

Spatio-temporal changes in macrobenthic communities of the Beagle Channel



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ABSTRACT

Macrobenthic communities of the Beagle Channel (BC), Garibaldi Fjord (GF), and the Shelf off the eastern entrance of the Beagle Channel (S) have been investigated. Seven giant box corer stations from the “FjordFlux” (FF) expedition in 2022 were analyzed and spatial differences in abundance, biomass, species composition and diversity studied. The aim of this study is to assess the current state of benthic communities of the BC, adjacent fjords and channels and identify the environmental factors influencing their distribution. The sediment composition, which varies from very fine sediment in fjords, to coarser sediment towards the Atlantic, had a significant impact on the distribution of different feeding types in 2022. A significant separation between the macrobenthic communities of the GF, BC and S-clusters were found. Due to high sedimentation processes in areas closer to glaciers, the GF community was dominated by small, mud-dwelling polychaetes, whereas higher hydrodynamic stress resulted in a more diverse community in the BC and S. The second goal of the study is to investigate changes in benthic communities of the region due to global warming induced environmental changes. Resampling of multibox corer stations of the “Joint Victor Hensen Campaign” (VH) in 1994 facilitated the investigation of changes in macrobenthic communities more than a quarter century later. Analysis of temporal data revealed a significant separation of the communities in 1994 and 2022. However, species composition showed a similar pattern in both years, with annelids, molluscs and arthropods dominating the communities in 1994 and 2022. Significantly higher abundances were found in 2022, whereas biomass was significantly less than in 1994. Deposit-feeding polychaetes, such as Capitellidae, Spionidae, Paraonidae and Cirratulidae, and the deposit-feeding bivalve *Yoldiella* indet. dominated the communities in 2022. The study area is subject to pronounced seasonal variability, particularly in the planktonic system. Due to the different sampling periods, seasonal variation in reproduction patterns of macrobenthic organisms may explain the high abundances and dispersion of juvenile mussels, especially *Yoldiella* specimens, throughout the study area in 2022. In the past 28 years, global warming amplified the retreat of glaciers in the region, which led to an increased input of sediments into the marine system, shifting the benthic system towards dominance of small, better adapted species. It is expected that both seasonal and long-term changes in the region are responsible for the distribution patterns observed in 2022.

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Abbreviations

AWI	Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung
BC	Beagle Channel
CDI	Cordillera-Darwin Icefield
FF	FjordFlux
GF	Garibaldi Fjord
MT	Morphotype
PERMANOVA	Permutational Multivariate Analysis of Variance
RDA	Redundancy Analysis
S	Shelf off the eastern entrance of the Beagle Channel
SIMPER	Similarity percentages
VH	Victor Hensen

1 INTRODUCTION

The Chilean fjord region (42° S – 56° S) is considered a biodiversity hotspot with diverse habitats and niches for marine organisms resulting in comparatively high species richness (Försterra et al., 2017) in both the benthic and pelagic system (Arntz and Gorny, 1996). Nevertheless, only little is known about its ecology and biogeography (Försterra et al., 2017). The BC, which extends east-west for approximately 200 km, is part of the Fuegian system of fjords and channels of the Magellan region (Diez et al., 2009; Bruno et al., 2018). Located at the southern tip of South America, the Magellan region (54° S – 55° S) belongs to the sub-Antarctic region (Diez et al., 2009). The channels and interior areas connect the Pacific and Atlantic water bodies through a westerly flow towards the Atlantic Ocean. Since the Magellan region is a geologically young system, the benthic organisms inhabiting the waters are colonizers from the Atlantic and Pacific (Montiel et al., 2001). During the Last Glacial Maximum around 20,000 – 18,000 years ago, the Patagonian Ice Sheet, an extensive ice cap, almost completely covered the Magellan region (Clapperton, 1993). Glaciers formed a land barrier to the Atlantic Ocean, so that the first sea water incursions into the Strait of Magellan only took place after the glaciers retreated about 8,000 years ago due to gradual warming (McCulloch and Davies, 2001). The Northern Patagonian Icefield, Southern Patagonian Icefield as well as the Cordillera-Darwin Icefield (CDI) are still remainders of the Patagonian Ice Sheet (Davies and Glasser, 2012).

Nowadays, the fjords and channels of the Magellan region are under increasing anthropogenic pressure due to infrastructure and industrialization, exploitation of natural resources as well as exponentially growing salmon farming (Försterra et al., 2017; Iriarte, 2018). In this way, large amounts of organic matter and nutrients are introduced into the system, resulting in higher turbidity as well as increased sedimentation and eutrophication rates, which can lead to anoxic conditions on the sea floor (Buschmann et al., 2009). Patagonian glaciers and icefields are shrinking rapidly due to global warming, significantly contributing to sea level rise (Rignot et al., 2003; Davies and Glasser, 2012). Increased sedimentation in areas adjacent to glaciers (Arntz and Gerdes, 2011) can limit the light availability, lowering photosynthetic rates and therefore food availability for many macroinvertebrates (Hopwood et al., 2020). Moreover, high sedimentation rates can alter sediment texture and stability, bury larvae and adult organisms and clog their feeding and respiratory organs (Włodarska-Kowalczyk et al., 2007), all in all resulting in lower

benthic biodiversity close to glaciers (Sahade et al., 2015). Apart from the input of allochthonous organic matter (Quiroga et al., 2012), river-runoff and ice melt also lead to a high inflow of freshwater into the fjords and channels. This large amount of freshwater dilutes the water masses and causes relatively low salinity throughout the study area (Antezana et al., 1994). The region's lowest salinities in surface waters (27) were measured in front of glaciers in the BC (Antezana et al., 1994). Since freshwater is less dense than seawater, a buoyant brackish surface layer forms in the upper 10 to 15 m (Försterra et al., 2017). The amount of freshwater input underlies seasonal variations influencing salinity, temperature and depth of the surface layer throughout the year, whereas the properties of deeper oceanic waters remain relatively stable (Betti et al., 2021). Arntz and Gerdes (2011) predict climate change induced changes in the pelagic and benthic system in the region with marked biological consequences for the shallow-water fauna.

Benthic organisms are often used as indicators of ecosystem changes since they are relatively site-specific and therefore exposed to environmental changes. Global warming can change the latitudinal distribution of species, influence their reproduction patterns or lead to regime shifts in the community (Birchenough et al., 2011). Rising temperatures, ice mass loss and thereby changes in the light penetration can trigger sudden shifts in a community to a contrasting state (Scheffer et al., 2001; Rocha et al., 2015). Rapid changes in the community structure of two Arctic fjords with a significant increase of macroalgae cover due to rising temperatures were reported by Kortsch et al. (2012). Moreover, Sahade et al. (2015) found a shift in an Antarctic benthic community due to increasing sedimentation rates caused by glacier retreat from a filter-feeder dominated community to a mixed assemblage. The distribution of benthic organisms based on differing feeding types is highly dependent on sediment composition and



Figure 1 – Under water images taken during the FF expedition showing the different habitat types (from fine sand [left] to hard cliffs [right]) and the associated fauna in the study area of the Magellan region, Photos: Nils Owsianowski.

current regime (McCave, 1976a; Wilde, 1976). Whereas filter-feeding organisms such as many bivalves are dependent on water currents that ensure a constant food supply, deposit feeders such as many polychaetes inhabit sediments that are less exposed to currents since they feed on deposited organic matter and detritus.

The seabed of the BC and the adjacent fjords provides various habitats for benthic organisms, from fine sediment to steep cliff habitats (Fig. 1), resulting in a high patchiness of species composition, density and biomass of benthic organisms (Gerdes and Montiel, 1999). Polychaetes dominate the communities of the region followed by molluscs, arthropods and echinoderms (Gerdes and Montiel, 1999; Thatje and Mutschke, 1999). Great areas of the shallow bottoms are covered by the kelp species *Macrocystis pyrifera* and the tube forming polychaete *Chaetopterus variepedatus*, offering refuge and food for many invertebrate species (Diez et al., 2009; Försterra et al., 2017). On hard substrates, bivalve and brachiopod species can be highly abundant and form habitats, so called Marine Animal Forests in the fjords and channels (Cárdenas and Montiel, 2017; Försterra et al., 2017). These biogenic constructions serve as an important site for spawning, nursery, feeding or shelter (Försterra et al., 2017). In terms of biomass, molluscs account for 75 % of the total benthic wet mass in the BC (Gerdes and Montiel, 1999). Thatje and Mutschke (1999) found an exponential decrease in abundance, biomass and species richness of the macrobenthic community in the Straits of Magellan and the BC with depth between 10 – 1500 m. Low water currents and high sedimentation rates in fjords shape the benthic community structure (Thatje and Mutschke, 1999; Gutt, 2001) with a dominance of small, opportunistic, mud-dwelling Polychaetes (Quiroga et al., 2012). In general, communities adjacent to glaciers are less diverse compared to richer channel communities (Thatje and Mutschke, 1999). Montiel et al. (2005) state that due to high sedimentation rates macrofauna assemblages persist in a stage of permanent early recolonization.

Spatio-temporal changes in macrobenthic communities due to the described environmental conditions and changes in the region were investigated in this thesis. Samples were taken on board of the German research vessel METEOR (Fig. 2) as part of the “FjordFlux” project in January/February 2022. The project aimed to describe flux dynamics of organic matter in the Magellan region under melt conditions in order to understand ecosystem functioning. A combination of physical hydrographic, chemical as well as biological surveys focusing both on the planktonic and benthic communities was carried out to investigate the current environmental state of the system. The FF campaign took place 28 years after the “Joint Victor Hensen Campaign” allowing a



Figure 2 – Pictures taken during the FF expedition 2022 showing the research vessel METEOR in the study area (top, bottom left) as well as the Garibaldi glacier (bottom right), Photos: Diego Nahuelhuén Díaz | Centro IDEAL.

historical comparison of benthic communities. The scientific objective of the “Joint Victor Hensen Campaign” in 1994 was, on the one hand, to gather information about the marine biota in the Magellan region, since knowledge about marine life and the ecosystem as such was limited at that time and therefore of great scientific interest. On the other hand, a comparison of the fauna and flora between the Antarctic and the Magellan region as well as latitudinal clines in invertebrate population dynamics and physiology were investigated (Arntz and Gorny, 1996). Since then, the Magellan region has become a more interesting study site, partly due to the ongoing regional effects of climate change.

The analysis of the FF box corer samples will provide the chance to compare the findings of the VH expedition more than a quarter century later and will reveal factors shaping the benthic communities of the Magellan region today, as well as anthropogenic and natural impacts that lead to possible predicted changes. The objectives of this thesis are, on the one hand, to reveal the current status of benthic communities in the BC and adjacent fjords and channels and, on the other hand, to use this status quo for the historical comparison. All available data from 1994 are compared and supplemented by new measured values to create a more detailed basis for later comparisons. It is hypothesized that due to increasing sedimentation, deposit feeders are dominating the present-day communities, while a decline in the abundances of filter-feeders occurred.

2 MATERIAL & METHODS

2.1 Study site and sampling

The study area (53,28° S – 55,20° S) is located in the Magellan region, southern Patagonia (Fig. 3a) (Krock, 2022). Benthic samples were taken with a giant box corer during the FF expedition on board of the R/V METEOR in January and February 2022. A total of 38 stations were sampled (Fig. 3b). Seven of these stations are historical stations that were resampled and analyzed for this work. These stations are located in the BC and on the S (Fig. 4). The historical samples from 1994 were taken during the "Joint Victor Hensen Campaign 1994" in November 1994 with a multibox corer (Gerdes, 1990) (Fig. 5a); the data is available (Arntz and Gorny, 1996).

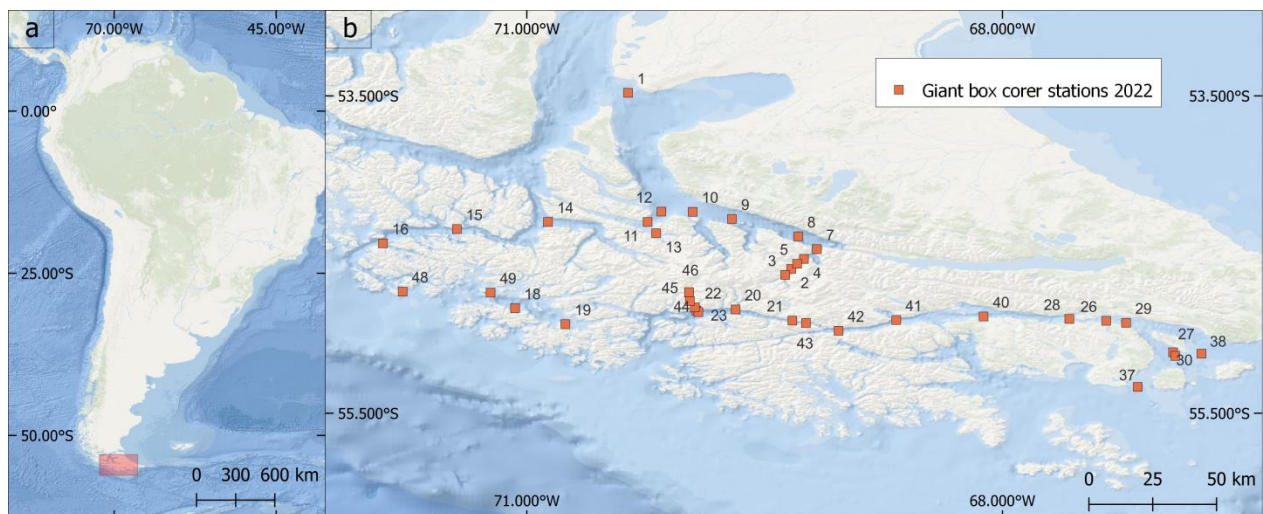


Figure 3 - Map of sampling stations in the study area: giant box corer stations of the FF expedition 2022 located in the Magellan region, numbers indicating the station ID.

Per giant box corer sample (0.5 m × 0.5 m × 0.6 m) (Fig. 5b) three contiguous Multicorer (MUC) cores with a diameter of 0.1 m each were taken ($0.00785 \text{ m}^2 \times 3 \text{ cores} = 0.024 \text{ m}^2$). This method was chosen to collect the same amount of sediment as with a multibox corer ($0.2 \text{ m} \times 0.12 \text{ m} = 0.024 \text{ m}^2$). The subsamples were sieved separately over 0.5 mm to extract the macrofauna. Samples were preserved on board in a 4% borax-buffered Formaldehyde-/seawater solution (Przeslawski et al., 2018). For sediment composition analysis, surface sediment samples (first 3 cm) from each giant box corer sample were taken with a 50 ml falcon tube and frozen at -20 °C until analysis. The samples were transported to Germany for further analysis.

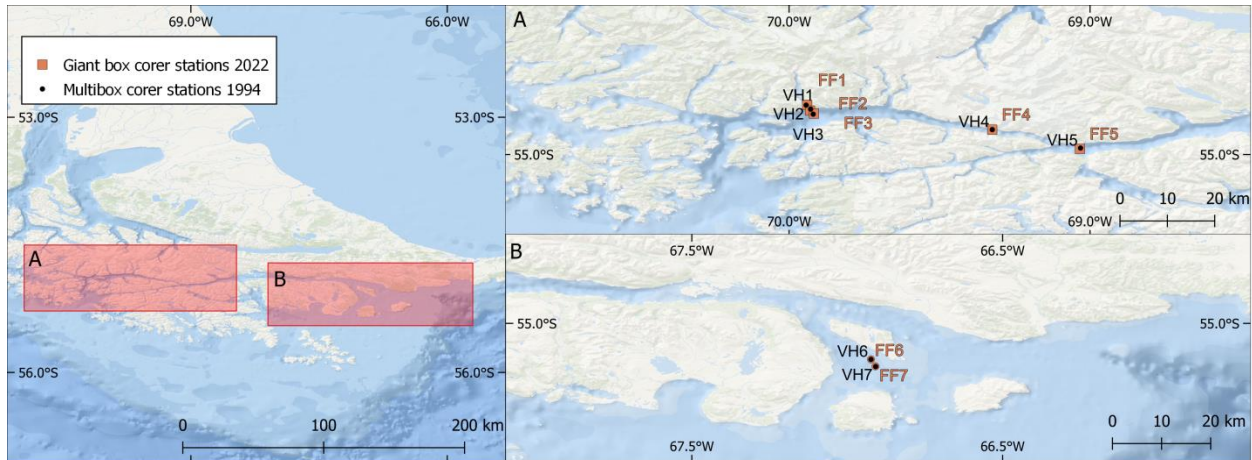


Figure 4 – Map of sampling stations in the study area: multibox corer stations of the VH expedition 1994 (black dots) and box corer stations of the FF expedition 2022 (orange squares) located in the BC (A) and on the S (B), VH1/FF1 located at the mouth of the GF, numbers indicating the station ID.

2.2 Sample processing

The macrofauna samples of the FF expedition were analyzed at the Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung (AWI) in Bremerhaven, Germany. To remove sediment residues and chemicals, the samples were rinsed over a 0.5 mm sieve and stained with Rose Bengal to simplify the sorting process. Half a table spoon of Rose Bengal powder was dissolved in approximately two liters of water. After placing the sample in the Rose Bengal/-water solution for about five minutes, it was rinsed again to remove excess color. Rose Bengal stains organic matter, allowing organisms to be distinguished more efficiently from sediment, empty shells and debris. After the rinsing process, the sample was filled into petri dishes. Organisms were sorted and identified preferably up to species level under a Leica MZ95 stereomicroscope (Leica Microsystems, Germany) and Zeiss Axioskop microscope (Carl Zeiss AG, Germany). If identification to species level was not possible and several taxa of one taxonomic unit were present, they were defined as different morphotypes

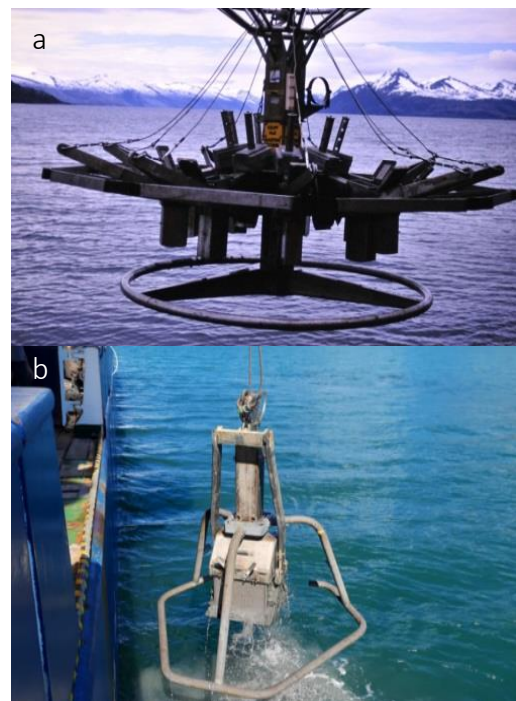


Figure 5 – Top: multibox corer, Photo: Wolf E. Arntz, bottom: giant box corer.

(MT). Pictures of the organisms were taken with a Leica IC80 HD camera (Leica Microsystems, Germany) and sent to experts of the corresponding phyla in Chile/Argentina for further identification. A list of identification literature and contacted experts is available (Appendix A1, A2). The organisms of each subsample were counted and weighed to obtain abundance (number of Individuals) and biomass (wet mass) data. Subsample size of 0.024 m^2 results in a conversion factor of 42 for calculating the abundance (Individuals $[\text{Ind.}]/\text{m}^2$) and biomass ($\text{g wet mass}/\text{m}^2$). Weighing was performed with a Sartorius CPA225D-OCE Competence Analytical Balance (Sartorius AG, Germany). The organisms were placed on a filter paper prior to weighing to remove excess water. If fragments could be identified, they were included for the determination of the biomass. Colonial organisms such as hydrozoans and bryozoans were only classified as present (p), but were counted as one individual for the statistical analysis of the data (Gerdes and Montiel, 1999). Since comprehensive sample sets in the study area are limited, samples were stored in 70 % denatured Ethanol after processing for additional taxonomic assessments on the organisms at a later stage.

2.3 Abiotic parameters

Depth (m), near bottom water temperature ($^{\circ}\text{C}$), dissolved oxygen near bottom (ml/l), salinity near bottom and salinity of surface water were measured with a Sea-Bird SBE 9 (Sea-Bird Scientific, USA) multi-probe for conductivity, temperature, and depth (CTD) on the FF expedition at each station. Salinity is expressed in the dimensionless Practical Salinity Unit (PSU). For station FF3, data on temperature, salinity and oxygen are missing because no CTD was deployed; however depth was measured with the ship sensors of R/V METEOR. In the abiotic parameters, 'near bottom' stands for the deepest water depth at which CTD measurements were taken at the respective station, a few meters above the seabed.

Granulometric analyses were carried out at the AWI in Sylt, Germany. The sediments were treated with hydrogen peroxide (H_2O_2) and acetic acid ($\text{C}_2\text{H}_4\text{O}_2$) prior to analysis to remove carbonates such as shell fragments and organic material. Grain sizes were measured with a CILAS1180 particle size analyzer (CILAS, France) using laser diffraction, determining grain sizes ranging between $0.04 \mu\text{m}$ and $2000 \mu\text{m}$. The results of the sediment analysis were evaluated using the GRADISTAT program (Blott and Pye, 2001). The sand fraction is defined smaller than 2 mm , the mud fraction smaller than $63 \mu\text{m}$. Folk and Ward method was used for sediment de-

scription (Folk and Ward, 1957). The C/N ratio and porosity of the sediment was measured at the AWI in Bremerhaven. For the porosity measurements, net weight of empty plastic weighing pans was determined. Three subsamples per station were measured and the mean value as well as the standard error calculated. Per subsample measurement, weight of 2 cm² of sediment was determined. Wet weight of the sediment sample was subtracted from the empty weight of the trays to obtain the net weight of the sediment. After drying at 60 °C for 48 hours, the samples were measured again to determine the net dry weight of the sediment. The difference between the net dry weight and the total wet weight of the sediment is the weight of the displaced pore water. The porosity is then calculated by dividing the weight of the displaced pore water by the net dry weight of the sediment. The result is a value between 0 and 1, with smaller values the less pore water present in the respective sediment. The dried sediment was pulverized and used for the C/N measurements. For the C/N analysis, 20 mg of sediment was weighed and packed into tin boats. Tungsten oxide (WO₃) served as a catalyst. Measurements were done with a VarioELcube Elemental Analyzer (Elementar GmbH, Germany). By combusting the sediment and detecting the resulting combustion gases, the C/N ratio of the sediment was quantified. The value obtained represents the ratio of carbon content to nitrogen content in the sediment sample.

2.4 Spatial data analysis

Maps of the study area and sampling locations were created in the Geographic Information System software QGIS 3.22.1. With the software Ocean Data View 5.3.0 the CTD data were analyzed and maps of the spatial differences of the abiotic parameters created. Microsoft Office Excel 2010 was used to create data tables of the raw abundance and biomass data; RStudio 4.0.3 was used to perform the transformation and statistical analysis of the data.

Taxa richness represents all taxa found in all three subsamples of a station. Since not all organisms were determined to species level, the term taxa richness (S) is used instead of species richness (S) in this work. Structure of the taxa lists is based on hierarchical classification according to Ruggiero et al. (2015). Biotic parameters were calculated from total abundance data of each subsample and the mean value of all subsamples of a station was used to obtain the mean abundance (Ind./m²), biomass (g wet mass/m²) and mean value for biodiversity indices (\pm standard error). Shannon index (H'), Pielou's evenness index (J) and Margalef's richness index (d) were chosen to assess biodiversity and community structure. The Shannon index (H') is a measure of biodiversity, representing the degree of diversity within a group of taxa. It is calculated as the ra-

tio between the number of individuals of a taxon to the sum of all individuals in the respective study area (Shannon, 1948). H' increases with higher taxa numbers (S) and increasing evenness (J), i.e. with increasing equal distribution of the relative abundances of the taxa. H' can range between values of 0 and $\ln(S)$, with values close to zero indicating low species diversity. A community is considered low in diversity if it is dominated by only a few taxa. Pielou's evenness (J) expresses the distribution of individuals among taxa (Pielou, 1966). J can take values between 0 (unequal distribution of individuals among taxa) and 1 (equal distribution). Since sample size can vary between stations and samples, Margalef's index (d) attempts to compensate for the effects of samples size (Margalef, 1958). Number of taxa (S) is divided by the natural logarithm of the number of organisms in the respective sample. Values close to zero indicate that only a few taxa are present in the sample, while higher values indicate higher taxa diversity.

Strong imbalances between highly abundant and rare taxa were adjusted by fourth root transformation of the abundance data prior to analysis. Non-metric multidimensional scaling (nMDS) based on the Bray-Curtis distance metric of abundance data of all subsamples of the FF stations was conducted to investigate clustering of the associations sampled at the stations (Bray and Curtis, 1957). Bray-Curtis distance was used, because it is well suited for heterogeneous abundance data with many zero value gaps. The stress value shown in the nMDS plots indicates how well the relationships between the assemblages of the stations, respectively their similarities, can be depicted in the two-dimensions of the nMDS plot. Stress values < 0.05 are considered as an excellent, stress < 0.1 a good and < 0.2 still a potential useful two-dimensional representation of the data (Clarke and Warwick, 2001). A Permutational Multivariate Analysis of Variance (PERMANOVA) was conducted to test for significant differences between the clusters. The null hypothesis H_0 , that there are no differences between the groups, is rejected if the calculated p-value is less than the significance level. The significance levels < 0.05 *, < 0.01 ** and < 0.001 *** were chosen. The F statistic is a measure of the strength of the grouping on the variance of the data, with a higher F-value indicating greater variance between the identified groups (Anderson, 2001). A hierarchical cluster dendrogram was conducted based on Bray-Curtis dissimilarities and Ward's agglomeration method. The ward.D2 method of the 'vegan package' in RStudio 4.0.3 was chosen, to minimize dispersion within groups (Murtagh and Legendre, 2014).

To determine taxa significantly associated with the predefined clusters, an Indicator species analysis was conducted using a multi-level pattern analysis. In the model, A is defined as the specificity reaching the value 1 when the respective taxon occurs only in the tested cluster. If

the indicator taxa are present in all stations/subsamples of the cluster, the fidelity B reaches the maximum value 1 (Dufrene and Legendre, 1997). Similarity percentages (SIMPER) analysis was performed to identify the discriminating taxa between clusters based on Bray-Curtis dissimilarities (Clarke, 1993). Shown are the cumulative contributions of each taxon up to 30 % of dissimilarity as well as the results of the pairwise PERMANOVA, testing for significant differences in community composition between clusters ($p = 0.05$). Pairwise PERMANOVA was as well conducted to test for significant differences between biotic parameters of the clusters. Redundancy Analysis (RDA) was carried out (Legendre and Legendre, 2012) to visualize the influence of environmental variables on the composition of the macrofauna communities. The direction and strength of the relationships are represented by arrows of distinct length. For standardization prior to RDA, abundance data were Hellinger-transformed and environmental variables were Z-transformed (Milligan and Cooper, 1988; Legendre and Gallagher, 2001). To test which environmental variables had significant effects on species composition, an envfit-analysis was carried out with the R-function envfit of the 'vegan package'. Since the first two axes explained most of the variation, only RDA axis 1 and 2 were displayed. Despite the correlations between the environmental variables, all parameters are depicted for visualization of interrelationships. The significances of correlations between the biotic and abiotic parameters were tested and are shown in a correlation matrix.

2.5 Analysis of temporal data

For the historical comparison, the 1994 macrofauna dataset is referred to as "Victor Hensen (VH)" and VH stations; 2022 as the "FjordFlux (FF)" dataset and stations of both years were numbered accordingly. As the number of multibox corer replicates varied between stations, three replicates per VH station were selected for better comparability of the VH and FF data. To ensure a representative and unbiased selection of multibox corer replicates, three replicates per VH station were selected in a randomized manner using the Analysis ToolPak in Microsoft Office Excel 2010.

The FF dataset was combined and split into the 34 defined taxonomic groups used by Gerdes and Montiel (1999). In 1994, "Vermes" was used for the classification of worm-like organisms that could not be grouped into any of the other taxonomic units. Although Vermes is no longer used as a taxonomic unit nowadays, it has been retained in the VH dataset for comparabil-

ity reasons, and worm-like taxa such as Phoronida, Nemertea and Oligochaeta of the FF dataset which could not be assigned to the other taxonomic units were grouped herein. The biotic parameters for the FF macrofauna data were recalculated because higher taxonomic levels were used for the historical comparison according to the available data and taxonomic units of 1994. For this reason, two different values for the biotic parameters calculated for the two different taxonomic levels are presented for the year 2022 in Chapter 3.2 and 3.3. The preparation of the taxa list, calculation of the biotic parameters, nMDS and hierarchical clustering were conducted as described in Chapter 2.4. Boxplots were created to investigate differences in the distribution of abundance and biomass among the most abundant phyla.

3 RESULTS

Results of the macrofauna community analysis of the FF expedition are described in Chapter 3.1, followed by the historical comparison of the VH and FF data in Chapter 3.2. To describe the spatial differences in the macrofauna community in 2022, a detailed dataset was created and the biotic parameters were compared between stations. Biotic parameters were recalculated for the temporal analysis due to the higher taxonomic classification based on the taxonomic units from 1994. Therefore two different values for the biotic parameters are presented for the two different taxonomic levels of the macrofauna data from 2022 in Chapter 3.1 and 3.2.

3.1 Spatial analysis

3.1.1 Abiotic parameters

Table 1 – Abiotic parameters and sediment composition of the FF stations: DSHIP ID, latitude (°S), longitude (°W), water depth (m), temperature near bottom (°C), salinity near bottom (PSU), dissolved oxygen near bottom (ml/l), fraction of sand particles < 2 mm (%), fraction of mud particles < 63 µm (%), median grain size of sediment particles D_{50} (µm), fraction of carbon C (%), fraction of nitrogen N (%), C/N ratio, porosity (standard error is given in parentheses) and description of sediment characteristics based on the Folk and Ward method. (*no CTD data available at station FF3, water depth measurement of the research vessel).

	FF1	FF2	FF3	FF4	FF5	FF6	FF7
DSHIP ID	44	22	23	21	42	27	30
Latitude (°S)	54°50.03	54°51.18	54°51.77	54°55.00	54°58.85	55°07.00	55°08.35
Longitude (°W)	069°56.40	069°55.82	069°55.06	069°19.50	069°02.01	066°55.40	066°54.53
Depth (m)	91	181	198*	187	198	107	107
Temperature (°C)	6.25	7.78	×	7.84	7.98	8.53	8.58
Salinity	30.93	33.17	×	33.11	32.32	32.58	32.57
Oxygen (ml/l)	4.41	6.03	×	5.9	5.75	5.91	5.9
Sediment composition							
Sand (< 2mm) (%)	1.2	1.7	4.9	20.3	23.4	28.6	68.0
Mud (< 63 µm) (%)	98.8	98.3	95.1	79.7	76.6	71.4	32.0
D_{50} (µm)	10.14	12.93	11.92	29.59	24.26	43.29	77.53
N (%)	0.15	0.13	0.15	0.05	0.08	0.24	0.08
C (%)	1.38	1.08	1.22	0.43	0.82	3.88	1.61
C/N	9.37	8.53	8.19	9.14	10.11	16.15	19.08
Porosity	0.59 (0.025)	0.58 (0.015)	0.59 (0.043)	0.87 (0.016)	0.80 (0.013)	0.80 (0.014)	0.70 (0.030)
Description (Folk and Ward Method)	medium silt	medium silt	medium silt	coarse silt	coarse silt	coarse Silt	very fine sand

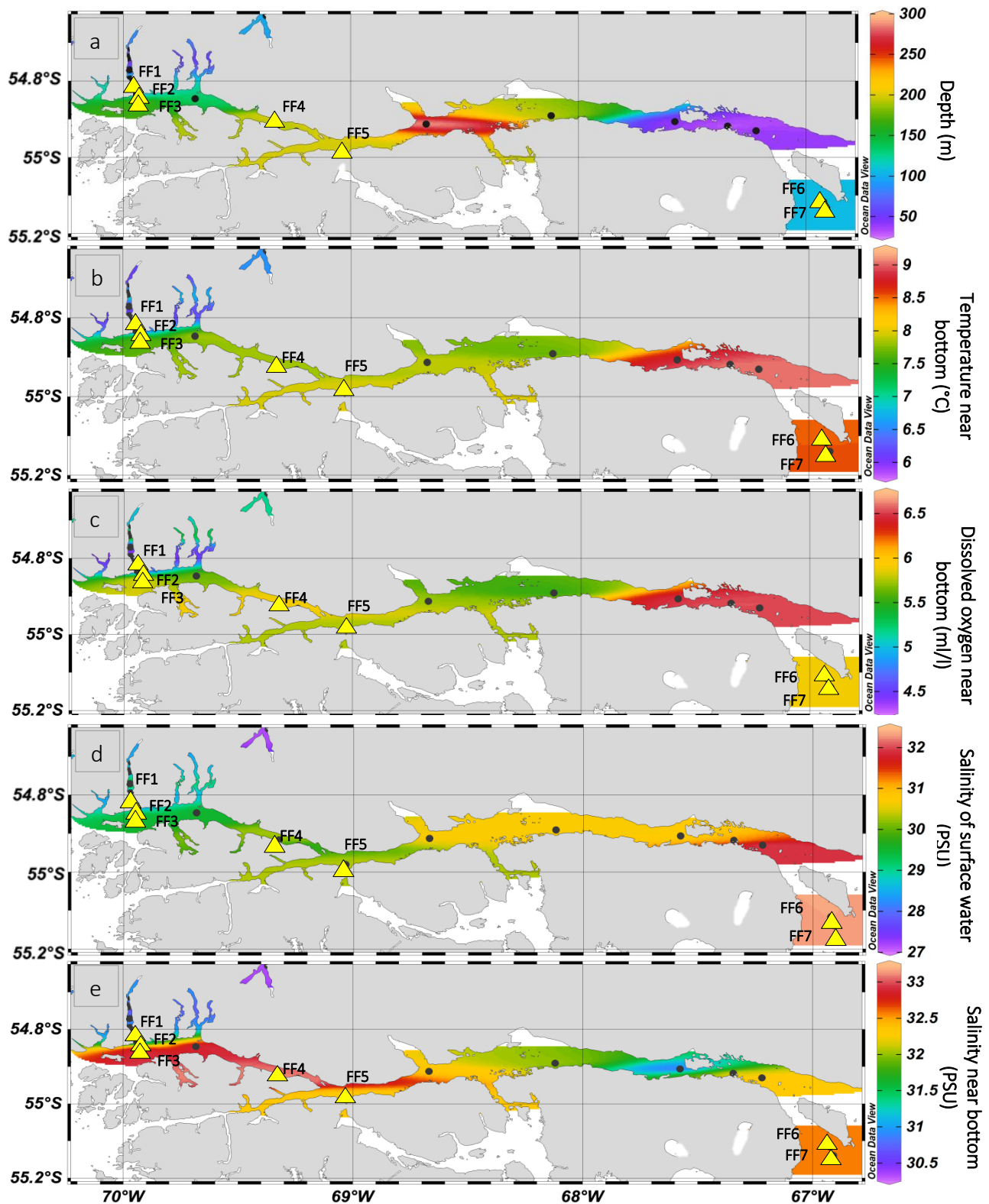


Figure 6 - Maps of the abiotic parameters of the FF stations: depth (m) (a), temperature near bottom (°C) (b), dissolved oxygen near bottom (ml/l) (c), salinity of surface water (PSU) (d) and salinity near bottom (PSU) (e); yellow triangles: giant box corer stations, black dots: CTD stations.

The analysis of the abiotic parameters showed differences between the stations and gradients for most of the measured parameters, which results from the geographical location of the stations in the study area from the central BC to the S (Table 1). The shallowest station was FF1 at the mouth of GF with a depth of 91 m, while the stations located in the BC (FF2 – FF5) were much deeper, with depths ranging from 181 m to 198 m. The two S stations, FF6 and FF7, were both 107 m deep (Fig. 6a). The same pattern was observed for salinity and oxygen in bottom water, with the highest values measured at the stations located in the BC. Temperature near bottom was lowest (6.25 °C) at FF1 and highest at station FF7 (8.58 °C). The sediment analysis showed a gradient of fine sediment in the BC to coarser sediment at stations closer to the Atlantic. Sediment at the stations FF1 – FF3 was described as medium silt, with a mud content of up to 98.8 %, while sediment at station FF7 was classified as very fine sand with a higher fraction of sand. The C/N ratio was highest at stations FF6 and FF7 (16.15 – 19.08).

Figure 6 illustrates the gradients of lower temperature and oxygen near the bottom (Fig. 6b, c) as well as lower salinity in the surface water and higher values eastwards towards the Atlantic (Fig. 6d). Low salinities (< 31) were measured in the GF up to station FF1 and an abrupt increase in salinity in the bottom water (> 31) in the BC, FF2 – FF5, was found (Fig. 6e).

3.1.2 Macrofauna community analysis

A total of 153 taxa belonging to nine phyla were found at the seven FF stations (Table 2). If taxa are not assigned to an order, 'Others' was noted in the taxa list and the taxa without order were listed below. Most taxa belong to the phyla Arthropoda, Annelida and Mollusca. The numbers given in the taxa list correspond to mean abundance per taxon per m². The according taxa list of the biomass data can be found in Appendix A3). Highest numbers of taxa per phylum were found in annelids, with 68 identified taxa. Out of these, 66 were polychaetes, while the remaining two were Clitellata and Sipuncula. Among the polychaetes, Capitellidae MT 1 (total abundance of 27,972 Ind./m² in all found stations), Spionidae MT 1 (17,724 Ind./m²), Paraonidae MT 2 (9,954 Ind./m²), and Cirratulidae MT 1 (5,502 Ind./m²) were most abundant. 44 arthropod taxa were found, 35 of these were Malacostraca, including amphipods and cumaceans. Among these, Urothoidae MT 1 (4,116 Ind./m²) and Diastylidae MT 1 (5,838 Ind./m²) were most abundant. 29 taxa of molluscs were found; 18 of those were bivalves. Among the bivalves, *Yoldiella* indet. was most abundant with a total of 31,500 Ind./m² found in 2022, constituting to 60.58 % of bivalves found.

Table 2 - Taxa list of macrofauna samples of the FF stations: mean abundance (Ind./m²).

	FF1	FF2	FF3	FF4	FF5	FF6	FF7
Cnidaria							
Hydrozoa	42	14	28	28	42	14	28
Arthropoda							
Pycnogonida							
Pantopoda	0	0	0	0	14	0	0
Malacostraca							
Decapoda							
Decapoda larvae	0	0	0	42	0	0	0
<i>Notiax santarita</i>	0	0	0	0	0	70	70
Amphipoda							
Ampeliscidae MT 1	0	0	0	0	0	0	14
<i>Cheidae</i> sp.	0	168	0	154	210	0	0
Photidae MT 1	0	0	0	0	28	0	0
<i>Pseudharpinia</i> sp.	0	0	0	28	0	0	0
Phoxocephalidae MT 1	0	14	84	28	140	0	56
<i>Lepidepecreoides</i> sp.	0	14	42	42	56	0	0
<i>Uristes</i> sp.	0	0	0	14	14	42	0
Urothoidae MT 1	0	308	0	238	574	0	252
Hyperiidea MT 1	0	0	0	0	0	0	14
Amphipoda MT 2	0	0	0	56	112	0	0
Amphipoda MT 6	0	0	0	14	0	0	0
Amphipoda MT 9	0	0	0	0	0	42	28
Amphipoda MT 10	28	14	0	14	0	70	126
Amphipoda indet.	14	14	14	84	14	14	0
Cumacea							
Diastylidae MT 1	0	0	0	294	1652	0	0
Diastylidae MT 2	14	14	0	112	56	0	0
Lampropidae MT 1	0	0	0	0	14	0	0
<i>Leucon</i> cf. <i>vasilei</i>	0	0	0	0	196	0	0
Leuconidae MT 1	0	0	56	154	56	0	0
Leuconidae MT 2	0	14	0	518	28	126	28
Nannastacidae MT 1	0	0	0	182	56	0	0
Nannastacidae MT 2	0	0	0	56	238	0	0
Nannastacidae MT 3	0	56	28	0	56	0	0
Cumacea indet.	0	0	0	0	42	0	0
Isopoda							
Munnidae MT 1	0	0	14	0	0	0	0
Paramunnidae MT 1	0	0	0	14	0	0	0
Isopoda MT 1	0	0	56	0	0	0	0
Valvifera	0	0	0	14	0	0	0
Mysida	0	0	0	0	0	14	42
Tanaidacea							
Tanaidacea MT 1	0	14	98	28	56	0	0
Tanaidacea MT 2	0	0	14	0	0	0	0
Leptostraca	0	0	0	0	0	14	0
Ostracoda							
Ostracoda MT 1	0	140	70	182	70	84	140
Ostracoda MT 2	0	0	0	14	14	0	0
Ostracoda MT 3	28	98	0	98	84	0	0

Table 2 (cont.)

	FF1	FF2	FF3	FF4	FF5	FF6	FF7
Arthropoda (cont.)							
Ostracoda MT 4	0	0	0	56	14	0	0
Ostracoda MT 5	0	0	0	0	140	0	0
Ostracoda MT 6	0	0	0	0	56	0	0
Ostracoda indet.	28	0	0	0	0	0	0
Priapulida	0	14	28	0	0	0	14
Annelida							
Clitellata							
Oligochaeta MT 1	14	84	476	0	56	0	0
Polychaeta							
Errantia							
Amphinomida							
Amphinomidae MT 1	0	14	28	0	0	0	0
Eunicida							
Dorvilleidae MT 1	0	0	0	14	0	0	0
Dorvilleidae MT 2	14	14	14	0	0	0	0
<i>Lumbrineris</i> sp.	574	70	154	210	154	266	154
<i>Ninoe</i> sp.	126	28	28	0	28	70	14
Oeonidae MT 1	14	0	14	0	0	0	0
Onuphidae MT 1	0	28	112	112	56	0	0
Onuphidae MT 2	98	56	0	14	0	0	0
Phyllodocida							
Hesionidae MT 1	0	14	0	0	0	0	28
Hesionidae MT 2	0	14	0	0	0	126	70
<i>Aglaophamus</i> sp.	0	0	28	42	28	112	56
Nereididae MT 1	0	14	0	0	0	0	14
Nereididae MT 2	0	0	14	0	0	28	14
Phyllodocidae MT 1	0	0	14	14	14	0	0
Phyllodocidae MT 2	0	0	28	28	42	0	0
Phyllodocidae MT 3	14	0	0	0	0	0	28
Pilargidae MT 1	42	28	0	56	42	0	0
Polynoidae MT 1	0	28	84	112	14	0	0
Polynoidae MT 2	14	0	42	0	0	0	28
Sigalionidae MT 1	42	0	0	0	0	28	0
Sphaerodoridae MT 1	0	14	0	70	28	0	0
Sphaerodoridae MT 2	392	56	0	0	112	0	0
Syllidae MT 1	196	0	0	0	0	0	0
Syllidae MT 2	0	14	0	0	0	0	0
Syllidae MT 3	0	0	84	0	14	0	0
Glyceriformia MT 1	0	0	28	0	42	14	42
Canalipalpata							
Sabellida							
Sabellida MT 1	0	0	70	0	0	0	0
Siboglinidae MT 1	0	0	0	0	14	0	0
Spionida							
Spionidae MT 1	1400	1246	154	672	2184	238	14
Spionidae MT 2	0	0	98	0	0	28	0
Terebellida							
Ampharetidae MT 1	0	0	0	14	0	0	0
Ampharetidae MT 2	0	14	28	0	14	0	0
Cirratulidae MT 1	294	0	42	168	84	392	854

Table 2 (cont.)

	FF1	FF2	FF3	FF4	FF5	FF6	FF7
Annelida (cont.)							
Cirratulidae MT 2	154	14	42	56	0	98	126
Cirratulidae MT 3	0	0	28	0	0	0	0
Cirratulidae MT 4	28	0	0	0	14	0	0
Flabelligeridae MT 1	70	0	0	0	0	0	28
<i>Melinna cristata</i>	0	0	14	0	14	0	0
Pectinariidae MT 1	0	0	84	0	14	0	0
Pectinariidae MT 2	0	0	14	0	0	0	0
<i>Sternaspis chilensis</i>	0	70	98	28	28	0	0
<i>Lanice</i> sp.	0	0	28	0	0	0	0
Polycirrini MT 1	0	0	0	0	0	0	14
Trichobranchidae MT 1	0	70	28	0	0	0	0
Terebelliformia MT 1	0	0	14	56	14	0	0
Terebelliformia MT 3	0	42	98	0	0	0	0
Terebelliformia MT 4	0	0	0	14	0	140	56
Terebelliformia MT 5	0	0	14	0	0	0	0
Terebelliformia indet.	0	0	0	0	210	0	0
Others							
Sabellariidae MT 1	0	0	14	0	42	0	0
Scolecida							
Capitellidae MT 1	5936	196	1008	686	1232	168	98
Capitellidae MT 2	0	0	14	14	0	0	0
Capitellidae MT 3	0	0	14	0	0	0	0
<i>Cossura</i> sp.	728	0	14	14	28	42	154
Maldanidae MT 1	0	0	28	28	70	28	0
Maldanidae MT 2	0	0	0	0	112	42	0
Opheliidae MT 1	0	294	84	98	0	0	14
Opheliidae MT 2	28	70	14	0	196	70	70
<i>Leitoscoloplos</i> sp.	70	0	0	14	70	0	0
<i>Phylo</i> cf. <i>felix</i>	0	0	0	0	0	0	84
Paraonidae MT 1	140	0	56	70	98	294	42
Paraonidae MT 2	3206	0	0	14	0	0	98
Paraonidae MT 3	0	14	14	42	56	1162	168
Scalibregmatidae MT 1	14	0	56	0	0	0	0
Scalibregmatidae MT 2	0	0	0	0	0	0	42
<i>Myriochele</i> sp.	0	0	0	0	14	0	0
Polychaeta indet.	0	0	56	0	0	0	28
Others							
Sipuncula	14	98	182	532	1344	14	0
Bryozoa	0	0	0	0	0	0	14
Mollusca							
Bivalvia							
Carditida							
<i>Cyclocardia thouarsii</i>	0	28	0	0	28	0	0
Galeommatida							
<i>Mysella</i> sp.	0	0	0	14	0	154	14
Lucinida							
<i>Notocina falkandica</i>	98	0	0	126	84	28	0
<i>Adontorhina pisum</i>	1078	700	98	294	798	406	518
<i>Mendicula sudamericana</i>	0	168	14	322	378	0	0
Arcida							
<i>Limopsis marionensis</i>	0	14	56	0	0	0	0

Table 2 (cont.)

	FF1	FF2	FF3	FF4	FF5	FF6	FF7
Mollusca (cont.)							
Nuculanida							
<i>Pseudoneilonella virens</i>	0	350	70	14	0	0	0
<i>Yoldiella</i> indet.	3542	840	84	154	1736	2940	1204
<i>Silicula patagonica</i>	0	0	0	0	28	0	0
Nuculida							
<i>Nucula</i> indet.	0	84	28	126	42	0	0
<i>Thracia</i> sp.	0	14	0	0	0	0	0
Others							
<i>Cuspidaria</i> sp.	14	0	28	0	0	0	0
Bivalvia MT 9	112	210	14	42	56	0	0
Bivalvia MT 15	0	0	0	0	0	28	14
Bivalvia MT 17	0	0	14	0	0	0	0
Bivalvia MT 18	0	0	14	0	14	0	0
Bivalvia indet.	28	14	56	0	0	0	0
Caudofoveata							
Chaetodermatida							
<i>Scutopus</i> sp. 1	0	56	14	14	28	0	0
<i>Scutopus</i> sp. 2	0	14	0	14	70	0	0
Others							
Caudofoveata MT 3	0	0	14	14	56	0	0
Gastropoda							
Littorinimorpha							
<i>Amauropsis</i> sp.	0	14	14	0	0	0	0
<i>Onoba</i> sp.	28	0	0	182	14	0	0
Neogastropoda							
<i>Admete magellanica</i>	0	0	14	14	0	0	0
Others							
<i>Turritella algida</i>	0	0	0	14	0	0	0
<i>Acteon</i> sp.	0	0	0	14	0	0	0
Gastropoda indet.	14	14	0	0	14	0	0
Polyplacophora							
<i>Leptochiton medinae</i>	0	0	42	0	0	0	0
Lepidopleurida							
Scaphopoda							
Dentaliida							
<i>Dentalium majorinum</i>	0	14	0	0	0	0	0
Gadilida							
<i>Siphonodentalium dalli</i>	616	84	0	28	280	0	0
Nemertea	42	42	28	42	42	42	28
Phoronida	0	0	0	0	14	0	0
Echinodermata							
Asteroidea							
Asteroidea larvae	0	0	0	14	0	0	0
Ophiuroidea							
Ophiuroidea MT 1	0	70	14	28	0	0	0
Ophiuroidea MT 2	0	0	14	0	0	0	0
Echinoidea							
Echinoidea larvae	0	0	0	14	14	0	0
Holothuroidea							
Dendrochirotida							
<i>Psolus</i> sp.	0	0	84	0	0	0	0

Table 3 lists the biotic parameters at the seven FF stations. Highest abundances occurred at station FF1 (19,404 Ind./m²) with values four times higher than in the least abundant community at station FF3 (4,816 Ind./m²). Large differences were also found in biomass. The biomass of taxa at station FF3 was 197.1 g wet mass per m², whereas the biomass of taxa at station FF4 was 7.25 g wet mass per m². Taxa richness was lowest at S station FF6 with 37 identified taxa per m² and highest at station FF5 with 80 taxa per m². Station FF3, FF4 and FF5, all located in the BC, had the highest taxa richness with more than 70 different taxa per station. Communities at these three stations also had the highest diversity ($H' > 3$, $d > 5$) with an even distribution of individuals among taxa ($J \geq 0.76$). Diversity was lowest in the community of station FF1, with a rather uneven distribution of species among taxa ($J = 0.65$). Both stations on the Shelf, FF6 and FF7, were more diverse than the station at the mouth of GF, FF1, but less diverse than the stations in the BC.

Table 3 - Biotic parameters of the macrofauna communities of the FF stations: Total taxa richness per station (S), abundance (Ind./m²), biomass (g wet mass/m²), Shannon index (H'), Pielou's evenness index (J) and Margalef's richness index (d); standard error is given in parentheses.

Station	Taxa richness (S)	Abundance (Ind./m ²)	Biomass (g wet mass/m ²)	Shannon index (H')	Pielou's evenness index (J)	Margalef's richness index (d)
FF1	42	19404 (759.49)	27.14 (3.25)	2.17 (0.07)	0.65 (0.01)	2.73 (0.20)
FF2	59	6258 (518.38)	44.96 (37.13)	2.91 (0.05)	0.80 (0.01)	4.12 (0.16)
FF3	77	4816 (824.93)	197.99 (101.03)	3.26 (0.08)	0.87 (0.03)	5.00 (0.37)
FF4	72	7140 (525.14)	7.25 (1.95)	3.40 (0.06)	0.88 (0.01)	5.26 (0.11)
FF5	80	14322 (1867.15)	9.67 (1.50)	3.02 (0.08)	0.76 (0.02)	5.62 (0.06)
FF6	37	7658 (1279.99)	92.35 (34.36)	2.35 (0.08)	0.72 (0.02)	2.88 (0.06)
FF7	45	5180 (656.21)	79.76 (19.98)	2.73 (0.11)	0.80 (0.03)	3.36 (0.19)

Cluster analysis using non-Metric Multidimensional Scaling (nMDS) revealed three clusters (Fig. 7). The stress of 0.1337 indicates a useful two-dimensional representation of the data (Clarke and Warwick, 2001). The clusters were named after the geographic location of the stations in the study area. The three subsamples of FF1 form a single cluster and were named *Garibaldi Fjord (GF)* – cluster. The four stations FF2, FF3, FF4 and FF5, located in the BC, were named *Beagle Channel (BC)* – cluster and stations FF6 and FF7 were named *Shelf (S)* - cluster. PERMANOVA showed that the separation between the communities of the three clusters was significant ($p = 0.0001^{***}$). Results of the hierarchical cluster analysis confirm the clusters identified with the nMDS (Fig. 8). The dendrogram shows that the subsamples of every station have high similarities and are clustered together. Compared to the S - cluster, the dissimilarity between FF3 and the other stations of the BC - cluster was relatively large. Moreover, the GF- and S-clusters were more similar to each other than to the BC-cluster.

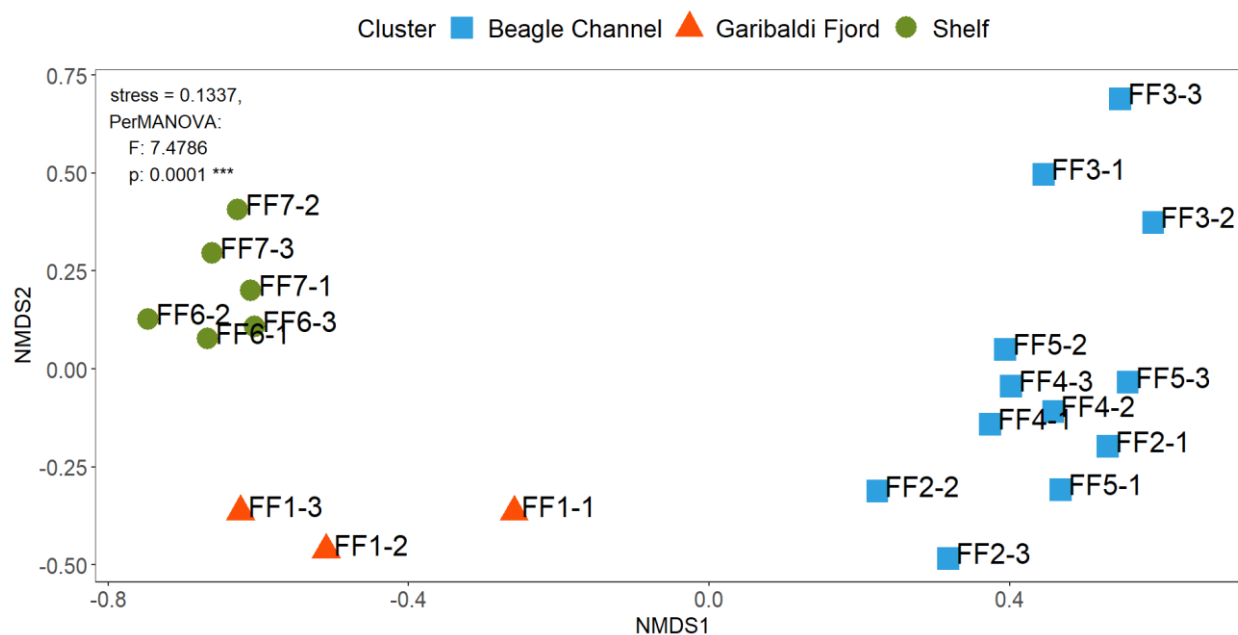


Figure 7 - Non-metric multidimensional scaling (nMDS) of the macrofauna communities of the FF stations. Shown are as well the stress value of the nMDS analysis as well as the results of the PERMANOVA indicating the F and p-value of the dissimilarity between the macrofauna communities of the clusters 'Beagle Channel' (blue squares), 'Garibaldi Fjord' (red triangles) and 'Shelf' (green dots); Signif. Codes: p -value $< 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$.

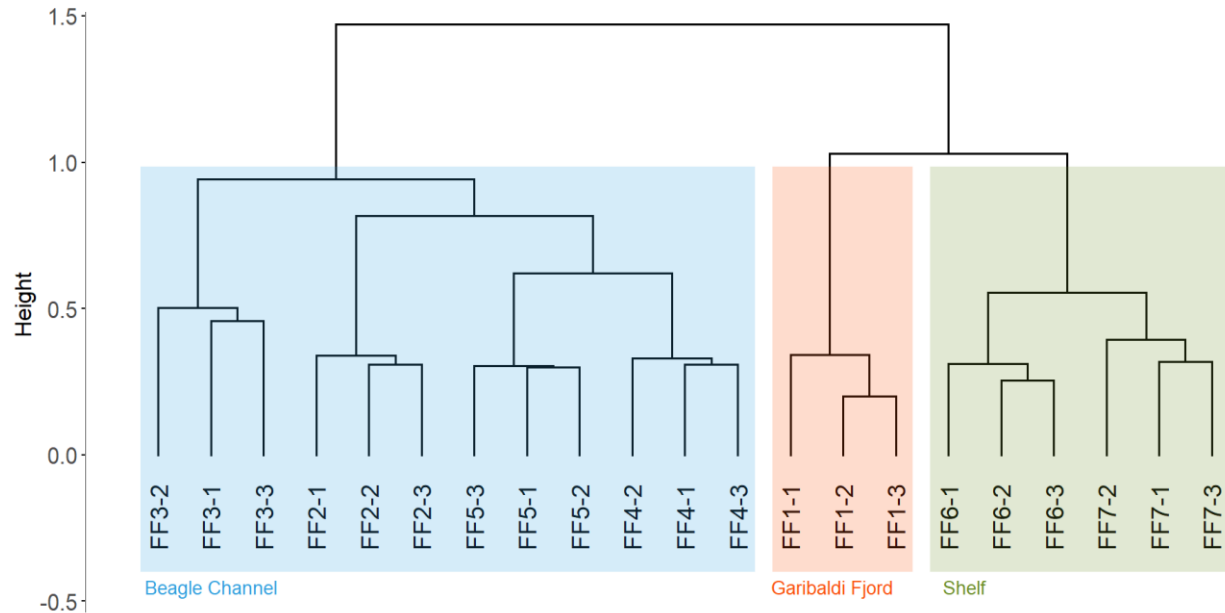


Figure 8 - Dendrogram: hierarchical clustering of the macrofauna communities of the FF stations, revealing the three clusters 'Beagle Channel' (blue box), 'Garibaldi Fjord' (red box) and 'Shelf' (green box).

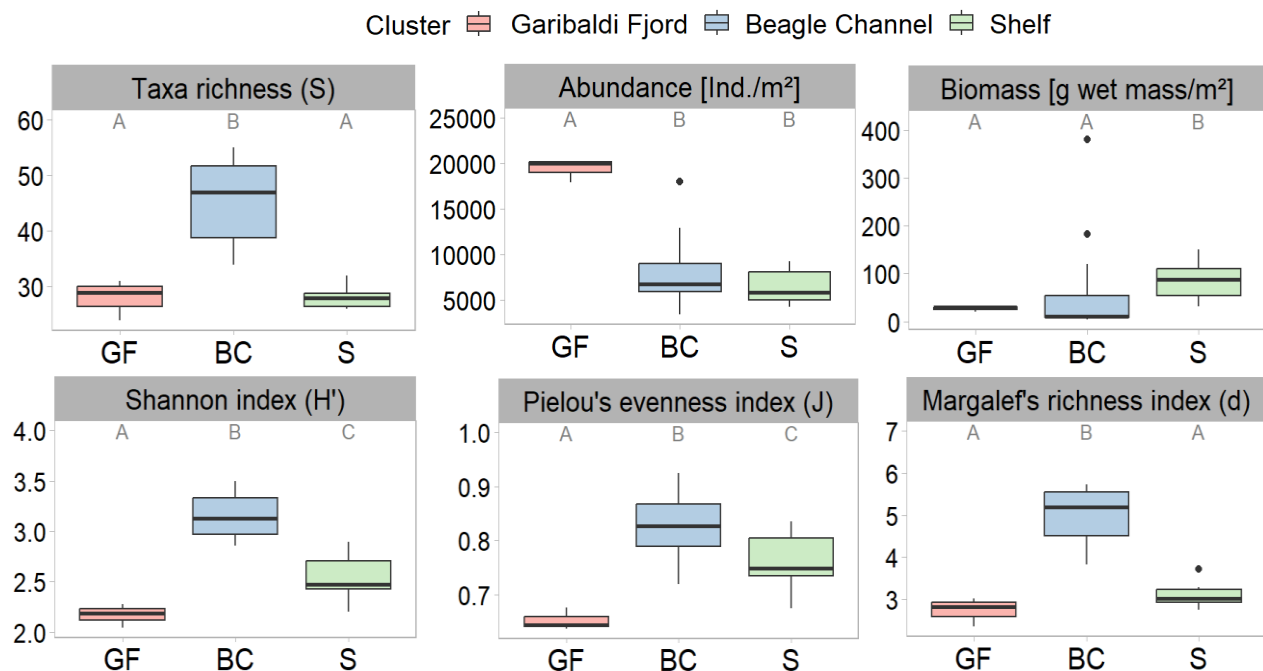


Figure 9 – Boxplots of the biotic parameters and biodiversity indices: Taxa richness (S), abundance (Ind./m²), biomass (g wet mass/m²), Shannon index (H'), Pielou's evenness index (J) and Margalef's richness (d) of the clusters 'Garibaldi Fjord (GF)' (n = 3), 'Beagle Channel (BC)' (n = 12) and 'Shelf (S)' (n = 6) of the macrofauna samples of the FF expedition. Results of the pairwise PERMANOVA shown in capital letters.

Figure 9 shows boxplots of the biotic parameters and biodiversity indices divided according to the identified clusters of the nMDS and hierarchical clustering. The results of the pairwise PERMANOVA indicate if differences in the parameters between the clusters were significant. The abundances of macrobenthic organisms in the GF-cluster were significantly higher than in the BC- and S-cluster. Most taxa per m² were present in the BC, where the diversity was also highest. Lowest biodiversity was found at the stations in the GF-cluster, which is reflected by the lowest values of all measured diversity indices in comparison to the BC- and S-cluster. The median biomass was relatively low for the BC, but two outliers indicate high biomass in two subsamples. Macrofauna organisms of the S-cluster stations had significantly higher biomass than those of the other two clusters.

At the stations of the GF-cluster, polychaetes were highly abundant and accounted for 70.26 % of the relative abundance and 94.41 % of the biomass (Fig. 10). Annelids were less abundant in the other two clusters, but still accounted for about 50 % of the abundance. The taxonomic classification of polychaetes into Errantia, Canalipalpata, and Scolecida can be found in the Appendix A4. Sipunculids were found more frequently in the BC, but only very few were present in the S- and GF - cluster. Molluscs, mostly bivalves, were highly abundant in all three clusters.

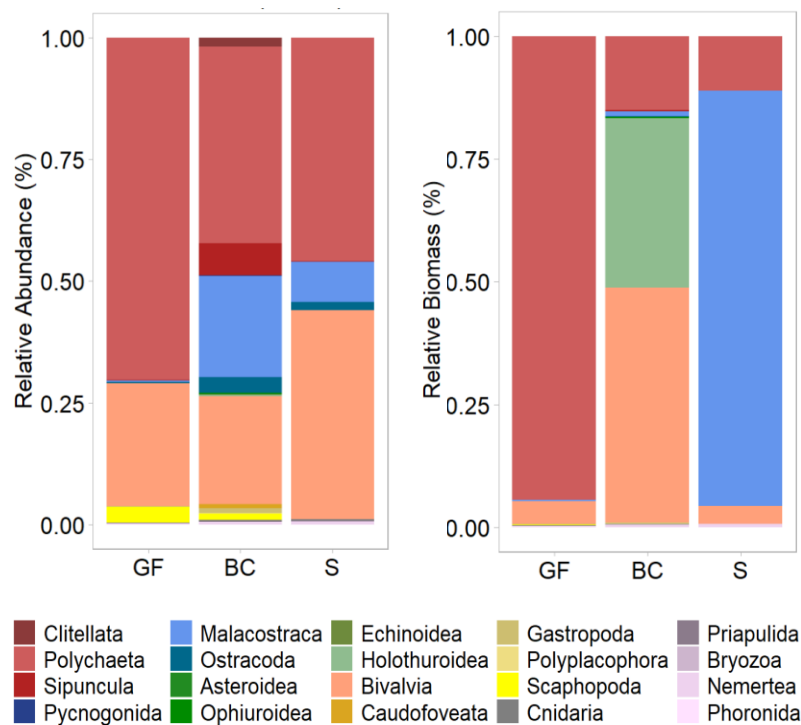


Figure 10 – Relative abundance (%) and relative biomass (%) of the 20 identified taxonomic units of the GF-, BC -, and S-cluster of the macrofauna samples of the FF expedition.

Caudofoveata, Gastropoda, Polyplacophora and Scaphopoda were absent at the S stations, but present in the BC. Of these taxa, only gastropods and scaphopods were found in the GF. Whereas arthropods were almost absent in the GF, 23.99 % of the organisms found in the BC stations and 10.06 % of the organisms found at S stations were arthropods. At the S stations, Malacostraca had a high relative biomass (84.52 %), indicating a few very heavy organisms. Echinoderms were

only present at the BC stations with only a few specimens of Asteroidea, Ophiuroidea, Echinoidea and Holothuroidea sampled. Though they had a relatively low abundance, a few organisms of Holothuroidea (*Psolus* sp.) contributed strongly to the relative biomass at these stations.

Indicator species analysis revealed a list of taxa significantly associated with each of the three defined clusters (Table 4). The indicator taxa of the GF-cluster belong exclusively to Annelida, whereas Arthropoda and Bivalvia were also significantly associated to the BC and S stations. A high specificity (A = 1), showed that eight taxa occurred only at the stations of the BC - cluster. This was the case for one polychaete morphotype (Syllidae MT 1) for the GF and two arthropods of the S stations. If all subsamples of the tested cluster included the according taxa, fidelity B reached the value 1, as for Paraonidae MT 2 at the GF and *Notiax santarita* in the S - cluster. Pictures of the indicator taxa are shown in Figure 11.

Table 4 - Result of the Indicator species analysis of the macrofauna samples from the FF expedition: listed are the taxa significantly associated to the clusters 'Garibaldi Fjord', 'Beagle Channel' and 'Shelf', the specificity (A) and fidelity (B); Signif. Codes: p -value $< 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$.

	specificity (A)	fidelity (B)	p-value
Garibaldi Fjord			
Syllidae MT 1	1.00	0.67	0.018*
Paraonidae MT 2	0.89	1.00	0.001***
Cirratulidae MT 4	0.89	0.67	0.028*
Flabelligeridae MT 1	0.80	0.67	0.039*
Onuphidae MT 2	0.77	1.00	0.003**
Sphaerodoridae MT 2	0.77	1.00	0.001***
<i>Leitoscoloplos</i> sp.	0.74	0.67	0.036*
Beagle Channel			
Onuphidae MT 1	1.00	0.87	0.002**
<i>Mendicula sudamericana</i>	1.00	0.83	0.001***
<i>Cheidae</i> sp.	1.00	0.75	0.003**
<i>Sternaspis chilensis</i>	1.00	0.75	0.001***
<i>Nucula</i> indet.	1.00	0.75	0.004**
Nannastacidae MT 3	1.00	0.67	0.018*
Polynoidae MT 1	1.00	0.67	0.020*
Leuconidae MT 1	1.00	0.58	0.044*
Opheliidae MT 1	0.86	0.75	0.039*
Shelf			
<i>Notiax santarita</i>	1.00	1.00	0.001***
Amphipoda MT 9	1.00	0.67	0.003**
Mysida	1.00	0.50	0.047*
Terebelliformia MT 4	0.94	1.00	0.001***
Hesionidae MT 2	0.93	1.00	0.001***
<i>Mysella</i> sp.	0.91	0.67	0.010**
<i>Aglaophamus</i> sp.	0.69	1.00	0.020*



Figure 11 - Indicator taxa identified by indicator species analysis of the macrofauna samples from the FF expedition for the clusters - BC: *Nannastacidae* MT 3 (A), *Mendicula sudamericana* (B), *Onuphidae* MT 1 (C), *Sternaspis chilensis* (D), *Cheidae* sp. (E), *Nucula* indet. (F), *Opheliidae* MT 1 (G), *Leuconidae* MT 1 (H); S: *Aglaophamus* sp. (I), *Hesionidae* MT 2 (J), *Amphipoda* MT 9 (K), *Mysella* sp. (L), *Terebelliformia* MT 4 (M); GF: *Syllidae* MT 1 (N), *Sphaerodoridae* MT 2 (O), *Flabelligeridae* MT 1 (P), *Paraonidae* MT2 (Q), *Leitoscoloplos* sp. (R), *Cirratulidae* MT 4 (S), *Onuphidae* MT 2 (T).

Table 5 – Results of the SIMPER analysis: taxa contributing up to 30% to the cumulative dissimilarity between the clusters ‘Beagle Channel’, ‘Garibaldi Fjord’ and ‘Shelf’. Also shown are the results of the pairwise PERMANOVA between the clusters (F and p-value, Signif. Codes: p value < 0.05*, < 0.01**, < 0.001***).

	Beagle Channel (n = 12)		Garibaldi Fjord (n = 3)	
Beagle Channel (n = 12)	x		x	
Garibaldi Fjord (n = 3)	F = 5.06, p = 0.001***			
	Taxa (n = 15)	cum diss. (%)		
	Paraonidae MT 2	4.60	x	
	<i>Cossura</i> sp.	7.00		
	Capitellidae MT 1	9.36		
	Sipuncula	11.45		
	<i>Mendicula sudamericana</i>	13.43		
	Sphaerodoridae MT 2	15.40		
	Urothoidae MT 1	17.36		
	<i>Yoldiella</i> indet.	19.27		
	Ostracoda MT 1	21.14		
	<i>Siphonodentalium dalli</i>	22.90		
	Syllidae MT 1	24.59		
	Opheliidae MT 1	26.26		
	<i>Cheidae</i> sp.	27.91		
	<i>Ninoe</i> sp.	29.41		
	Onuphidae MT 1	30.86		
Shelf (n = 6)	F = 9.49, p = 0.002**		F = 8.39, p = 0.019*	
	Taxa (n = 18)	cum diss. (%)	Taxa (n = 8)	cum diss. (%)
	Sipuncula	2.33	Paraonidae MT 2	5.79
	Paraonidae MT 3	4.42	Capitellidae MT 1	10.89
	<i>Mendicula sudamericana</i>	6.42	<i>Siphonodentalium dalli</i>	15.08
	Spionidae MT 1	8.35	Sphaerodoridae MT 2	18.80
	Cirratulidae MT 1	10.17	Paraonidae MT 3	22.33
	Terebelliformia MT 4	11.99	Spionidae MT 1	25.52
	<i>Notiax santarita</i>	13.78	Ostracoda MT 1	28.21
	Hesionidae MT 2	15.55	Onuphidae MT 2	30.81
	Oligochaeta MT 1	17.22		
	<i>Cheidae</i> sp.	18.89		
	Opheliidae MT 1	20.43		
	Urothoidae Mt 1	21.95		
	Amphipoda MT 10	23.46		
	Capitellidae MT 1	24.97		
	Onuphidae MT 1	26.44		
	<i>Nucula</i> indet.	27.86		
	<i>Yoldiella</i> indet.	29.26		
	Bivalvia MT 9	30.63		

Pairwise PERMANOVA revealed that macrofauna communities of all clusters tested against each other differed significantly. However, the difference between the GF and S-cluster (F = 8.39, p = 0.019 *) is less promoted than the ones between the BC and the S (F = 9.49, p = 0.002**), as well

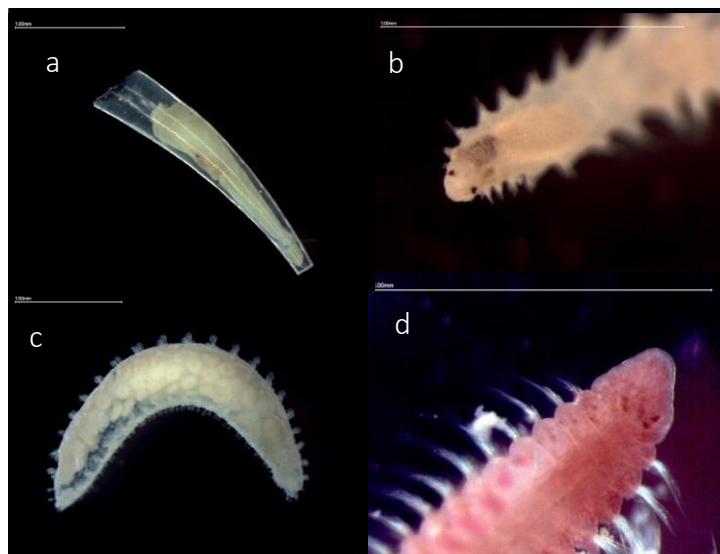


Figure 12 - Discriminating taxa I : *Siphonodentalium dalli* (a), Syllidae MT 1 (b), Sphaerodoridae MT 2 (c), Paraonidae MT 2 (d).

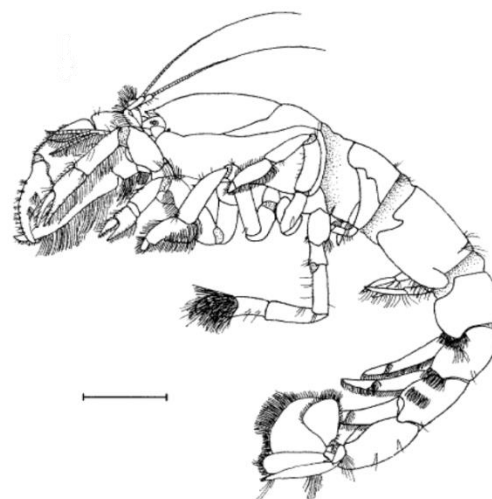


Figure 13 - Discriminating taxa II : *Notiax santarita*, Thatje (2000).

as the BC and GF ($F = 5.06$, $p = 0.001^{***}$). For a better overview, only parts of the SIMPER results were depicted in table 5; the detailed results can be found in the Appendix A5. For the comparison between the GF and BC, 15 taxa were necessary to reach a cumulative dissimilarity of 30 % between the two locations. Six of these taxa were not found at any of the GF stations. Syllidae MT 1 was the only taxon of the 15 taxa tested that occurred only in the GF, but not the BC or S stations. If the contribution of a taxon to the mean dissimilarity was large in combination with a small standard deviation (see Appendix A5), the respective taxon contributed much and consistently to the dissimilarity and can be considered a good discriminating species/taxon (Clarke, 1993). Paraonidae MT 2, another indicator taxon of the GF, can be classified as a discriminating taxon between GF and BC, since it was highly abundant in the GF, but only one single organism was found in one of the subsamples of the BC-cluster (Fig. 12). The SIMPER analysis revealed 18 taxa contributing to a 30 % dissimilarity between the BC- and S-cluster. Six of these taxa were found only at the BC stations. Only one of the taxa was found at the Shelf but not in the BC, *Notiax santarita*, an indicator species of the S and a good discriminating species between BC and S stations (Fig. 13). Despite the smaller differences between GF and S, only eight taxa were required to reach a dissimilarity of 30 %. Three indicator taxa of GF contributed to these differences. Discriminating taxa between GF and S were the scaphopod *Siphonodentalium dalli* and the polychaete Sphaerodoridae MT 2. These two taxa occurred in high abundances at GF, but were not present at the S stations.

3.1.3 Correlation between abiotic and biotic parameters

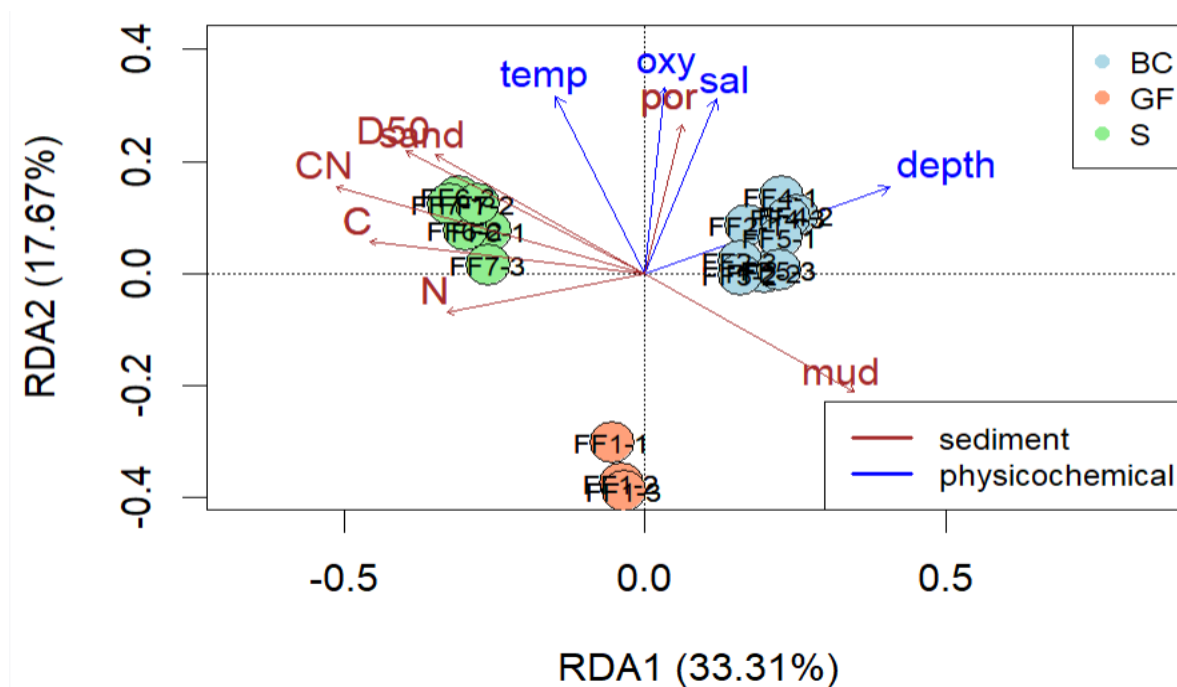


Figure 14 - Redundancy Analysis (RDA): distribution of FF macrofauna communities. Blue arrows: physicochemical variables depth (depth), temperature near bottom (temp), salinity near bottom (sal) and dissolved oxygen near bottom (oxy); red arrows: sediment parameters median grain size (D_{50}), proportion of sand particles (sand), proportion of mud particles (mud), carbon C and nitrogen N concentrations, C/N ratio and porosity.

The Redundancy Analysis (RDA) was used to reveal the correlations between the variation of the macrofauna species community in the FF data and the environmental variables studied. For the analysis, the sediment parameters D_{50} , sand and mud content, C/N ratio, carbon and nitrogen concentration as well as the physico-chemical parameters depth, temperature, near-bottom dissolved oxygen and near-bottom salinity were tested (Fig. 14). The first two axes of the RDA explained 50.45 % of the data variation. The envfit analysis showed that all tested environmental parameters had a significant influence on the abundance data (Appendix A6). The R^2 value in the envfit analysis indicates how much of the variation in the abundance data can be explained by the environmental variables. The environmental variables depth, temperature, salinity, oxygen, C/N ratio and the median grain size D_{50} have an R^2 value of 0.7 or higher, indicating a strong influence on species abundance. The proportion of sand and mud as well as the carbon content had a moderate influence on species abundance, with R^2 values between 0.59 and 0.64. Nitrogen content of the sediment and the porosity had the least influence on species abundance, with R^2

values of 0.34 and 0.39, respectively.

Figure 15 shows the correlation matrix for all biotic and abiotic parameters investigated. In the study area, the bottom water of deeper stations was significantly saltier; however, depth had no significant influence on water temperature. In deeper waters, the sediment had lower N and C contents and a lower C/N ratio, but higher porosity. At stations where near-bottom water was warmer, higher near-bottom salinities, dissolved oxygen contents and C/N ratio was measured. Moreover, the C/N ratio was positively correlated with the median grain size D_{50} and the sand content. The more taxa were found at a station, the lower was the measured biomass. However, diversity increased significantly with higher taxa richness. Significantly more taxa were found at

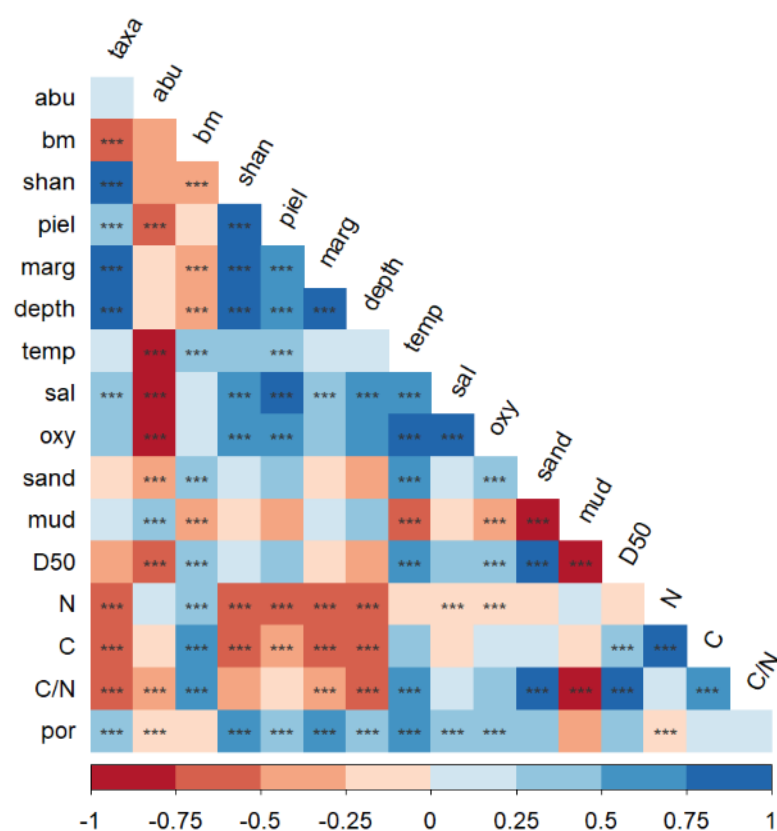


Figure 15 – Correlation matrix of the tested biotic parameters: Taxa richness (taxa), abundance (abu), biomass (bm), Shannon index H' (shan), Pielou's evenness index J (piel), Margalef's richness d (marg) and the abiotic parameters: depth (depth), temperature near bottom (temp), Salinity near bottom (sal), oxygen near bottom (oxy), proportion of sand (sand), proportion of mud (mud), median grain size D_{50} (D_{50}), nitrogen content (N), carbon content (C), C/N ratio (C/N) and porosity (por). Positive correlations: $r > 1$ (blue), negative correlations: $r < 1$ (red). Signif. Codes: p -value $< 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$.

stations with higher near-bottom salinity, whereas significantly negative correlations were found between sediment nitrogen and carbon content, the C/N ratio and taxa richness. About 50 % to 75 % of the variability in taxa richness can be explained by the three sediment parameters, with lower nitrogen and carbon contents, as well as a lower C/N ratio leading to higher taxa richness. On the other hand, less taxa were present at stations with higher sediment porosities. About 75 % to 100 % of variability in total abundances of a station was explained by near-bottom water temperature, salinity and dissolved oxygen content. In deeper waters with higher near-bottom salinity and higher near-bottom dissolved

oxygen contents, significantly fewer organisms were found. Moreover, coarser sediments with a higher proportion of sand resulted in significantly lower abundances, but significantly higher biomass. Since mud and sand content are inversely related, significantly higher abundance and lower biomass were found in finer sediments. Weak but significant correlations were also found for the C/N ratio as well as porosity and the abundance. Higher biomass was found in shallower waters with comparably higher temperature and sediments with higher nitrogen and carbon contents as well as higher C/N ratios. The diversity indices Shannon index, Pielou's evenness index as well as Margalef's index are significantly positive correlated with each other. Higher salinity and dissolved oxygen contents near the bottom resulted in higher diversity of the macrofauna community of the respective station, while higher nitrogen and carbon content as well as a higher C/N ratio had significantly negative influence on the diversity.

3.2 Temporal analysis

The taxa list of the macrofauna samples from the VH expedition and the FF expedition is shown in Table 6. In 1994, 24 taxa belonging to nine phyla were found at the seven stations. In 2022, 22 of the predefined taxonomic units of 1994 were present. In 1994, a few Anthozoa, Harpacticoidea, Echiurida and Hemichordata were sampled, in 2022 none were present. Pantopoda and Polyplacophora were absent at the seven stations of 1994, but were present in 2022.

Table 6 - Taxa list of the VH and FF macrofauna indicating the abundance (Ind./m²) per station; colonial organisms (hydrozoans and bryozoans) were only classified as present (p).

	VH							FF						
	VH1	VH2	VH3	VH4	VH5	VH6	VH7	FF1	FF2	FF3	FF4	FF5	FF6	FF7
Cnidaria														
Anthozoa	0	0	0	0	14	0	0	0	0	0	0	0	0	0
Hydrozoa	p	0	0	0	p	p	p	p	p	p	p	p	p	p
Arthropoda														
Pantopoda	0	0	0	0	0	0	0	0	0	0	0	14	0	0
Crustacea	0	28	0	14	0	0	111	0	0	0	42	0	98	112
Amphipoda	14	42	0	167	472	63	0	42	532	140	672	1148	168	490
Cumacea	0	0	14	209	639	0	83	14	84	84	1316	2394	126	28
Isopoda	0	0	0	0	70	0	0	0	0	70	28	0	0	0
Tanaidacea	0	0	0	0	42	21	0	0	14	112	28	56	0	0
Harpacticoidea	0	0	0	0	0	0	14	0	0	0	0	0	0	0
Ostracoda	0	14	0	56	56	0	719	56	238	70	350	378	84	140
Priapulida														
Priapulida	0	0	0	0	14	0	0	0	14	28	0	0	0	14
Annelida														
Polychaeta	3179	180	1542	1903	3250	1769	2144	13594	2422	2898	2660	5082	3346	2338
Echiurida	0	0	0	0	14	0	0	0	0	0	0	0	0	0
Sipuncula	14	0	14	292	1875	0	14	14	98	182	532	1344	14	0
Brachiopoda														
Brachiopoda	0	28	0	0	0	0	0	0	0	0	0	0	0	0
Bryozoa														
Bryozoa	0	0	0	0	p	0	0	0	0	0	0	0	0	p
Mollusca														
Bivalvia	373	1680	264	319	736	749	4012	4872	2422	476	1092	3164	3556	1750
Aplacophora	0	0	0	28	111	0	0	0	70	28	42	154	0	0
Gastropoda	0	153	14	0	56	0	194	42	28	28	224	28	0	0
Polyplacophora	0	0	0	0	0	0	0	0	0	42	0	0	0	0
Scaphopoda	14	0	14	14	139	0	0	616	98	0	28	280	0	0

Table 6 (cont.)

	VH1	VH2	VH3	VH4	VH5	VH6	VH7	FF1	FF2	FF3	FF4	FF5	FF6	FF7
Echinodermata														
Asteroidea	0	0	0	0	0	0	0	0	0	0	14	0	0	0
Ophiuroidea	14	0	14	0	0	21	0	0	70	28	28	0	0	0
Echinoidea	0	0	0	0	28	0	0	0	0	0	14	14	0	0
Holothuroidea	0	14	0	0	0	0	0	0	0	84	0	0	0	0
Hemichordata														
Hemichordata	0	0	0	0	14	0	0	0	0	0	0	0	0	0
Others														
Vermes	0	0	0	125	473	0	0	56	126	504	42	112	42	28
Unidentified	0	0	0	14	139	0	0	0	42	28	0	42	0	42

Table 7 and Figure 16 show the biotic parameters of 1994 and 2022. Taxa richness, abundance and diversity was significantly higher in 2022. The most abundant and most diverse station in 1994 was VH5 with 8,211 Ind./m². Lowest abundance of the seven VH stations was recorded at station VH2 with 2,139 Individuals per m². Macrofauna community at station VH1 at the mouth of the GF had the lowest values for the diversity indices, which is also true for the resampled station FF1 in 2022. Although macrofauna community at station VH1 was less diverse, the taxa were evenly distributed. The biomass of the macrofauna organisms was significantly higher in 1994. The highest biomass in 1994 was measured at station VH5 with 317.7 g wet mass/m², whereas the highest biomass in 2022 was recorded at station FF3 with 197.99 g wet mass/m².

All biotic variables tested differ significantly between 1994 and 2022. The boxplots indicate higher values for all variables except biomass. The median biomass in 1994 was 107.94 g wet mass/m², while in 2022 it was significantly less with 30.82 g wet mass/m² (Fig. 16). The median number of individuals found was 7,266 in 2022 and 4,117 in 1994. For taxa richness, the VH boxplots show a median line at six taxa per subsample, eleven for FF. Diversity was higher in 2022, indicating more diverse communities, whereas evenness was not significantly different.

Table 7 - Biotic parameters of the macrofauna communities of the VH and FF stations: total taxa richness per station (S), abundance (Ind./m²), biomass (g wet mass/m²), Shannon index (H'), Pielou's evenness index (J) and Margalef's richness index (d); standard error in brackets.

	Station	Taxa richness (S)	Abundance (Ind./m ²)	Biomass (g wet mass/m ²)	Shannon index (H')	Pielou's evenness index (J)	Margalef's richness index (d)
1994	VH1	7	3622 (884.67)	53.64 (22.25)	0.42 (0.05)	0.37 (0.07)	0.32 (0.10)
	VH2	8	2139 (619.40)	168.02 (76.86)	0.76 (0.07)	0.46 (0.04)	0.57 (0.02)
	VH3	7	1876 (1086.68)	182.5 (82.38)	0.44 (0.11)	0.45 (0.10)	0.37 (0.16)
	VH4	10	3140 (1972.74)	163.55 (117.79)	1.12 (0.19)	0.59 (0.05)	0.73 (0.10)
	VH5	19	8211 (781.46)	317.7 (157.58)	1.73 (0.12)	0.65 (0.05)	1.52 (0.11)
	VH6	6	2664 (1665.00)	11.76 (7.73)	0.83 (0.09)	0.54 (0.12)	0.52 (0.08)
	VH7	9	7318 (611.95)	190.71 (56.19)	1.00 (0.10)	0.52 (0.04)	0.64 (0.04)
2022	FF1	10	19348 (734.43)	27.14 (3.25)	0.75 (0.10)	0.37 (0.02)	0.67 (0.12)
	FF2	14	6230 (527.00)	44.96 (37.13)	1.47 (0.01)	0.6 (0.01)	1.22 (0.03)
	FF3	16	4802 (813.09)	197.99 (101.03)	1.43 (0.12)	0.6 (0.04)	1.14 (0.08)
	FF4	17	7140 (525.14)	7.25 (1.95)	1.82 (0.03)	0.71 (0.02)	1.36 (0.14)
	FF5	14	14210 (1913.38)	9.66 (1.50)	1.69 (0.05)	0.67 (0.02)	1.19 (0.05)
	FF6	9	7448 (1287.77)	92.34 (34.37)	0.99 (0.02)	0.5 (0.02)	0.71 (0.06)
	FF7	10	4942 (717.01)	79.74 (19.98)	1.24 (0.06)	0.63 (0.03)	0.75 (0.08)

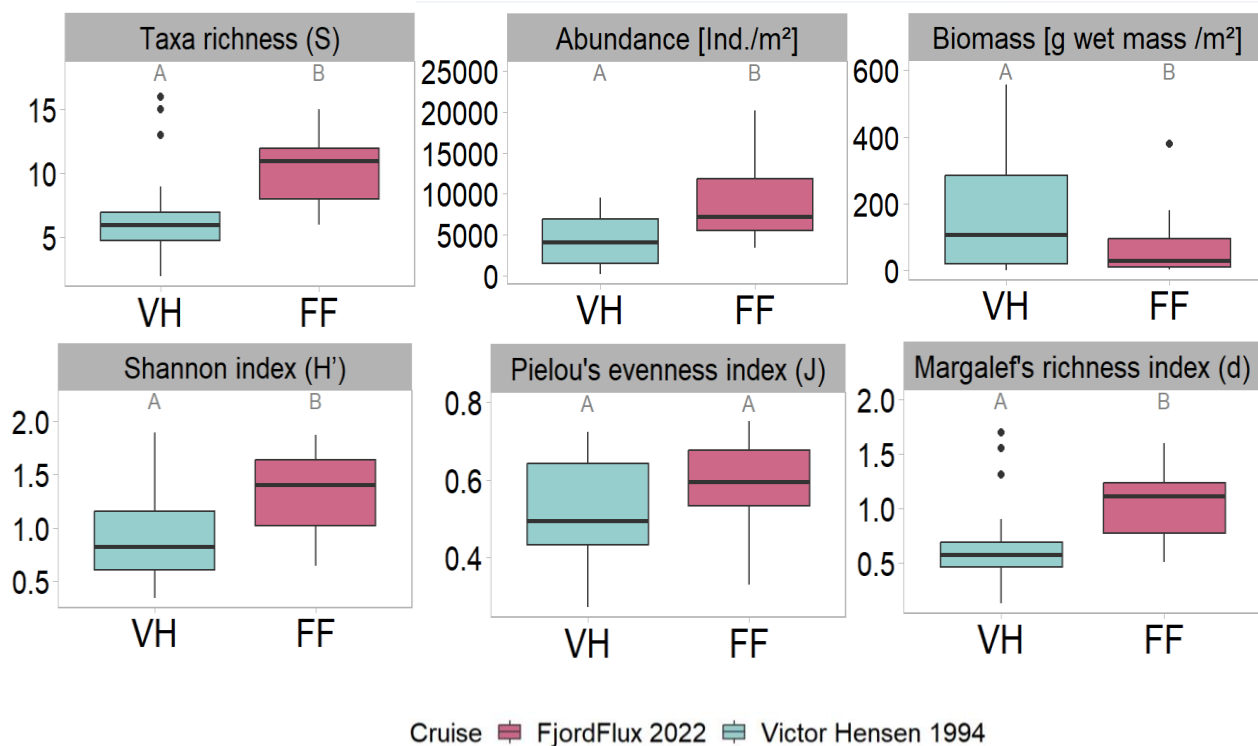


Figure 16 - Boxplots of the biotic parameters and biodiversity indices: taxa richness (S), abundance (Ind./m²), biomass (g wet mass/m²), Shannon index (H'), Pielou's evenness index (J) and Margalef's richness index (d) of the VH (turquoise) and FF (violet red) macrofauna (n = 21). Results of the pairwise PERMANOVA shown in capital letters.

Figure 17 shows that abundance was higher at all FF stations than at the according VH station, with the exception of station VH7/FF7. Considering the relative abundance of all stations from 1994 and 2022, the proportions of the phyla were stable. Annelids accounted for almost 50 % of all organisms found in both years, followed by molluscs. Only a few echinoderms were found in both years. At station VH1/FF1, annelids dominated. While molluscs accounted for about 86 % of the relative abundance at station VH2, molluscs and annelids each made up both around 40 % of the relative abundance of station FF2 in 2022. At station VH3/FF3 to VH6/FF6, annelids had a higher proportion of the stations' relative abundance in 1994 than in 2022. In contrast to that,

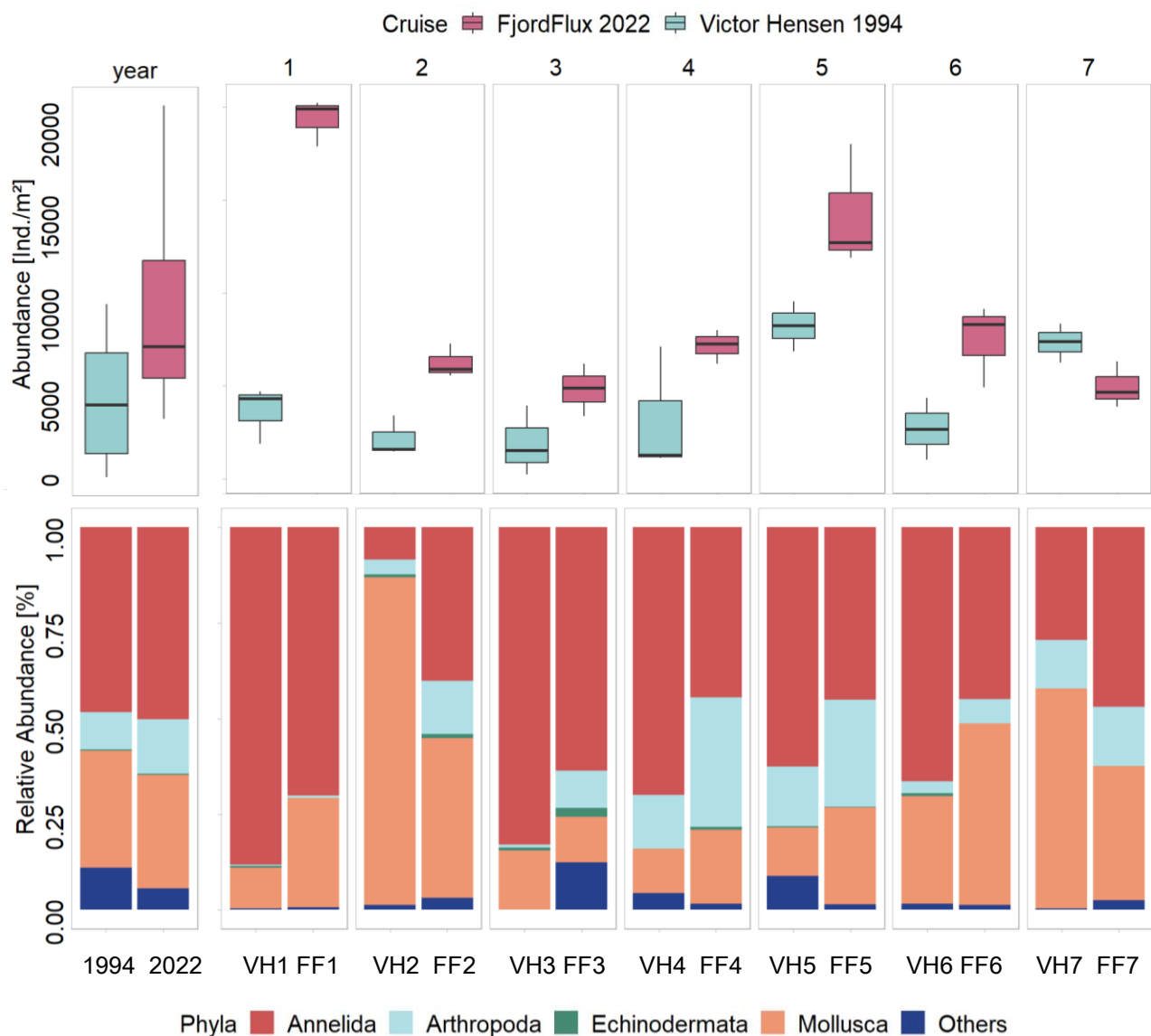


Figure 17 – top: Boxplots of VH (turquoise) and FF (violet red) abundance (Ind./m²) per station and per year; bottom: relative abundance of VH (left) and FF (right) stations.

at the same stations, arthropods and molluscs had higher proportions in 2022 than in 1994. Molluscs were most abundant at station VH7 with 57 %, followed by annelids with 30 %, while annelids accounted for 47 % of the relative abundance and molluscs for 35 % at FF7. Highest contributions to the relative abundance of Arthropoda were found at station FF4 and FF5 with 34 % and 28 %, respectively.

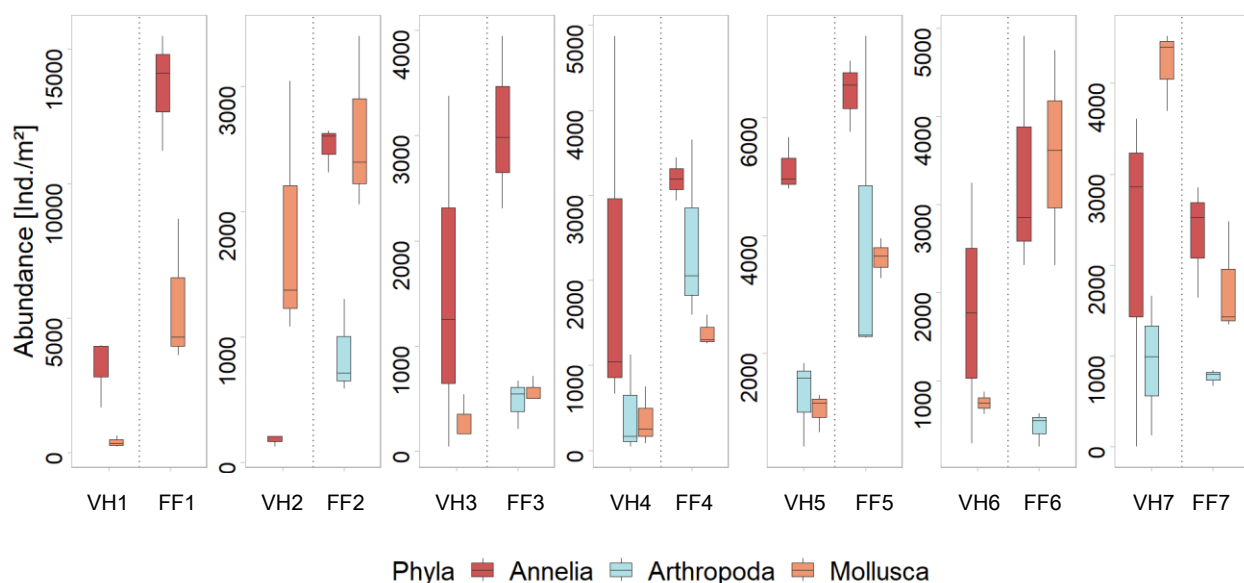


Figure 18 – Boxplots of the phyla contributing more than 90% to the abundance (Ind./m²) of the VH (left) and FF (right) stations.

Figure 18 shows how the dominating phyla Annelida, Arthropoda and Mollusca contributed to the total abundance of the respective station and how the abundance of a station differed between years. Although relative abundance of annelids was higher at most VH stations than at FF stations, total abundances of annelids was higher at all stations except VH7/FF7.

The analysis of biomass showed the reverse picture as for the abundance data. At all stations, except of VH6/FF6, the biomass was higher in 1994 than in 2022 (Fig. 19). At station FF6, Arthropoda made up 85 % of the biomass, whereas at station VH6 polychaetes contributed 90 %. Apart from the differences in total biomass, the proportions of phyla contributing to the relative biomass of both years remained relatively stable. In both years Arthropoda and Mollusca contributed more than 25 % to the biomass, Mollusca accounted for almost 50 % in 1994. At station VH1/FF1 Annelida contributed highly to the biomass, accounting for more than 90 %. VH2 and FF3 were the only stations where echinoderms contributed substantially to the biomass; however comparison of the abundance and biomass indicates that only a few echinoderms with

a high biomass were present, which also applies to molluscs at VH5.

At station VH4, FF6 and VH7/FF7, Arthropoda contributed strongly to the biomass. Figure 20 illustrates the phyla that contributed more than 90 % to the overall biomass at the stations. Although annelids had only a small contribution to the relative biomass at station FF6, the total biomass of annelids was higher than at station VH6 in 1994. Apart from the same proportional distribution of phyla to the relative biomass at station VH7/FF7, the total biomass of Arthropoda and Annelida was higher in 1994.

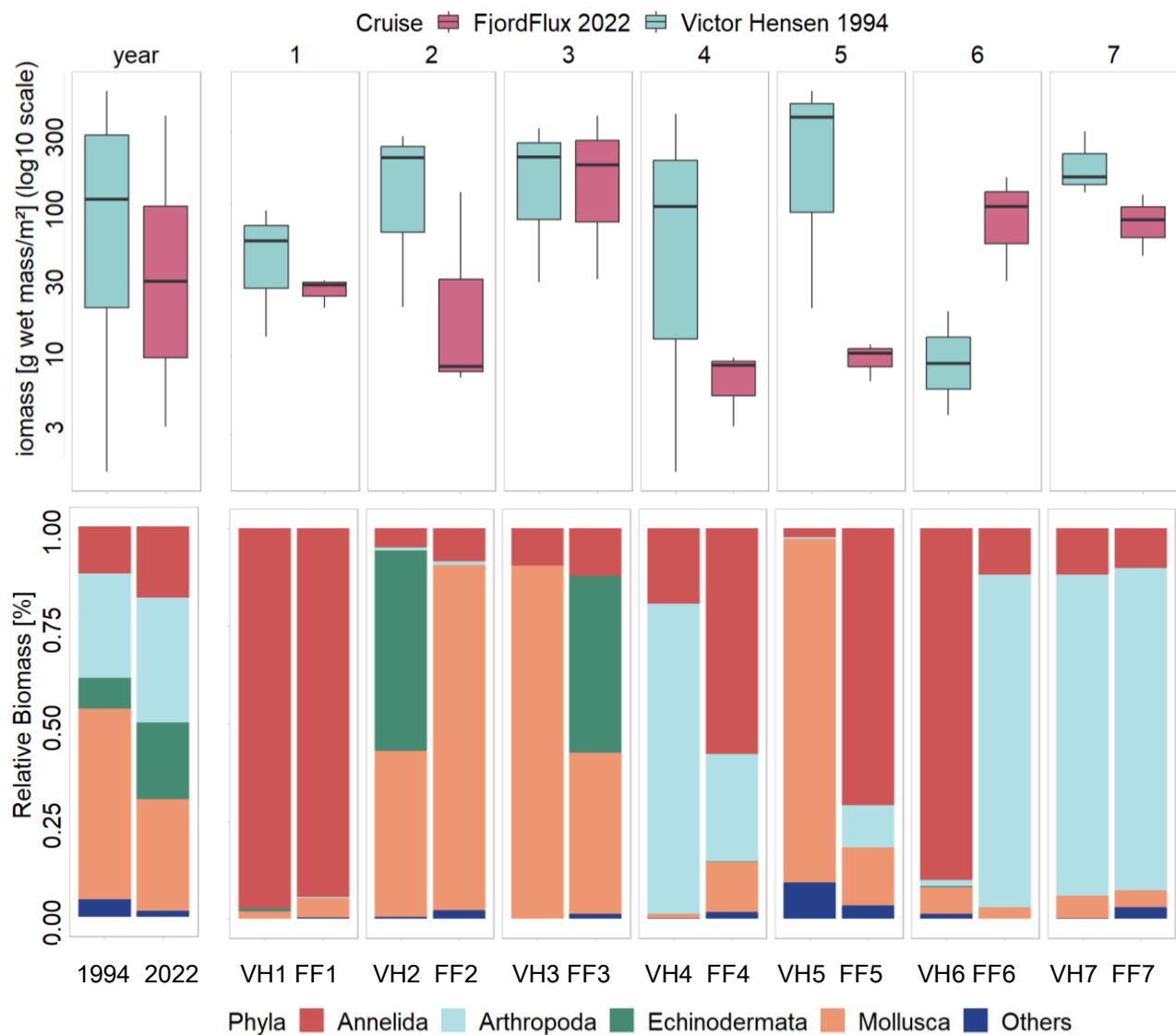


Figure 19 – top: Boxplots of VH (turquoise) and FF (violet red) biomass (g wet mass/m²) per station and per year; bottom: relative biomass of VH (left) and FF (right) stations.

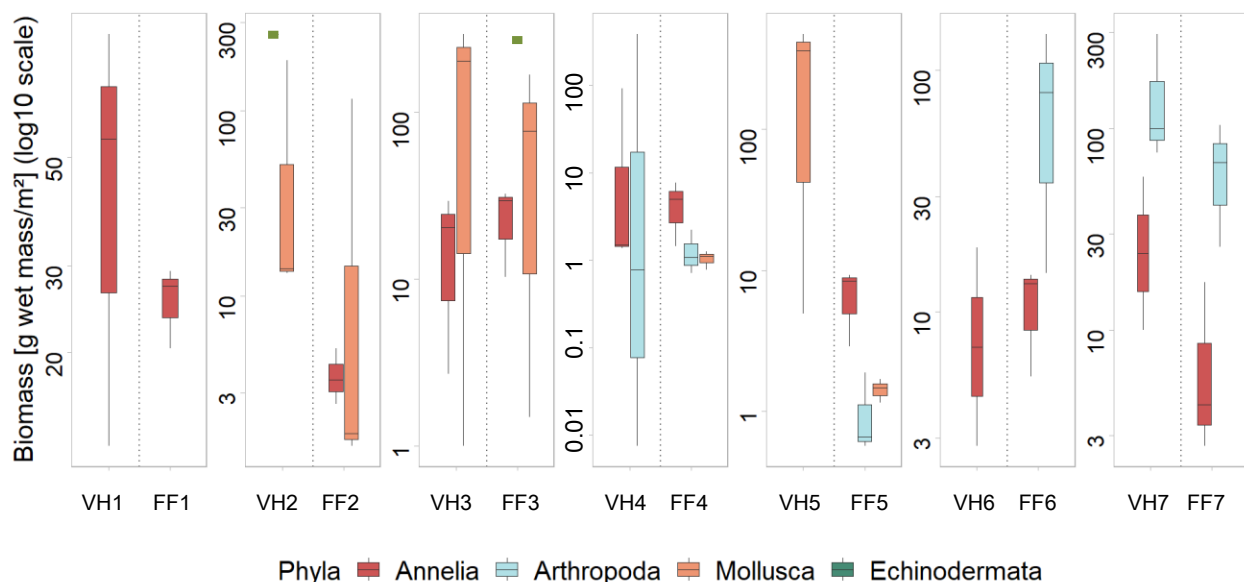


Figure 20 - Boxplots of the phyla contributing more than 90% to the biomass (g wet mass./m²) of the VH (left) and FF (right) stations.

Non-metric multidimensional scaling (nMDS) of the abundance data from 1994 and 2022 does not show a clear differentiation of the clusters between the stations, sites or the two years (Fig. 21). However, PERMANOVA results show a significant difference between the two years. The FF subsamples are closer together than the VH replicates, indicating less variance. The stress value of 0.1689 indicates a still useful two-dimensional representation of the data (Clarke and Warwick, 2001). Hierarchical clustering shows the formation of three possible clusters (Fig. 22). All FF subsamples of a station show low dissimilarity and form a common cluster. The replicates of VH2 were separated between two of the clusters, and the replicates of VH4 were distributed between all three clusters. FF2, FF3, FF4 and FF5 form a cluster together. All of these stations are situated in the BC. FF1 as well as the S stations FF6, FF7 and VH7 form a cluster, with FF6 and FF7 having greater similarities. The stations VH1, VH3 and VH6 form a single cluster; combining stations from all three locations of the study area (GF, B, S).

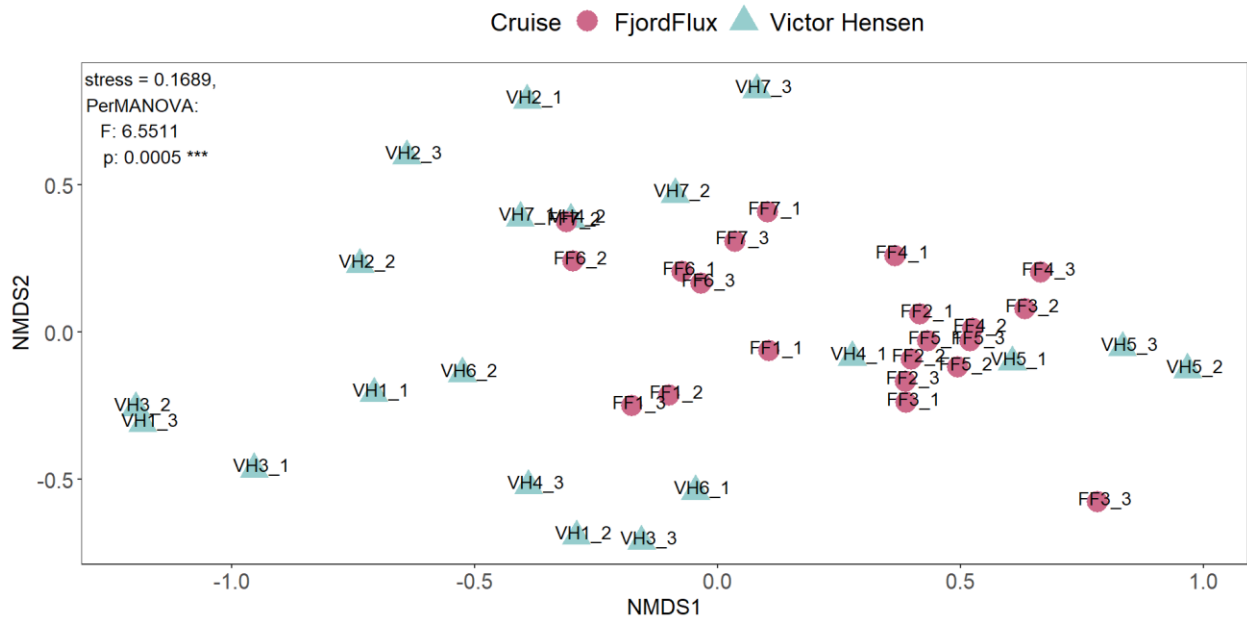


Figure 21 - Non-metric multidimensional scaling (nMDS) of VH (turquoise) and FF (violet red) macrofauna communities. Shown are as well the stress value and results of PERMANOVA indicating the F and p-value of the dissimilarity between the macrofauna communities of the two years; Signif. Codes: p-value < 0.05*, < 0.01**, < 0.001***.

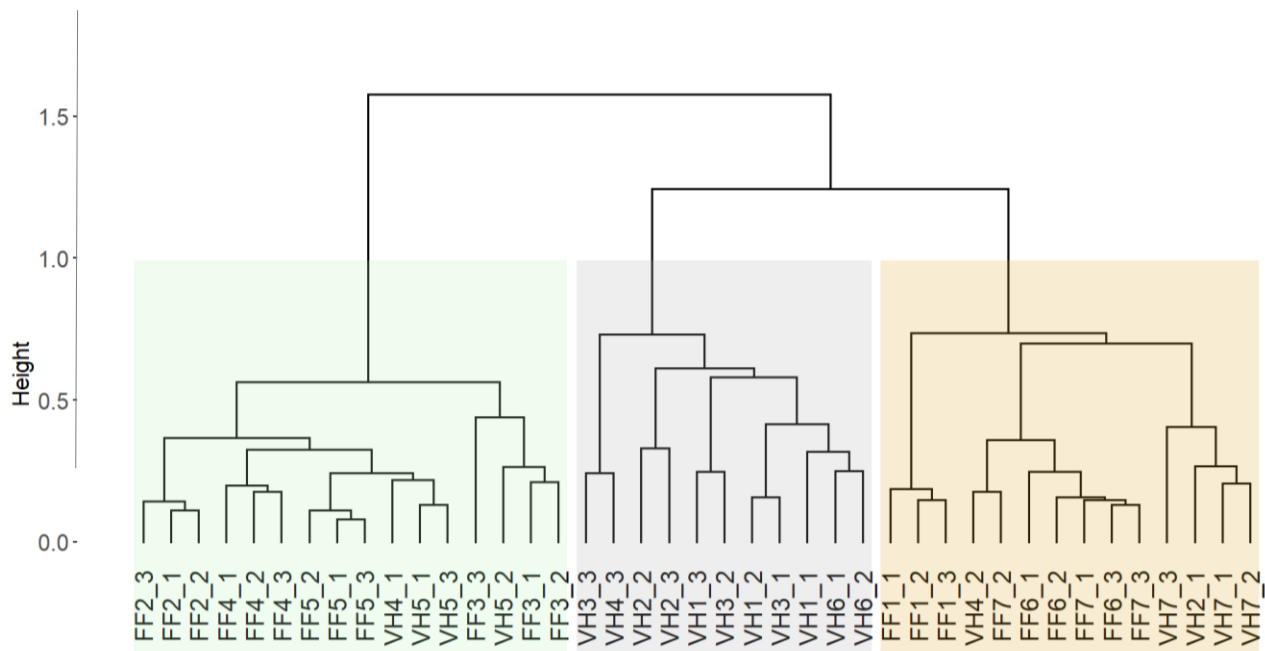


Figure 22 - Hierarchical cluster dendrogram of the macrofauna communities of the VH and FF stations.

4 DISCUSSION

4.1 Evaluation of Methodology

Since the number of stations analyzed for 2022 is limited to the historical stations, it is important to examine the additional 30 samples taken during the FF expedition to confirm the patterns of the spatial distribution depicted. For example, the GF-cluster consisted only of the subsamples of one station, which must be critically evaluated due to the high patchiness in the area. The different number of subsamples in the clusters tested against each other also led to limitations in the statistical analysis of the data. Since the subsamples were taken of a single giant box corer, they are strictly speaking pseudoreplicates, as they do not meet the requirement of independence (Hurlbert, 1984). According to Hurlbert (1984), pseudoreplicates are nevertheless suitable to investigate differences between locations.

In 1994 and 2022, different sampling devices were used. During the VH expedition in 1994, samples were taken with a multibox corer, while during the FF expedition in 2022 a giant box corer was used due to logistical limitations. Despite the limitation of different sampling devices, care was taken to obtain the same sample size as in 1994 (0.024 m^2 per subsample). Due to the pronounced patchiness of the seafloor it is of utmost importance to re-sample the same location for historical comparison. Since no coordinates were measured for the sampling device itself, drifting due to currents cannot be excluded. However, the comparison of the sampling coordinates of 1994 and 2002 measured with the ship sensors shows high accuracy of the resampled stations and drifting is expected to be minor. Additionally, the number of historical stations is limited to a total of eight and more historical stations would be desirable to underline the results. Due to rocks that damaged the sampling equipment or stones hindering the boxes to close, not all historical stations could be resampled. Nevertheless, samples of the region and especially historical samples are very rare and are therefore of great importance to study changes of the benthic community in the area due to ongoing climatic changes. In addition, numerous abiotic parameters were measured, and a more detailed sediment description than in previous studies was conducted. Despite its limitations, this study presents a valuable baseline for future comprehensive comparisons and investigations.

4.2 Spatial analysis

The community analysis of macrofauna data from the seven stations sampled during the FF expedition revealed three significantly distinguishable clusters separated according to the geographical location of the stations. In the following, these results are interpreted, discussed and related to the abiotic parameters to interpret how this clustering occurs and which factors influence the abundances, biomass, diversity and species composition of the corresponding macrofauna communities.

Warm, oxygen-poor, nutrient-rich Pacific water with high salinity enters the BC via Bahia Cook, a bay forming the western entrance of the BC. Arntz (1999) describes an entrapment of warm water with high salinity under cold, brackish water in the eastern BC. This pattern of high salinity near the bottom and less saline surface water is also reflected in the CTD measurements of this study at the stations FF1 to FF4 located in the eastern BC (Fig. 7). Moreover, surface water is diluted by precipitation, river discharge and glacial melt water (Antezana, 1999), leading to a decrease in salinity and temperature towards the innermost regions of the channel (Arntz, 1999). Findings of Antezana et al. (1994) with surprisingly high salinities at the eastern entrance of the channel, despite eastward currents, were confirmed in 2022. This may be due to the northward flow from the Atlantic along the western tip of Picton Island leading to a circular mixing of Atlantic water and BC water that leaves the channel north-east of Picton Island (Cucco et al., 2022). Western parts of the BC are surrounded by the CDI, whose glaciers are connected to the BC via fjords or direct river tributaries (Giesecke et al., 2021). The oxygen-rich, nutrient-poor surface water mix in the central BC due to the eastward flow, leading to lower salinity near the bottom in the central BC (Antezana, 1999). Lowest salinity in surface waters and strong stratification have been described especially close to glaciers in the region (Antezana et al., 1994), with more pronounced stratification in summer months due to higher freshwater input (Giesecke et al., 2021). Hydrographic data collected during the FF cruise in the GF support these findings. Lowest dissolved oxygen concentrations found in GF may therefore be due to the high stratification during summer months, which isolates the bottom water and prevents mixing of oxygen-rich surface water with the bottom layer. Due to the described influence of different water masses and mixing processes as well as the geomorphology of the study area, the distribution of water temperatures and salinities in the BC deviates the generally accepted idea, that cold, saline water forms the lower part of the water masses, while warmer, less saline water rises and forms the upper water layers (Broecker, 1991). As the correlations of abiotic parameters have shown, there is a

significant positive correlation between water depth and bottom salinity, but no significant correlation between water temperature and depth. This is because the coldest water was present at the shallowest stations in the GF (6.25 °C).

In general, sediment composition is strongly affected by the strengths of currents in a given location, with higher wave actions leading to coarser sediments by preventing the deposition of fine sediments (McCave, 1976b). The sediment analysis revealed fine sediments and a high proportion of mud at the station at the mouth of the GF. Surprisingly lowest porosity was found in the finer sediments, whereas one would generally expect low porosities in coarser sediments (Berner, 1976). Especially at station FF1, the recorded low porosity may indicate a dense and tight packing of the relatively fine sediment grains (Berner, 1976). Some of the GF sediments were mixed with glacial clay, due to abrasive erosion (personal observation). In the GF-cluster, polychaetes have the largest contribution to the abundance and biomass of the sampling site. Indicator species analysis supports these findings, with exclusively polychaetes representing the GF-cluster. Quiroga et al. (2012) found a dominance of small-bodied polychaetes such as paraonids, capitellids and cirratulids in a glacially influenced fjord mouth in northern Patagonia. Indeed, Paraonidae and Cirratulidae morphotypes were indicator taxa of the GF, and also Capitellidae occurred in large abundance at the GF station (5,936 Ind./m²). Moreover, Spionidae MT 1 accounted for 10.30 % of the polychaetes at GF and 32.76 % in the BC. Spionids feed at the sediment-water interface on both deposited and suspended particles (Dauer et al., 1981). About 83 % of the polychaetes inhabiting the station located at the fjord mouth belong to the Scolecida, such as Capitellidae and Paraonidae, which mainly include burrowing and deposit-feeding taxa (Weigert and Bleidorn, 2016). Better adaptation and tolerance of these small-sized, opportunistic species to the constant physical disturbance caused by high sedimentation rates (Giangrande et al., 2005; Quiroga et al., 2012) may explain the community pattern found in the GF-cluster.

Underwater images (Fig. 23) support the discussed distribution patterns of sediments and deposits of fine debris at the fjord mouth, but shows as well the occurrence of fine sediments in the BC. Coarser sediments were found at the S stations, as already observed by Gutt et al. (1999). In general, the current regime and sediment composition have a major influence on the occurrence of different macrofauna organisms, as filter feeders depend on water currents ensuring a constant food supply (McCave, 1976a; Wilde, 1976). In the BC, the filter-feeding holothurian *Pso-lus* sp. accounts for most of the relative biomass, and higher relative abundances of bivalves were found both, in the BC and at the S stations. Furthermore, the analysis revealed that the indicator

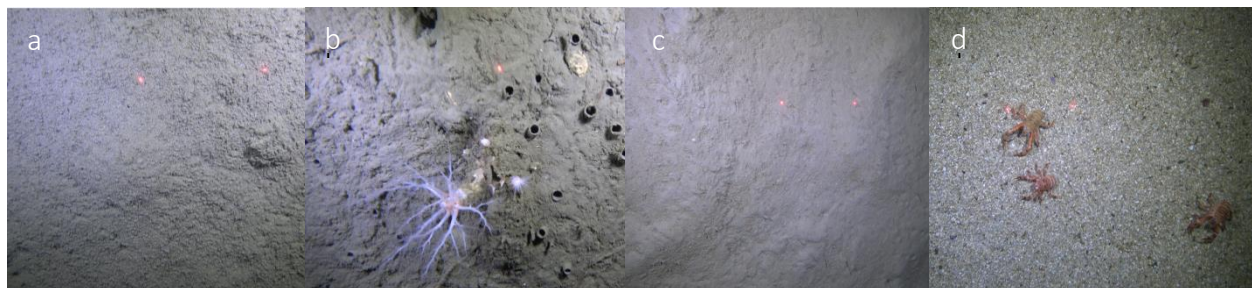


Figure 23 – Underwater images taken during the FF expedition 2022 showing the different habitat types at the mouth of the Garibaldi Fjord (a), in the BC (b-c) and at the Shelf off the eastern entrance of the BC (d), Photos: Nils Owsianowski.

species of the BC belong to several taxonomic units, such as bivalves, amphipods and cumaceans besides polychaetes. These findings go hand in hand with the highest biodiversities of the three clusters found in the BC, as already mentioned by Thatje and Mutschke (1999) who also found a richer community in the BC and a rather impoverished fjord community. Moreover, the significantly higher diversity in the BC may result from its central location between the Pacific and Atlantic, allowing species from both oceans to enter the channel and mix. Of the stations, the macrofauna community at FF4 is the most diverse and the sediment had the highest measured porosity. Sediments with a higher porosity have more voids and pores between the grains (Berner, 1976) and therefore provide more space for organisms to live and interact within. Furthermore, higher porosity and capability for water penetrating the sediment enhance the oxygen content in the sediment, which could lead to higher habitat complexity and more suitable habitats for macroinvertebrates (McCave, 1976b). The pattern of more complex communities characterized by different size classes and feeding modes in areas of greater disturbance (Quiroga et al., 2012) could explain higher diversity in the current-influenced BC and S stations, in contrast to the polychaete-dominated fjord community. However, also in BC and S stations, polychaetes contribute to about 50 % of the relative abundance. In contrast to the polychaetes inhabiting GF, the analysis of polychaete composition showed a higher contribution of Errantia, free-moving and predatory forms, and Canalipalpata, which bury and are deposit feeders or sessile, tube-dwelling filter feeders (Weigert and Bleidorn, 2016). For example the indicator taxa *Hesionidae* MT 2 and *Aglaophamus* sp. are carnivorous (Fig. 11). The most abundant amphipods of the BC *Cheidae* sp., Phoxocephalidae MT 1 and Urothoidae MT 1 belong to the Haustorioidea and have a burrowing lifestyle (Barnard and Karaman, 1991). Most cumaceans also live burrowed in the first few centimeters of the sediment (Watling and Gerken, 2023). Bivalves accounted for about 25 % of the relative abundance in the GF and BC and about 45 % at the S stations. *Yoldiella* indet. had the

highest total abundance of bivalves found at all stations and was described as a deposit feeder adapted to fine sediments (Reed et al., 2014).

The discriminating taxa Syllidae MT 1, between GF and BC, and Sphaerodoridae MT 2 between Shelf and the GF, live in various sediments and habitats (Martin et al., 2021). Moreover, the indicator species of the S stations, *Notiax santarita*, was also described by Thatje (2000) to be present in the BC, but was presently only found at the S. Therefore the absence of this decapod at certain sampling sites in this study could be due to the low number of sampling stations. *Notiax santarita*, a callianassid with a burrowing lifestyle, plays an important role in shaping community structure via bioperturbation (Hernández, 2018). The high water temperatures and dissolved oxygen contents in the water column at the S stations may fuel phytoplankton growth and enhance the activity and metabolic rate of organisms, leading to comparably higher productivity and the highest biomass at the Shelf. RDA supports these findings, showing a positive relationship and influence of coarse sediment as well as a higher C/N value at the S stations with the highest biomass. Moreover, the results show that depth, temperature, salinity, oxygen, the C/N ratio and the median grain size have the highest influence on the variation in the community. Arntz et al. (2005) state that the macrofauna assemblages in the Magellan region are mainly determined by food supply, which in turn is influenced by depth. However, only 50.45 % of the variation was explained by the environmental variables measured during this study. Biological processes and interactions such as competition, predation, intraspecific as well as interspecific interactions may therefore also influence community structure (Gray, 1981).

In conclusion it can be assumed that the spatial distribution of the macrofauna community at the mouth of GF is strongly influenced by increased sedimentation and therefore mud-dwelling polychaetes dominate at this study site. In contrast, the BC and S stations are more exposed to hydrodynamic stress, resulting in more diverse communities than the GF. Since the BC is still more exposed to sedimentation than the S, more deposit feeding organisms with burrowing lifeforms such as amphipods and cumaceans are present. The macrofauna community at the Shelf is less influenced by sedimentation than in the fjords and channels due to geographical location and current regime, resulting in highest relative abundances of bivalves. The high productivity in this area results in the highest biomass and it is assumed that the community pattern is more influenced by species interaction.

4.3 Historical comparison

The analysis of the FF macrofauna data is a basis for the historical comparison with the VH data set from 1994. Spatial differences in macrobenthic communities of the region with low diversity adjacent to glaciers and a more diverse channel community was described for 1994 (Thatje and Mutschke, 1999) and was supported by present findings (Chapter 4.2). Community analysis showed a significant distinction between the macrofauna communities of the two years. In the following, the changes in environmental conditions in the region over the last 28 years and their effects on the macrofauna communities inhabiting the BC and adjacent areas are discussed.

The species composition shows a similar pattern in both years, with annelids, molluscs and arthropods dominating the communities in 1994 and 2022. However, significant differences were found in total abundance, species diversity and biomass. Abundance and diversity was significantly higher in 2022, whereas biomass was significantly lower than in 1994. As in 2022, polychaetes and molluscs dominated the community in 1994 (Gerdes and Montiel, 1999), while abundance of polychaetes (on average 1,995 Ind./m² in 1994, 4,620 Ind./m² in 2022) and bivalves (1,162 Ind./m² in 1994, 2,476 Ind./m² in 2022) were significantly higher in 2022 and mainly contributed to the described differences in total abundances. High abundances of polychaetes are expected to result from rising sedimentation in the region due to rising temperatures: Strelin and Iturraspe (2007) described an increase in air temperature in Ushuaia, located at the central BC, of 0.8 °C since 1970. This goes hand in hand with the rising global air surface temperatures of 0.19 °C per decade from 1979 to 2022 (Copernicus Climate Change Service, 2023). Since 1990, annual precipitation has been decreasing in combination with a decline in snowfall and higher rainfall in austral winter (Garreaud et al., 2013; González-Reyes et al., 2017). The continued rise in temperatures over the last 28 years is exacerbating the loss of ice mass from glaciers and icefields. Glacier retreat at a rate of 1.21 ha/year has been described for the Cordón Martial glaciers, located north of the central BC, due to a significant reduction in precipitation and an increase in temperature (Strelin and Iturraspe, 2007). Moreover, the CDI surrounding the western part of the BC lost 3.9 GT of ice per year between 2000 and 2011 (Melkonian et al., 2013). The ice mass loss was more pronounced in glaciers at the northern and eastern sites of the CDI, whereas smaller changes or even glacier advance was observed in the southern parts (Holmlund and Fuenzalida, 1995; Melkonian et al., 2013). In contrast to many north-eastern glaciers of the CDI, the Garibaldi glacier showed a trend towards thickening between 2001 and 2011 (Melkonian et al., 2013), due to orographic effects in which the southern slopes of the icefield receive com-

paratively more precipitation, while drier conditions prevail on the northeastern side (Holmlund and Fuenzalida, 1995). Retreating and advancing glaciers in close proximity to each other have also been described for glaciers in Alaska and Greenland due to prevailing trends in regional climate (Truffer and Motyka, 2016).

The most abundant polychaete taxa of 2022, Capitellidae MT 1 (28.91 % of all polychaetes found), Spionidae MT 1 (18.32 %), Paraonidae MT 2 (10.29 %) and Cirratulidae MT 1 (5.69 %), are described to be well adapted and more tolerant to constant physical disturbance from high sedimentation rates (Quiroga et al., 2012). Significantly higher abundances of bivalves in 2022 consisted to 60 % of the bivalve *Yoldiella* indet., which is described to live in glacial influenced sediments (Fetzer et al., 2002) and is capable of consuming large amounts of sediment (Reed et al., 2014), resulting in a good adaptation of the taxa to increasing sedimentation. Gerdes and Montiel (1999) found that bivalves contributed highly to the biomass in 1994, especially in the BC, while reptant decapods were very abundant at the S stations and contributed almost 16 % of total biomass. However, no reptant decapods were found at the S stations in 2022. Amphipods and cumaceans contributed to higher diversity in 2022, especially at station FF4 and FF5. Since the most abundant amphipod taxa of 2022 *Cheidae* sp., Phoxocephalidae MT 1 and Urothoidae MT 1 as well as many cumaceans have burrowing lifeforms (Barnard and Karaman, 1991; Watling and Gerken, 2023), this might indicate a good adaptation of these organisms to fine sediments. The significantly higher species diversity in 2022 could therefore be related to the increasing physical disturbance caused by continuous sedimentation, resulting in more complex communities (Quiroga et al., 2012). This goes hand in hand with the theory that intermediate disturbance maintains high biodiversity in a community, as described by Robinson et al. (2021) for ice scour disturbance on the Antarctic Peninsula and Laudien et al. (2007) for an Arctic glacial fjord. On the S stations, the influence of increasing sedimentation is expected to be lower due to the current regime. However, also at the S station FF6 total abundance was higher than in 1994, but it was the only station with a higher biomass than in 1994. The higher biomass in 2022 is almost only based on a few specimens of *Notiastrea antarctica*. On the other hand, VH7 is the only station where abundances were higher in 1994 than in 2022, with polychaetes and bivalves being most abundant in 1994. The variation found at the two S stations indicate that more samples would be necessary to confirm a trend in this respect.

Changes in temperature can alter the latitudinal distribution of species, influence their reproduction patterns (Birchenough et al., 2011) or lead to regime shifts in the community. For

example Kortsch et al. (2012) found rapid changes in the community structure of two Arctic fjords with a significant increase in macroalgae cover and increasing macrofauna community diversity due to climate warming. Moreover, rising temperatures can lead to an increase in metabolism of ectothermic organisms resulting in a faster development and maturation at a smaller size (Sheridan and Bickford, 2011; Verberk et al., 2021). However, bottom water temperature data of the BC is limited. Satellite-derived sea surface temperature data show no differences between 1994 and 2022 (Copernicus Climate Change Service, 2023), but these measurements are limited especially in autumn and winter, due to clouds present in the region.

It has to be taken into account that sampling time of the VH and FF expedition differed. In 1994, the samples were taken in November (austral spring) while in 2022 samples were taken in February (austral summer). Water temperatures of the BC are subject to strong seasonal variability with temperatures ranging from ~ 6 °C to ~ 9 °C in the upper 200 m of the water column (Giesecke et al., 2021). From September to November, the highest abundance of merozooplankton is induced by the highest chlorophyll-a concentrations (Aguirre et al., 2012; Pineda-Metz and Montiel, 2021). Indeed, during the VH sampling period, the planktonic system was in a successional stage with high abundance of meroplankton in the water column (Richter, 1996). High macrofauna abundance in 2022 combined with low biomass, indicate more juvenile organisms than in 1994, where organisms had higher biomass but lower abundances. As the detailed community data from 1994 containing the wet mass of individual organisms was not available for this thesis, the hypothesis of different sampled age classes due to seasonal variability cannot be tested. However, the vast majority of bivalves were ≤ 1 mm in 2022. An analysis of the age structure of the bivalve taxa need to be carried out to determine whether the organisms collected may originate from the same cohort. Several *Yoldiella* species have pelagic lecithotrophic larvae, such as *Yoldiella valettei* (Reed et al., 2014), which occurs in the Magellan region (Aldea et al., 2020). In this way, larvae may be dispersed over wide distances and explain the distribution of the *Yoldiella* specimens throughout the study area, including the S stations.

In conclusion, significantly higher abundances of deposit feeding polychaetes and bivalves in 2022 may be an effect of increased sedimentation due to increasing glacial melt through global warming. However, the study area is subject to strong seasonal variability, which has implications on benthic community structure and reproduction patterns and may partly contribute to the high abundances of juvenile bivalves. To determine whether the significant differences in community structure observed between 1994 and 2022 are due to seasonal variation or whether the com-

munity has shifted towards smaller organisms, better adapted to their changing habitat, it is important to continue monitoring the benthic communities of the region.

4.4 Conclusion

In the coming years, the Magellan region will be subject to many changes due to direct anthropogenic pressure as well as environmental and climatic changes, highlighting the importance of future investigations in an area that until recently was undisturbed and pristine. The Intergovernmental Panel on Climate Change (IPCC) states in its latest synthesis report, that global warming will continue to increase in the coming years in almost all scenarios considered (Lee et al., 2023). Moreover, industrial pressure from aquaculture is rapidly expanding towards southern Patagonia (Iriarte, 2018). The findings presented herein provide valuable insights into changes in benthic community structure in response to the effects of climatic changes such as rising sedimentation. Changes in the benthic community structure of the BC, adjacent fjords, and surrounding areas were identified. Particularly, areas impacted by increased sedimentation are presently dominated by small, opportunistic polychaetes. The study provides a comprehensive data set of biotic and abiotic parameters providing a solid foundation for future years to enhance the description and understanding of forthcoming changes. The findings underscore the significance of monitoring benthic communities in these dynamic environments, offering valuable insights into the responses of these organisms to environmental disturbances.

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7 APPENDIX

Appendix A1: List of Identification literature

- Aldea, C., Novoa, L., Alcaino, S., & Rosenfeld, S. (2020). Diversity of benthic marine mollusks of the Strait of Magellan, Chile (Polyplacophora, Gastropoda, Bivalvia): a historical review of natural history. *ZooKeys*, 963, 1.
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Appendix A2: List of contacted experts

Table A2: Experts of the respective phyla contributing to the taxonomic identification of the macrofauna samples.

Phylum	Expert
Polychaeta	Americo Montiel , Instituto de la Patagonia, Universidad de Magallanes, Chile
Mollusca	Diego Zelaya , Universidad de Buenos Aires, Argentina Renán Peña , Andrés Bello National University, Chile
Crustacea	Jan Beermann , Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Germany
Others	Sandra Silva Klenner , Universidad Austral de Chile, Chile (specialized in the identification of macrofauna from marine benthic sediments, lakes and rivers)

Appendix A3: Taxa list FF – biomass data

Table A3: Taxa list of macrofauna samples of the FF stations 2022: biomass (g wet mass/m²).

	FF1	FF2	FF3	FF4	FF5	FF6	FF7
Cnidaria							
Hydrozoa	0.025	0.005	0.259	0.019	0.110	0.001	0.022
Arthropoda							
Pycnogonida							
Pantopoda	0	0	0	0	0.003	0	0
Malacostraca							
Decapoda							
Decapoda larvae	0	0	0	0.205	0	0	0
<i>Notiax santarita</i>	0	0	0	0	0	78.176	65.071
Amphipoda							
Ampeliscidae MT 1	0	0	0	0	0	0	0.086
<i>Cheidae</i> sp.	0	0.015	0	0.010	0.028	0	0
Photidae MT 1	0	0	0	0	0.004	0	0
<i>Pseudharpinia</i> sp.	0	0	0	0.057	0	0	0
Phoxocephalidae MT 1	0	0.001	0.041	0.013	0.079	0	0.018
<i>Lepidepecreoides</i> sp.	0	0.007	0.034	0.047	0.052	0	0
<i>Uristes</i> sp.	0	0	0	0.025	0.058	0.024	0
Urothoidae MT 1	0	0.137	0	0.022	0.05824	0	0.023
Hyperiidea MT 1	0	0	0	0	0	0	0.001
Amphipoda MT 2	0	0	0	0.029	0.041	0	0
Amphipoda MT 6	0	0	0	0.001	0	0	0
Amphipoda MT 9	0	0	0	0	0	0.149	0.195
Amphipoda MT 10	0.033	0.078	0	0.021	0	0.272	0.274
Amphipoda indet.	0.001	0.003	0.001	0.031	0.001	0.001	0
Amphipoda fragments	0	0.002	0	0.028	0.014	0	0
Cumacea							
Diastylidae MT 1	0	0	0	0.033	0.149	0	0
Diastylidae MT 2	0.033	0.048	0	0.442	0.188	0	0
Lampropidae MT 1	0	0	0	0	0.014	0	0
<i>Leucon</i> cf. <i>vasilei</i>	0	0	0	0	0.109	0	0
Leuconidae MT 1	0	0	0.011	0.124	0.009	0	0
Leuconidae MT 2	0	0.007	0	0.085	0.006	0.014	0.002
Nannastacidae MT 1	0	0	0	0.030	0.008	0	0
Nannastacidae MT 2	0	0	0	0.005	0.033	0	0
Nannastacidae MT 3	0	0.012	0.008	0	0.014	0	0
Cumacea indet.	0	0	0	0	0.063	0	0
Cumacea fragments	0	0	0	0.001	0.002	0	0.007
Isopoda							
Munnidae MT 1	0	0	0.0001	0	0	0	0
Paramunnidae MT 1	0	0	0	0.003	0	0	0
Isopoda MT 1	0	0	0.009	0	0	0	0
Valvifera	0	0	0	0.001	0	0	0
Mysida	0	0	0	0	0	0.004	0.067
Tanaidacea							
Tanaidacea MT 1	0	0.0001	0.004	0.003	0.005	0	0
Tanaidacea MT 2	0	0	0.002	0	0	0	0
Leptostraca	0	0	0	0	0	0.001	0

Table A3 (cont.)

	FF1	FF2	FF3	FF4	FF5	FF6	FF7
Arthropoda (cont.)							
Ostracoda							
Ostracoda MT 1	0	0.043	0.023	0.078	0.019	0.021	0.097
Ostracoda MT 2	0	0	0	0.007	0.004	0	0
Ostracoda MT 3	0.006	0.019	0	0.027	0.018	0	0
Ostracoda MT 4	0	0	0	0.015	0.002	0	0
Ostracoda MT 5	0	0	0	0	0.037	0	0
Ostracoda MT 6	0	0	0	0	0.01	0	0
Ostracoda indet.	0.001	0	0	0	0	0	0
Crustacea fragments	0.001	0.001	0.002	0	0.006	0.008	0.012
Priapulida	0	0.004	0.013	0	0	0	0.009
Annelida							
Clitellata							
Oligochaeta MT 1	0.001	0.015	0.080	0	0.008	0	0
Polychaeta							
Amphinomida							
Amphinomidae MT 1	0	0.007	0.011	0	0	0	0
Eunicida							
Dorvilleidae MT 1	0	0	0	0.007	0.005	0	0
Dorvilleidae MT 2	0.001	0.002	0.007	0	0	0	0
<i>Lumbrineris</i> sp.	0.082	0.063	0.017	0.212	0.616	0.045	0.511
<i>Ninoe</i> sp.	0.289	0.012	0.008		0.004	0.238	0.308
Oeonidae MT 1	0.026	0.000	0.011	0	0	0	0
Onuphidae MT 1	0.000	0.026	0.048	0.053	0.053	0	0
Onuphidae MT 2	11.578	2.136	0	1.988	0	0	0
Phyllodocida							
Hesionidae MT 1	0	0.127	0	0	0	0	0.015
Hesionidae MT 2	0	0.004	0	0	0	0.036	0.035
<i>Aglaophamus</i> sp.	0	0	0.022	0.171	2.716	0.283	0.195
Nereididae MT 1	0	0.063	0	0	0	0	0.001
Nereididae MT 2	0	0	0.007	0	0	0.035	0.024
Phyllodocidae MT 1	0	0	0.018	0.011	0.002	0	0
Phyllodocidae MT 2	0	0	0.002	0.012	0.012	0	0
Phyllodocidae MT 3	0.001	0	0	0	0	0	0.006
Pilargidae MT 1	0.034	0.094	0	0.026	0.009	0	0
Polynoidae MT 1	0	0.011	0.009	0.037	0.002	0	0
Polynoidae MT 2	0.003	0	0.080	0	0	0	0.04004
Sigalionidae MT 1	0.384	0	0	0	0	1.3104	0
Sphaerodoridae MT 1	0	0.001	0	0.021	0.006	0	0
Sphaerodoridae MT 2	0.086	0.022	0	0	0.053	0	0
Syllidae MT 1	0.008	0	0	0	0	0	0
Syllidae MT 2	0	0.003	0	0	0	0	0
Syllidae MT 3	0	0	0.033	0	0.002	0	0
Glyceriformia MT 1	0	0	0.097	0	0.032	0.002	0.240
Sabellida							
Sabellida MT 1	0	0	0.022	0	0	0	0
Siboglinidae MT 1	0	0	0	0	0.001	0	0
Spionida							
Spionidae MT 1	0.106	0.242	0.074	0.174	0.217	0.059	0.002
Spionidae MT 2	0	0	0.566	0	0	0.00434	0

Table A3 (cont.)

	FF1	FF2	FF3	FF4	FF5	FF6	FF7
Annelida (cont.)							
Terebellida							
Ampharetidae MT 1	0	0	0	0.018	0	0	0
Ampharetidae MT 2	0	0.034	0.574	0	0.067	0	0
Cirratulidae MT 1	0.033	0	0.002	0.027	0.018	0.029	0.080
Cirratulidae MT 2	0.009	0.003	0.005	0.028	0	0.013	0.013
Cirratulidae MT 3	0	0	6.100	0	0	0	0
Cirratulidae MT 4	0.073	0	0	0	0.0314	0	0
Flabelligeridae MT 1	0.004	0	0	0	0	0	0.055
<i>Melinna cristata</i>	0	0	0.014	0	0.487	0	0
Pectinariidae MT 1	0	0	0.023	0	0.003	0	0
Pectinariidae MT 2	0	0	2.702	0	0	0	0
<i>Sternaspis chilensis</i>	0	0.160	0.332	0.004	0.011	0	0
<i>Lanice sp.</i>	0	0	1.875	0	0	0	0
Polycirri MT 1	0	0	0	0	0	0	0.444
Trichobranchidae MT 1	0	0.281	0.074	0	0	0	0
Terebelliformia MT 1	0	0	0.0001	0.057	0.002	0	0
Terebelliformia MT 3	0	0.003	0.253	0	0	0	0
Terebelliformia MT 4	0	0	0	0.233	0	0.295	0.158
Terebelliformia MT 5	0	0	0.156	0	0	0	0
Terebelliformia indet.	0	0	3.878	0	0.039	0	0
Others							
Sabellariidae MT 1	0	0	0.001	0	0.011	0	0
Capitellidae MT 1	0.477	0.007	0.057	0.053	0.086	0.008	0.005
Capitellidae MT 2	0	0	0.008	0.052	0	0	0
Capitellidae MT 3	0	0	0.018	0	0	0	0
<i>Cossura sp.</i>	0.022	0	0.001	0.003	0.004	0.024	0.052
Maldanidae MT 1	0	0	0.267	0.238	0.070	6.997	
Maldanidae MT 2	0	0	0	0	0.037	0.003	0
Opheliidae MT 1	0	0.047	0.012	0.017	0	0	0
Opheliidae MT 2	0.006	0.052	0.016	0	0.024	0.046	0.063
<i>Leitoscoloplos sp.</i>	0.004	0	0	0.012	0.043	0	0
<i>Phylo cf. felix</i>	0	0	0	0	0	0	0.121
Paraonidae MT 1	0.008	0	0.003	0.010	0.048	0.021	0.006
Paraonidae MT 2	0.633	0	0	0.001	0	0	0.020
Paraonidae MT 3	0	0.001	0.001	0.006	0.013	0.115	0.040
Scalibregmatidae MT 1	0.001	0	0.034	0	0	0	0
Scalibregmatidae MT 2	0	0	0	0	0	0	0.043
<i>Myriochele sp.</i>	0	0	0	0	0.0001	0	0
Polychaeta indet.	0	0	0.391	0	0	0	4.920
Polychaeta fragments	11.753	0.390	5.958	1.089	1.736	1.338	0.682
Others							
Sipuncula	0.008	0.008	0.226	0.143	0.394	0.006	0
Bryozoa	0	0	0	0	0	0	0.001
Mollusca							
Bivalvia							
Carditida							
<i>Cyclocardia thouarsi</i>	0	0.020	0	0	0.005	0	0
Galeommatida							
<i>Mysella sp.</i>	0	0	0	0.003	0	0.173	0.003
Lucinida							
<i>Notocina falkandica</i>	0.01	0	0	0.02	0.02	0.01	0

Table A3 (cont.)

	FF1	FF2	FF3	FF4	FF5	FF6	FF7
Mollusca (cont.)							
<i>Adontorhina pisum</i>	0.08	0.03	0.03	0.08	0.14	0.18	2.62
<i>Mendicula sudamericana</i>	0	0.16	0.01	0.30	0.26	0	0
Arcida							
<i>Limopsis marionensis</i>	0	38.255	79.744	0	0	0	0
Nuculanida							
<i>Pseudoneilonella virens</i>	0	0.605	0.263	0.030	0	0	0
Yoldiella indet.	1.014	0.284	0.017	0.117	0.613	2.178	0.803
<i>Silicula patagonica</i>	0	0	0	0	0.157	0	0
Nuculida							
<i>Nucula</i> indet.	0	0.175	0.291	0.167	0.069	0	0
<i>Thracia</i> sp.	0	0.042	0	0	0	0	0
Others							
<i>Cuspidaria</i> sp.	0.133	0	1.179	0	0	0	0
Bivalvia MT 9	0.030	0.116	0.006	0.034	0.034	0	0
Bivalvia MT 15	0	0	0	0	0	0.208	0.010
Bivalvia MT 17	0	0	0.011	0	0	0	0
Bivalvia MT 18	0	0	0.010	0	0.0001	0	0
Bivalvia indet.	0.001	0.001	0.002	0.001	0	0	0
Bivalvia fragments	0	0	0	0.001	0	0	0
Caudofoveata							
Chaetodermatida							
<i>Scutopus</i> sp. 1	0	0.038	0.048	0.058	0.011	0	0
<i>Scutopus</i> sp. 2	0	0.003	0	0.020	0.033	0	0
Others							
Caudofoveata MT 3	0	0	0.022	0.012	0.027	0	0
Gastropoda							
Littorinimorpha							
<i>Amauropsis</i> sp.	0	0.019	0.012	0	0	0	0
<i>Onoba</i> sp.	0.007	0	0	0.114	0.003	0	0
Neogastropoda							
<i>Admete magellanica</i>	0	0	0.008	0.010	0	0	0
Others							
<i>Turritella algida</i>	0	0	0	0.045	0	0	0
<i>Acteon</i> sp.	0	0	0	0.028	0	0	0
Gastropoda indet.	0.001	0.014	0	0	0.002	0	0
Polyplacophora							
<i>Leptochiton medinae</i>	0	0	0.343	0	0	0	0
Lepidopleurida							
Scaphopoda							
Dentaliida							
<i>Dentalium majorinum</i>	0	0.008	0	0	0	0	0
Gadilida							
<i>Siphonodentalium dalli</i>	0.047	0.011	0	0.012	0.071	0	0
Nemertea	0.090	0.069	1.067	0.119	0.015	0.012	1.121
Phoronida	0	0	0	0	0.018	0	0
Echinodermata							
Asteroidea							
Asteroidea larvae	0	0	0	0.006	0	0	0
Ophiuroidea							
Ophiuroidea MT 1	0	0.008	0.018	0.005	0	0	0

Table A3 (cont.)

	FF1	FF2	FF3	FF4	FF5	FF6	FF7
Echinodermata (cont.)							
Ophiuroidea MT 2	0		0.672	0	0	0	0
Echinoidea							
Echinoidea larvae	0	0	0	0.001	0.001	0	0
Holothuroidea							
Dendrochirotida							
<i>Psolus</i> sp.	0	0.000	88.900	0	0	0	0
Unidentified	0	0.903	0.829	0	0.186	0	1.224

Appendix 4: Polychaeta

Table A4: Proportion of polychaetes (%) at the clusters GF, BC and S belonging to the subclasses Errantia and Sedentaria.

	GF	BC	S
Errantia	11.23	17.78	35.15
Sedentaria (Canalipalpata)	14.32	45.91	19.31
Sedentaria (Scolecida)	74.46	36.31	54.46

Appendix A5: SIMPER

Table A5: SIMPER Analysis: taxa contributing up to 50 % to the cumulative dissimilarity between the Clusters 'BC', 'GF' and 'S'. Listed are the average contribution of a specific taxon to the overall dissimilarity (Average), standard deviation (sd), ratio of the contribution of a taxon to the dissimilarity compared to the total dissimilarity (ratio), average abundance of the taxon in each of the two clusters (ava,avb), cumulative dissimilarity (cumsum), (Signif. Codes: p value $< 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$).

GF vs. BC	Average	sd	ratio	ava	avb	cumsum	p
Paraonidae MT 2	0.029	0.005	6.043	7.520	0.212	0.046	0.010**
<i>Cossura</i> sp.	0.015	0.008	1.854	4.630	0.849	0.070	0.010**
Capitellidae MT 1	0.015	0.006	2.498	8.718	5.018	0.094	0.100.
Sipuncula	0.013	0.007	1.953	0.849	4.112	0.114	0.040*
<i>Mendicula sudamericana</i>	0.013	0.006	2.109	0.000	3.243	0.134	0.010**
Sphaerodoridae MT 2	0.012	0.007	1.854	4.397	1.296	0.154	0.030*
Urothoidae MT 1	0.012	0.007	1.663	0.000	3.212	0.174	0.070.
<i>Yoldiella</i> indet.	0.012	0.007	1.816	7.594	4.583	0.193	0.010**
Ostracoda MT 1	0.012	0.004	2.681	0.000	2.970	0.211	0.020*
Siphonodentalium dalli	0.011	0.007	1.550	4.939	2.200	0.229	0.120
Syllidae MT 1	0.011	0.008	1.369	2.755	0.000	0.246	0.030*
Opheliidae MT 1	0.011	0.007	1.555	0.000	2.535	0.263	0.030*
<i>Cheidae</i> sp.	0.010	0.006	1.668	0.000	2.705	0.279	0.030*
<i>Ninoe</i> sp.	0.009	0.006	1.614	3.287	0.929	0.294	0.010**
Onuphidae MT 1	0.009	0.006	1.627	0.000	2.340	0.309	0.040*
<i>Nucula</i> indet.	0.009	0.006	1.586	0.000	2.279	0.323	0.030*
Cirratulidae MT 2	0.009	0.006	1.358	2.597	1.168	0.337	0.200
Oligochaeta MT 1	0.009	0.007	1.266	0.849	2.576	0.350	0.240

Table A5 (cont.)

GF vs. BC	Average	sd	ratio	ava	avb	cumsum	p
Diastylidae MT 1	0.009	0.009	0.925	0.000	2.407	0.364	0.310
<i>Phoxocephalidae</i> sp.	0.009	0.005	1.668	0.000	2.219	0.377	0.070.
Onuphidae MT 2	0.008	0.005	1.677	3.058	0.889	0.391	0.050*
<i>Sternaspis chilensis</i>	0.008	0.005	1.585	0.000	2.125	0.404	0.010**
Tanaidacea MT 1	0.008	0.005	1.607	0.000	2.097	0.417	0.040*
Flabelligeridae MT 1	0.008	0.006	1.337	2.049	0.000	0.430	0.050*
Cirratulidae MT 1	0.008	0.007	1.106	3.997	2.105	0.443	0.660
Polynoidae MT 1	0.008	0.006	1.312	0.000	1.945	0.455	0.110
<i>Leitoscoloplos</i> sp.	0.008	0.006	1.204	2.126	0.744	0.467	0.050*
<i>Pseudoneilonella virens</i>	0.008	0.008	0.914	0.000	1.776	0.479	0.300
Sigalionidae MT 1	0.007	0.006	1.341	1.858	0.000	0.491	0.070.
Ostracoda MT 3	0.007	0.006	1.191	1.009	2.058	0.502	0.290
Paraonidae MT 2	0.034	0.008	4.102	7.520	0.690	0.058	0.010**
Capitellidae MT 1	0.030	0.008	3.598	8.718	2.726	0.109	0.010**
<i>Siphonodentalium dalli</i>	0.025	0.003	9.244	4.939	0.000	0.151	0.010**
Sphaerodoridae MT 2	0.022	0.002	13.065	4.397	0.000	0.188	0.010**
Paraonidae MT 3	0.021	0.011	1.958	0.000	4.179	0.223	0.010**
Spionidae MT 1	0.019	0.009	2.073	6.108	2.352	0.255	0.010**
GF vs. S							
Ostracoda MT 1	0.016	0.002	7.923	0.000	3.185	0.282	0.010**
Onuphidae MT 2	0.015	0.002	6.513	3.058	0.000	0.308	0.010**
Terebelliformia MT 4	0.015	0.002	6.696	0.000	3.058	0.334	0.010**
Hesionidae MT 2	0.015	0.003	4.980	0.000	3.024	0.360	0.010**
<i>Aglaophamus</i> sp.	0.015	0.002	7.130	0.000	2.962	0.385	0.010**
<i>Notiax santarita</i>	0.014	0.001	9.708	0.000	2.840	0.409	0.010**
Syllidae MT 1	0.013	0.010	1.369	2.755	0.000	0.431	0.010**
Pilargidae MT 1	0.013	0.001	19.299	2.546	0.000	0.453	0.010**
<i>Cossura</i> sp.	0.012	0.008	1.418	4.630	2.571	0.473	0.150
Bivalvia MT 9	0.011	0.009	1.332	2.337	0.000	0.492	0.060.
<i>Leitoscoloplos</i> sp.	0.011	0.008	1.353	2.126	0.000	0.511	0.010**
BC vs. S							
Sipuncula	0.016	0.007	2.281	4.112	0.424	0.023	0.010**
Paraonidae MT 3	0.014	0.009	1.631	1.393	4.179	0.044	0.020*
<i>Mendicula sudamericana</i>	0.014	0.006	2.129	3.243	0.000	0.064	0.010**
Spionidae MT 1	0.013	0.008	1.576	5.323	2.352	0.083	0.010**
Cirratulidae MT 1	0.012	0.009	1.442	2.105	4.858	0.102	0.010**
Terebelliformia MT 4	0.012	0.004	3.146	0.212	3.058	0.120	0.010**
<i>Notiax santarita</i>	0.012	0.002	6.778	0.000	2.840	0.138	0.010**
Hesionidae MT 2	0.012	0.004	2.985	0.212	3.024	0.156	0.010**
Oligochaeta MT 1	0.011	0.008	1.460	2.576	0.000	0.172	0.010**
Cheidae sp. 1	0.011	0.007	1.678	2.705	0.000	0.189	0.010**
Opheliidae MT 1	0.010	0.007	1.439	2.535	0.424	0.204	0.010**
Urothoidae MT 1	0.010	0.008	1.278	3.212	1.869	0.219	0.150
Amphipoda MT 10	0.010	0.006	1.713	0.424	2.668	0.235	0.010**
Capitellidae MT 1	0.010	0.007	1.562	5.018	2.726	0.250	0.660
Onuphidae MT 1	0.010	0.006	1.636	2.340	0.000	0.264	0.010**
<i>Nucula</i> indet.	0.010	0.006	1.592	2.279	0.000	0.279	0.010**
<i>Yoldiella</i> indet.	0.009	0.006	1.465	4.583	6.580	0.293	0.060.

Table A5 (cont.)

BC vs. S	average	sd	ratio	ava	avb	cumsum	p
Bivalvia MT 9	0.009	0.007	1.293	2.124	0.000	0.306	0.050*
Diastylidae MT 1	0.009	0.010	0.933	2.407	0.000	0.320	0.120
<i>Siphonodentalium dalli</i>	0.009	0.007	1.367	2.200	0.000	0.333	0.580
<i>Sternaspis chilensis</i>	0.009	0.006	1.593	2.125	0.000	0.347	0.010**
<i>Mysella</i> sp.	0.009	0.007	1.306	0.212	2.151	0.360	0.010**
Tanaidacea MT 1	0.009	0.006	1.613	2.097	0.000	0.373	0.010**
Leuconidae MT 2	0.009	0.007	1.201	1.829	1.727	0.386	0.310
<i>Cossura</i> sp.	0.009	0.006	1.353	0.849	2.571	0.399	0.450
Ostracoda MT 3	0.009	0.006	1.333	2.058	0.000	0.412	0.030*
Polynoidae MT 1	0.009	0.006	1.321	1.945	0.000	0.424	0.020*
Cirratulidae MT 2	0.009	0.006	1.346	1.168	2.706	0.437	0.120
<i>Pseudoneilonella virens</i>	0.008	0.009	0.920	1.776	0.000	0.449	0.090.
Paraonidae MT 1	0.008	0.007	1.159	1.973	2.990	0.461	0.100.
Phoxocephalidae MT 1	0.008	0.006	1.325	2.219	0.983	0.472	0.050*
Nannastacidae MT 3	0.008	0.006	1.364	1.777	0.000	0.484	0.020*
Amphipoda MT 9	0.008	0.006	1.363	0.000	1.777	0.495	0.010**
Leuconidae MT 1	0.008	0.007	1.145	1.858	0.000	0.506	0.040*

Appendix A6: Envfit

Table A6: Results of the envfit analysis: Shown are the coordinates of the first RDA axis (RDA1), coordinates of the second RDA axis (RDA2,) proportion of variation in the data explained by the environmental variable (r2), Signif. Codes: p value < 0.05*, < 0.01**, < 0.001***.

	RDA1	RDA2	r2	p
Depth (m)	0.89244	0.45117	0.9529	0.001***
Temperature near bottom (°C)	-0.32976	0.94406	0.9161	0.001***
Salinity near bottom (PSU)	0.28325	0.95904	0.8576	0.001***
Oxygen near bottom (ml/l)	0.08193	0.99664	0.908	0.001***
Sand (< 2mm) (%)	-0.7808	0.62478	0.5967	0.003**
Mud (< 63 µm) (%)	0.7808	-0.62478	0.5967	0.003**
D ₅₀ (µm)	-0.81112	0.58488	0.723	0.002**
N (%)	-0.96187	-0.2735	0.3475	0.04*
C (%)	-0.98788	0.1552	0.6396	0.002**
C/N	-0.93129	0.36428	0.9088	0.001***
Porosity	0.1788	0.98388	0.3938	0.029*

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