L of dissolved oxygen

are considered critical, but hypoxic conditions ( $< 3\text{mg/L}$ ) can also cause faunal changes (Diaz and Rosenberg, 1995). However, several studies suggest that changes can be induced with even higher oxygen concentrations, with values of 2-6 mg/L leading to oxygen deficiency (Wu, 2002; Molvær et al., 2007). The inner-most basin of Tysfjord, therefore, falls into this last category, with values between 4 and 6 mg/L (Fig. 8). However, oxygen values during late summer may be much lower than the ones found for May, leading to potentially anoxic conditions. At the same time, it is possible that during winter, when stratification is potentially of lower magnitude, denser water flows above the Musken sill and replaces the stagnated water either partially or completely. Whether the inner-most basin is subjected to periodic deep-water renewals is something to further investigate. No oxygen deficiency has been observed in the deepest basin of Tysfjord (this study; Gitmark et al., 2014), indicating good ventilation of the deepest and middle basins all year-round.

The poor oxygenated inner-most basin of Tysfjord was dominated by *Thyasira cf. rotunda* (Fig. 20). This thyasirid is known to have symbiont bacteria in their gills that helps the species to tolerate high amounts of  $\text{H}_2\text{S}$  in the environment, being able to occur in sediment almost depleted of oxygen (Keuning et al., 2011). The siboglinid polychaete *Siboglinum cf. ekmani* also could tolerate hypoxic conditions with the help of sulphur-oxidizing autotrophic symbiont bacteria in their postannular region (Southward et al., 1986). The abundant polychaete *Terebellides stroemi* is also known to tolerate low levels of oxygen (Bremec and Elias, 1999).

*H. filiformis* in this basin might be exploiting big particles of refractory material (Levinton 1989) deposited from the adjacent rivers, making it readily available for the surface deposit feeder *T. stroemi*, which collects detritus with its long tentacles (Fauchald and Jumars 1979). *H. filiformis* seems to cope well with a poor-nutrient food source with large amounts of indigestible and inorganic material (like lignin rich material) due to a low-cost energetic feeding mechanism (Taghon, 1989; in Neira and Höpner, 1994). The high amounts of plant detritus (leaves and pieces of wood) found in the samples of this basin supports this theory. At the same time, sinking kelp from the surrounding coast should not be discarded as potential high C/N carbon source for benthic fauna (Renaud et al., 2015). Especially, this basin has a quite long coastline in comparison with the narrow surface area of the basin itself (Fig. 2), which could have accumulated POM of sinking kelp detritus. The highly motile burrower polychaete *Lumbrineris mixochaeta*, which was also abundant in this basin, seems to be mainly carnivorous. However, some species of lumbrinerids have been reported to feed on plant fragments or detritus (Fauchald and Jumars, 1979). Whether in this case this species also feeds on the refractory material accumulated in this basin is an open question.

The inner-most basin benthic fauna composition seems, therefore, to be influenced by oxygen deficiency and relatively high amounts of rather refractory material in the sediments. This reflects

that the sill depth of a basin can play an important role determining the conditions of the deeper water and consequently the fauna living in it.

#### 4.2.5. The Musken sill and shallowest stations

The cluster group of the Musken sill and the two inner-most stations of Tysfjord were highly dominated by the spionid *Prionospio cirrifera* (Fig. 20). The distribution of this polychaete in Northern Norway seems to vary significantly with depth with high abundances recorded at 100 m depth in Ranafjord (Helland et al., 1994). The burrowing anemone *Edwardsia* spp. is reported to occur in association with spionid and maldanid polychaetes in Antarctic waters (Williams, 1981). It is known that the genus *Edwardsia* predates on relatively large prey like polychaetes, gastropods and even small benthic crustaceans (Oliver et al., 1982). It could be a possibility that this anemone feeds on the spionid worms abundant in these stations. This genus of anthozoa is also known for inhabiting brackish waters and is reported to be tolerant to low salinities (Shick, 1991). These stations may still have relatively high amounts of plant/kelp particulate organic matter, and the omnivorous sub-surface deposit feeder (Fauchalds and Jumars, 1979) amphinomid *Paramphinome jeffreysii* may be also utilizing this food source together with *H. filiformis*.

Some ophiurid species were also abundant in these last stations and in the Helland Sill and Drag Channel cluster groups (Fig. 20). Although Larsen (1997) observed a lower number of echinoderms in fjords when comparing to adjacent shelf areas, the shallowest parts of Tysfjord showed high abundances of this phylum. *O. cf. carnea* has a depth range of 40–2857 m (Simirnov et al., 2014) which means that potentially this species could also be found at the deepest stations of Tysfjord. However, the only ophiurid found in stations deeper than 400 m was *Amphilepis norvegica* (Fig. 16),, a species commonly found at the deep regions of the Skagerrak (Petersen 1915). This species, however, was also quite frequent at the shallower stations around the Helland sill. Maybe *O. cf. carnea* has a different preference for sediment composition, preferring coarser sediments, while *A. norvegica* might prefer a wide range of mud content in the sediments.

## 5. Conclusions

The present study showed that Tysfjord is inhabited by a benthic fauna characteristic of deep fjords, like the deepest fjords of Norway, Sognefjord and Hardangerfjord. Although depth may be an important factor structuring the benthic community of the fjord, it seems to do it in a secondary plane. In fact, the taxonomic diversity and species composition of soft-bottom communities in Tysfjord seem to be mainly determined by the oxygen conditions of the water and the distribution of organic matter in the seafloor sediments. While the oxygen content might be ultimately controlled by the sill depth, organic matter content depends on the carbon import from



off-shore waters into the fjord, the riverine supply of plant material, kelp from the shore line and/or local primary production. The stratification in the upper layer of the water-column might play an important role in the distribution of the sediments along Tysfjord, especially at the middle basin, where turbidity levels could be high. In this basin, only organisms tolerant to this condition may prevail, excluding the more suspension feeding types. Measurements of turbidity with the CTD or measurements with sediment traps could elucidate this theory.

However, each basin in Tysfjord is inhabited by different benthic communities, reflecting the prevailing environmental conditions in the basins. Since the organic matter seems to play an important role in the fjord benthos, care should be taken in monitoring possible organic enrichment from the fish farms and other potential anthropogenic sources. An additional input of organic waste products released by these facilities could modify this environmental driver, having a potential impact in the functioning and ecology of the soft-bottom communities of Tysfjord.

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