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Investigating the influence of sea ice cover on benthic community and trophic structure

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Abstract

The extent of Antarctic sea ice has decreased rapidly since 2014, reaching a record low of 10.7 × 10^6 km^2 in 2017. The duration and extent of sea ice cover are directly linked to primary production and the subsequent vertical transfer of organic matter to the deep sea. Through this close benthic-pelagic coupling, climate-driven variability in the upper ocean can therefore be expected to directly impact benthic macrofaunal community composition and diversity. To investigate the impact of sea ice cover and primary productivity on community structure, food sources and trophic levels of benthic macrofauna, benthic sampling and experimentation was carried out at 4 stations in the Weddell Sea along a gradient of sea ice cover and primary productivity. Here, community structure parameters (abundance and biomass) were compared between the station with the longest (station 6) and shortest (station 38) period of ice coverage (>50%). Both abundance and biomass were significantly higher at station 38. Polychaetes were more dominant at station 38 and together with larger bivalve specimens strongly contrasted the more varied taxonomic distribution at station 6. In addition, the expected identification of decreasing levels of biomass and abundance with increasing sediment depth were confirmed. Furthermore, stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) and community parameters were compared between station 6 and the Prince Gustav Channel (PGC). Overall, the benthic community at the PGC was dominated by polychaetes, attributed to higher productivity levels benefiting polychaete families, particularly the Maldanidae family. This pattern of polychaete dominance in terms of biomass and abundance was not as pronounced for station 6. The depleted $\delta^{13}C$ and $\delta^{15}N$ signatures at the PGC demonstrate the increased variation in food sources utilised at the PGC, including the possibility of a chemosynthetic and/or terrestrial input in the area. The polychaete family Cirratulidae, in particular, showed a significantly higher $\delta^{13}C$ signature. As a result of climate variability it is to be expected that the identified community shift of increasing biomass and abundance as well as changing taxonomic distributions and stable isotope signatures with varying sea ice cover will be more pronounced in the future. This study provides a baseline for how benthic polar macrofaunal communities will change in response to increasing open water conditions.

Key words: · Antarctica · Benthic · Macrofauna · Climate change · Sea ice cover

Introduction

Polar areas are particularly strongly affected by climate change and loss of ice mass is one of the most prominent symptoms of warming (Hanna et al. 2013, Parkinson 2019). In the Arctic, sea ice loss is unanimously predicted to move towards a summer ice-free Arctic Ocean by 2040 (Zhang & Walsh 2006, Overland & Wang 2013). In the Antarctic, however, the response of Antarctic sea ice coverage to atmospheric greenhouse gas (GHG) loading has not been as straightforward as within the Arctic. Long-term satellite-based sea ice cover records reveal that overall Antarctic sea ice extent increased between 1979 and 2018, but a rapid decline was found during the 2014 to 2017 period, equalling 89% of the total yearly Arctic sea ice extent lost between 1982 and 2016 (Parkinson 2019). As one of only three areas of recent rapid regional (RRR) warming within the higher latitudes, the Antarctic Peninsula has been experiencing significant reductions in sea-ice duration and the adjacent Weddell Sea, the focus of this study, has been experiencing ice extent decreases since 2015 (Vaughan et al. 2003, Parkinson 2019). This loss of sea ice has been identified as one of three major factors expected to affect biodiversity and ecosystem functioning in the Southern Ocean (Convey & Peck 2019). In addition, recent studies have revealed the instability of nearly a quarter of West Antarctic glacier ice, with direct ecological consequences, such as diversity reductions of specialist species. (Bromwich et al. 2013, Shepherd et al. 2019, Cauvy-Fraunie & Dangles 2019). The increasing loss of the West Antarctic Ice Sheet has been found to be connected to the increasing amount of greenhouse gas concentrations through the 20th century; thus, its collapse is found to be a result of anthropogenic influence (Holland et al. 2019).

Primary production efficiency in the Antarctic is dictated by strong seasonal variations of environmental conditions together with nutrient inputs (Priddle et al. 1992). Sea ice duration and extent coupled with light availability and the timing of spring melt are linked to primary production in the Southern Ocean from an environmental perspective (Arrigo et al. 2008, Smith & Comiso 2008, Venables et al. 2013). The key nutrient inputs at the West Antarctic Peninsula consist of iron (Fe) flux, macronutrient and carbon supply, with the latter two transported to the upper ocean via Circumpolar Deep Water (Sherrell et al. 2018, Henley et al. 2018). The productivity of the deep sea depends on organic matter (OM) produced via primary production in the euphotic zone, which is then transported to the deeper layers (Constable et al. 2014). Therefore, benthic-pelagic coupling refers to the exchange of nutrients between the water column and the seabed, playing a prominent role in facilitating nutrient cycling and the transfer of energy in food webs (Graf 1992, Griffiths et al. 2017). Vertical OM transfer is a closely coupled process, with, for example, sinking speed of fast-sinking particulate organic carbon (POC) identified at 85 ± 11 m d^{-1} (DeVries & Weber 2017). Close benthic pelagic coupling means that changes in the euphotic zone, such as increasing primary productivity in newly ice-free areas, will rapidly cascade down to the deep layers (Smith Jr. et al. 2009). Benthic invertebrates in the Southern Ocean receive pulsed organic inputs as a consequence of the seasonality of Antarctic sea ice cover, relying mainly on phytoplankton and sea ice algae as primary food sources (Clarke 1988, Dayton 1990, Arntz et al. 1994, Gili et al. 2001). Johnson et al. (2007) identified how abundance of sediment fauna in the deep sea is dictated by upper ocean primary productivity. In addition, the flux of POC to the deep layers is a major determinant of sediment biomass given its connectivity to the benthic community energy demand (Smith Jr. et al. 2002).

The deep ocean floor (>200 m depth) is the largest habitat on earth, encompassing over 60% of earth's surface, and plays an essential role in bio-geochemical fluxes, such as carbon sequestration, nutrient cycling and trophic linkages (Thurber et al. 2014). Deep-sea benthic assemblages in the Southern Ocean are expected to be strongly influenced by climate-driven environmental changes and predictions for a changing benthic environment range from species extinctions to major shifts in diversity and trophic positions (Ingels et al. 2012). The composition and diversity of deep-sea polar benthic macrofaunal communities is primarily determined by sea ice conditions, ice algae input, organic matter supply, oxygen and salinity (Dayton et al. 1986, Norkko et al. 2007, Kohlbach et al. 2016, Mäkelä et al. 2017a).

Whereas climate variability impacts on the pelagic Antarctic ecosystem have been studied extensively, far less is known about the impact of declining sea ice coverage and resulting increases in primary productivity on benthic communities, specifically within the Weddell Sea (Turner et al. 2009). There remains a lack of research of the impact climate change has and will have on the structure of macrofaunal communities, food sources utilised and food web links surrounding the Antarctic Peninsula with exception to the West Antarctic Peninsula shelf area (Glover et al. 2008, Smale & Barnes 2008). Research on how benthic organisms will cope with environmental changes entails for the majority experimental work via temperature manipulation scenarios (Turner et al. 2009, Ingels et al. 2012). Most benthic organisms on the shelf are expected to benefit from a declining sea ice cover, given increased amounts of algal blooms and resulting increases in shelf phytodetritus (Turner et al. 2009).

The disintegration of Larsen B from the Larsen Ice Shelf in 2002 induced benthic system responses, such as temporary increased deep-sea species growth as a response to a shift towards a eutrophic system and associated phytoplankton blooms (Hauquier et al. 2011, Turner et al. 2014). Seasonal sea ice-cover in polar ecosystems blocks sunlight from reaching the water column, therefore periodically controlling primary production (Smith & Comiso 2008). In response to earlier Antarctic sea ice loss, regime shifts from benthic invertebrate to algae-dominated communities have been identified in shallow seabed ecosystems (Clark et al. 2013). Attributed to the strong connectivity between surface organic carbon production and the deep-sea benthos, reduced sea ice cover and subsequently higher levels of primary productivity may possibly increase benthic biomass (Yasuhara et al. 2012). Benthic foraminifera, for example, have been identified as indirect indicators of sea ice cover (Ishman & Domack 1994). Although primary production levels increase with ice-free open-water conditions, this will not necessarily induce higher biomass and abundance for all benthic species, as the timing and composition of food reaching the seafloor may not be advantageous for all (Gutt et al. 2011, Ingels et al. 2012).

Stable isotope analysis is a well-established tool in trophic ecology for identifying ecosystem fluxes of carbon and nitrogen, therefore enabling the reconstruction of diets and elucidating food source and trophic positioning in food webs (Tieszen et al. 1983, Peterson & Fry 1987, Fry 1991). In contrast to stomach content analyses or behavioural studies, which can be expensive and only reveal the nature of recently ingested food, stable isotope analysis of tissues offers an integrated long-term picture of OM sources assimilated into tissues (Mäkelä et al. 2017). Dual analysis of carbon (C) and nitrogen (N) stable isotope ratios can provide insights into both food sources and trophic position (Post 2002). The minimal increase of <1‰ of $\delta^{13}C$ between primary and secondary consumers enables the quantification of the primary production source and primary food source (Hobson et al. 1995, McMahon et al. 2006). In contrast, there is significantly greater trophic step enrichment of +3.4‰ for $\delta^{15}N$, and $\delta^{15}N$ signatures are therefore a convenient tool to investigate trophic positioning and food web structure within a set community (Zanden & Rasmussen 2001).

The samples analysed in this study are part of a larger international research endeavour led by Professor Ursula Witte (University of Aberdeen) to investigate the influence of sea ice cover and primary productivity on benthic food-web structure and ecosystem functioning. Besides the analysis of the macrofaunal community structure, natural stable isotope signatures and isotope tracing experiments (ITEs) with labelled algal biomass were used to investigate the structure of the benthic food web as well as rates and pathways of OM degradation through the benthic community (Mäkelä et al. 2017b, Mäkelä et al. 2017c).

The focus was to assess community structure, trophic positions in the food web and food source utilization of benthic metazoan macrofauna at one of four transect stations from a subset of samples collected in the Weddell Sea. Another honours student analysed a second station and community structure parameters could therefore be compared between two stations of varying sea ice cover to predict changes of benthic macrofauna assemblages in the face of climate change. Trophic structure of the benthic food web and additional community structure parameters were compared with data from a 2018 expedition to the Prince Gustav Channel, whereby stable isotope ratios were used to derive primary production source ($\delta^{13}C$) and trophic position in the food web ($\delta^{15}N$) of sampled macrofauna (Middelburg 2014).

Specifically, this project tested the following hypotheses:

H1 Abundance and biomass will increase with decreasing median sea ice cover and subsequently, increasing primary productivity between stations.

H2 Abundance and biomass will decrease with sediment depth.

By establishing and comparing community structure, food sources and trophic levels of benthic macrofauna along a gradient of sea ice cover, this study provides a baseline for future research into the ecosystem functioning in a constantly changing environment.

Materials and Methods

Study site and sample collection

Benthic sampling was performed by Professor Ursula Witte in March 2019 during cruise no. PS118 with RV *Polarstern* (for details see Dorschel 2019). The initial target area of the cruise was the break-off point of iceberg A68 in the Larsen C ice shelf. Due to the sea ice conditions encountered, the *Polarstern* was unable to reach the target area and an alternative sampling programme along a gradient of sea ice cover and primary productivity (chlorophyll layer) in the Weddell Sea was devised (Fig. 1). Sediment cores were retrieved using a multiple corer (MUC10, core liner diameter 94 mm, 0.0078 m² surface area) at 4 stations along a gradient of varying sea ice cover and primary productivity. The total number of cores retrieved from the deep Antarctic continental shelf (benthic bathyal) was fifteen per site at depths between 414 and 426 metres. The background sediment cores used for this study were sliced at 0-2, 2-5 and 5-10 cm intervals, sieved through 500 µm mesh size and residues were stored in 5% buffered formaldehyde on board *Polarstern*. Station 6 was sampled on 5th March, 2019 (Table 1). Besides retrieving the macrofaunal control and ITE cores, physical parameters, including sediment oxygen flux via incubations and water column measurements were taken. At best, 5 cores with algae (ITEs) and 6 control cores without algae were incubated for 96 hours at every station. The cores with algal additions were analysed for tracer ^{13}C and ^{15}N incorporated by benthic organisms and background stable isotope ratios were derived from metazoan macrofauna from the control cores.

The focus of this project is the community structure and natural stable isotope signatures of the macrofauna community at station 6 (details of the subset of samples analysed for this project are given in Table 1), the station with the longest ice cover (median sea ice extent >50% from November to March). The macrofauna referred to in this paper are benthic metazoa. Foraminifera, usually regarded as meiofauna, have been excluded from analyses even where large enough to be retained on a 500 µm sieve. The subset of macrofauna samples from the Prince Gustav Channel were collected on the research cruise JR17003 aboard the RV *James Clark Ross* (British Antarctic Survey) in March 2018.

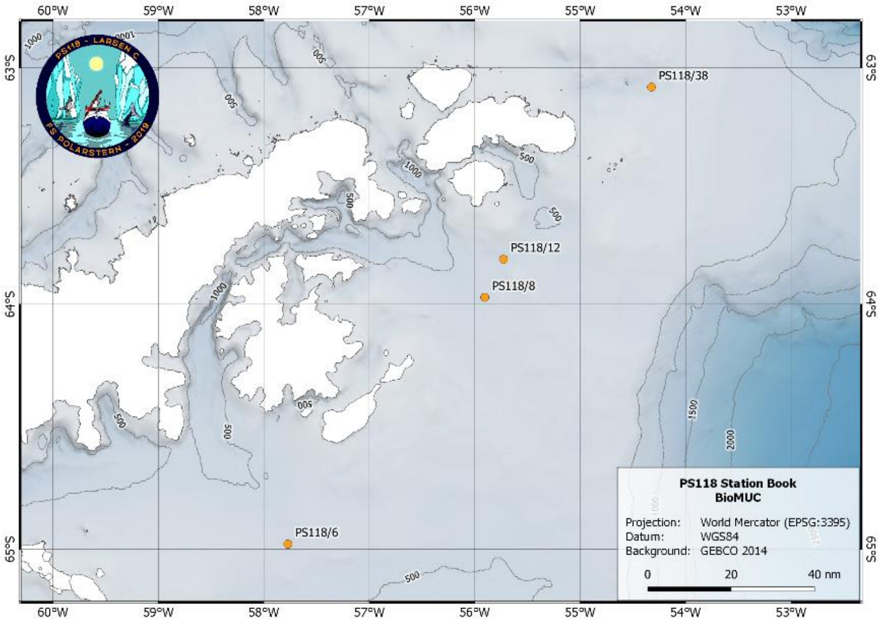

Figure 1. Location of stations of sediment sampled during RV *Polarstern* expedition PS118

Table 1. Background benthic samples from station 6 used in this study, collected by a multi-corer (MUC) at 426 metres depth in the southern Weddell Sea on 5th March, 2019 during RV *Polarstern* expedition PS118

#	Station no.	Core ID	Slice (cm)	Longitude	Latitude
1	PS 118_6_2	J	00-02	64° 58.724' S	57° 46.379' W
2	PS 118_6_2	J	02-05	64° 58.724' S	57° 46.379' W
3	PS 118_6_2	J	05-10	64° 58.724' S	57° 46.379' W
4	PS 118_6_3	I	00-02	64° 58.612' S	57° 46.363' W
5	PS 118_6_3	I	02-05	64° 58.612' S	57° 46.363' W
6	PS 118_6_3	I	05-10	64° 58.612' S	57° 46.363' W
7	PS 118_6_4	G	00-02	64° 58.612' S	57° 46.363' W
8	PS 118_6_4	G	02-05	64° 58.612' S	57° 46.363' W
9	PS 118_6_4	G	05-10	64° 58.612' S	57° 46.363' W

Sample analysis

Taxonomic analysis

Samples were removed from the sample containers and sieved over 250 µm mesh size with artificial seawater. For the duration of taxonomic identification under a dissecting microscope, specimens were kept in petri dishes with artificial seawater. First, macrofauna were sorted into major taxa (polychaetes, echinoderms, oligochaetes, crustaceans and bivalves) and stored in labelled glass vials. In a next step, specimens were identified to the lowest possible taxonomic rank (genus or species for bivalves, families for polychaetes and orders for crustaceans) and stored in 5% buffered formaldehyde. All bivalves present were photographed and species identification was confirmed by Dr. Katrin Linse (British Antarctic Survey), an expert on the taxonomy of Antarctic bivalves and gastropods. Specimen fragments were included in biomass estimates but excluded from abundance estimates.

Biomass

Biomass was determined as dry weight during sample preparation for the stable isotope analysis using pre-weighed tin or silver cups (silver for organisms requiring acidification). Depending on the size of the organisms, specimens were dried in a drying oven for a maximum of 48 hours at a temperature of 60°C. After the specimens were dried, the cups containing the organisms were re-weighed and dry weight was specified.

Stable isotope analysis

For further stable isotope analysis preparation, specimens requiring acidification of the calcium carbonate shell (molluscs, crustaceans and echinoderms) were treated with 50 µl of 1 mol^{-1} hydrochloric acid (HCL) on average. The amount of HCL applied varied with specimen size, with another 50 µl HCL added to organisms exhibiting bubble formation post-acidification. Additional amounts of HCL were added to the specimens until the formation of bubbles ceased and calcified structures had been completely removed. The acceptable range of sample weights for the dual isotope analysis (^{15}N and ^{13}C) by the UC Davis Stable Isotope Facility was set between 0.5 and 1.5 mg. Macrofaunal organisms weighing less than 0.5 mg in dry weight were pooled with the same family, if possible within the same sediment layer and always within a core, to attain the necessary minimum weight for the stable isotope analysis. Macrofaunal specimens with a dry weight >1.5 mg were homogenised and a sub-sample was taken. Final preparations for the dual stable isotope analysis included encapsulating the specimens with tin or silver and tin cups (non-acidified and acidified specimens respectively). The well plates were subsequently sent to the UC Davis Stable Isotope Facility (University of California). Macrofaunal tissue was analysed for carbon (^{13}C) and nitrogen (^{15}N) stable isotope ratios by way of a PDZ Europa ANCA-GSL elemental analyser connected to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Limited, Cheshire, UK). Combustion of samples arranged with chromium oxide and silvered copper oxide at 1000°C was followed by the removal of oxides via a reduction reactor in form of an oxidizing atmosphere at 650°C. Next, by means of a water trap the helium carrier was removed and chromatographic separation of N_2 and CO_2 via a carbon molecular sieve was performed, preparing the samples for the isotope ratio mass spectrometer (IRMS). For high accuracy during the analytical process, samples were intermixed with replicates containing a minimum amount of 4 reference materials, all calibrated against international reference material standards as defined by the International Atomic Energy Agency, including IAEA-600, USGS-40, USGS-41, USGS-42, USGS-43, USGS-61, USGS-64 and USGS-65 reference materials. Provisional isotopic ratios were adjusted to ratio scales of reference gas peak followed by modifying the values by incorporating known laboratory reference materials. Long-term standard deviations for ^{13}C and ^{15}N are 0.2 (0.0002 atom%) and 0.3 (0.0003 atom%) respectively.

Statistics

Analysis of macrofaunal community structure was based on biomass and abundance calculations measured in milligram per square metre (mg m^{-2}) and individuals per square metre (ind m^{-2}) respectively. Data analysis performed in this project was centred around statistical comparisons of abundance, biomass and natural stable isotope signatures between stations 6 and 38. Normal distributions of data were assessed visually and statistically (Anderson–Darling test) with adequate transformations applied when necessary. Stable isotope ratios were used to derive primary production source ($\delta^{13}C$) and trophic position in the food web ($\delta^{15}N$) of sampled macrofauna (Middelburg 2014).

Statistical packages applied for this analysis include Microsoft Excel (v.16.0), Minitab (v. 19.2.0) and R (3.6.1).

Results

Benthic community structure

Total macrofauna abundance at station 6 was 2564 ± 59.68 (SE) ind. m^{-2}. Specimens of the class Polychaeta were most abundant, representing over a third of the total density within the station (36.67%) closely followed by bivalve species (31.67%). Polychaetes and bivalves together amounted to 68.34% of all encountered macrofauna specimens at station 6 (Fig. 2). Isopods, amphipods and cumacea of the class Malacostraca represented 15% of total abundance, whereby 5 brittle stars (class Ophiuroidea) and a single gastropod (superfamily Rissooidea) comprised 8.33% and 1.67% of total abundance respectively.

The mean macrofauna biomass of all classes was 1618.44 ± 106.92 (SE) mg m^{-2} with percentage contributions similar to the pattern described for mean abundance (Fig. 2). Polychaetes comprised just over a third of total macrofauna biomass (34.28%). Jointly, polychaetes and bivalves contributed to 67% of sediment biomass analysed, 31.67% of which is attributed to bivalve families. Brittle stars (11.72%) and crustaceans (13.94%) represented over a quarter of present macrofauna biomass. Oligochaetes (5.78%) and gastropods (<2%) had the lowest overall contributions to macrofauna biomass at station 6 (Fig. 2).

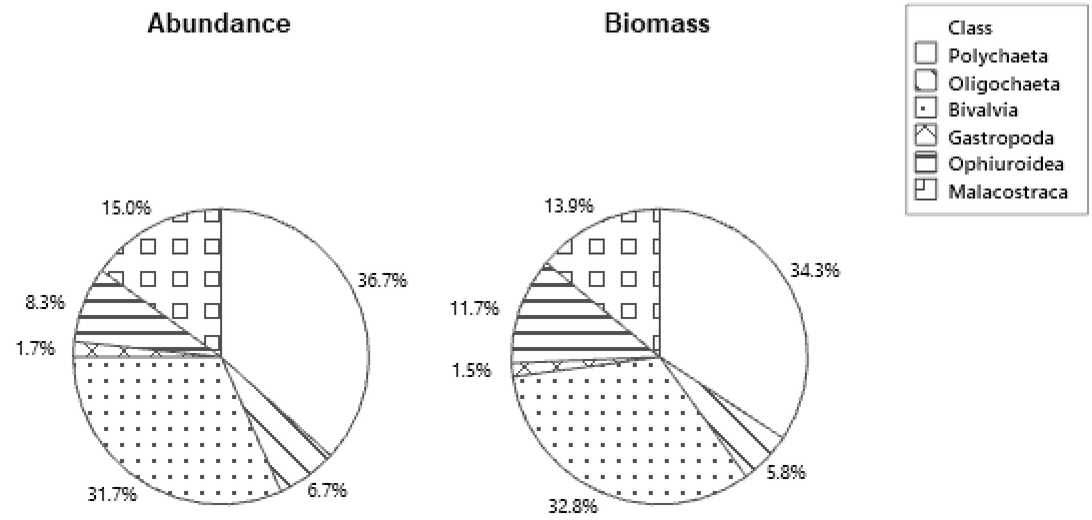

Figure 2. Relative abundance (ind. m^{-2}) and biomass (mg m^{-2}) of macrofauna classes

Altogether, 7 polychaete families were encountered at st. 6, for relative abundances and biomass see Fig. 3. Cirratulidae and Opheliidae were most abundant, comprising approximately 10% of total macrofauna each while jointly representing 50% of all polychaetes. Although Maldanidae comprised the lowest abundance, covering <2% of seabed macrofauna, specimens of this family were found to have the second highest biomass of all polychaete families. Polychaetes of the family Paraonidae contributed to just 3% of macrofauna abundance, nonetheless, constituted the single highest polychaete biomass contributor at 8.87% of all macrofauna biomass.

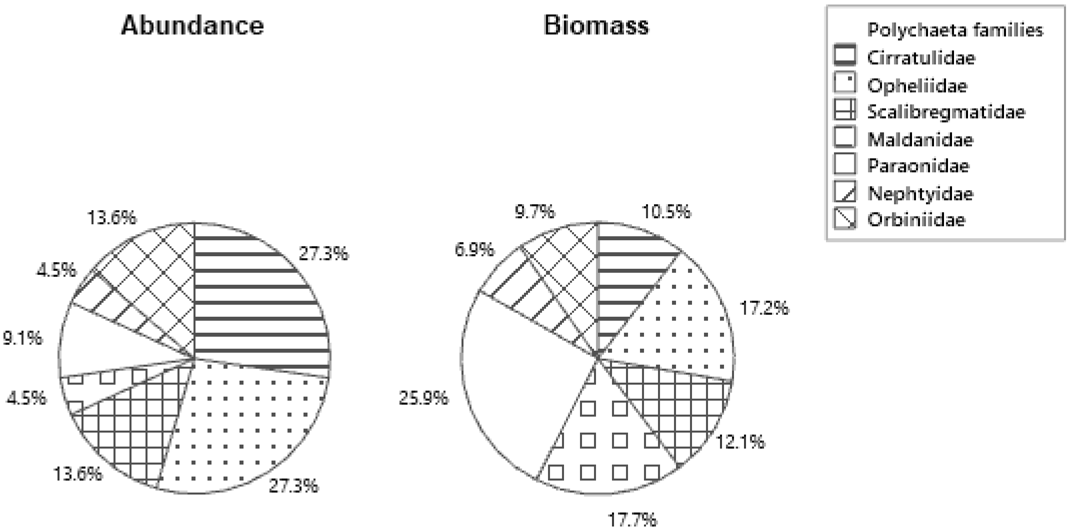

Figure 3. Relative abundance (ind. m^{-2}) and biomass (mg m^{-2}) of polychaete families

Approximately one third of macrofauna biomass consisted of bivalves, 85.4% of which was attributed to the family Yoldiidae which comprised 28% of all macrofauna (Fig. 4). In addition, Yoldiidae specimens had the highest density of all bivalve taxa at 470 ± 156.23 (SE) ind. m^{-2} (18.33% of all macrofauna). Thyasiridae represented the second most abundant bivalve family, accounting for 36.84% of bivalve density, yet making up for only 11.51% of bivalve seabed biomass (Fig. 4). The lowest mean macrofauna abundance and biomass is given by the single Cuspidariidae specimen, figured at 1.67% and 1.03% respectively (Fig. 4).

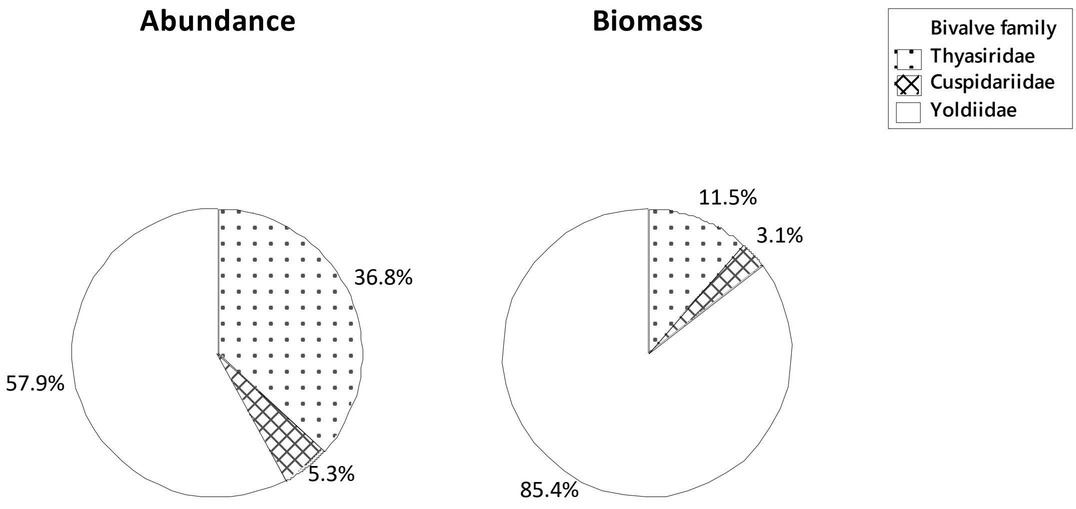

Figure 4. Relative abundance (ind. m^{-2}) and biomass (mg m^{-2}) of bivalve families

Vertical distribution

Of the 60 specimens found in station 6, 80% were present in the 0-2 and 2-5 cm layers. For the two upper layers, mean abundance was 1025.68 ind. m^{-2} each ± 114.08 (SE; 0-2 cm layer) and ± 130.85 (SE; 2-5 cm layer). The lowest depth represented only 20% of encountered macrofauna, figured at 512.84 ind. m^{-2} ± 97.92 (SE) (Fig. 5).

The uppermost layer contained the majority of measured macrofauna biomass, at 46.71% of all biomass measured in the 0-2 cm layer. The 2-5 and 5-10 cm layers contained reduced biomass, representing 29.63% and 23.66% of total biomass respectively, hence biomass decreased significantly with increasing sediment depth (Fig. 5).

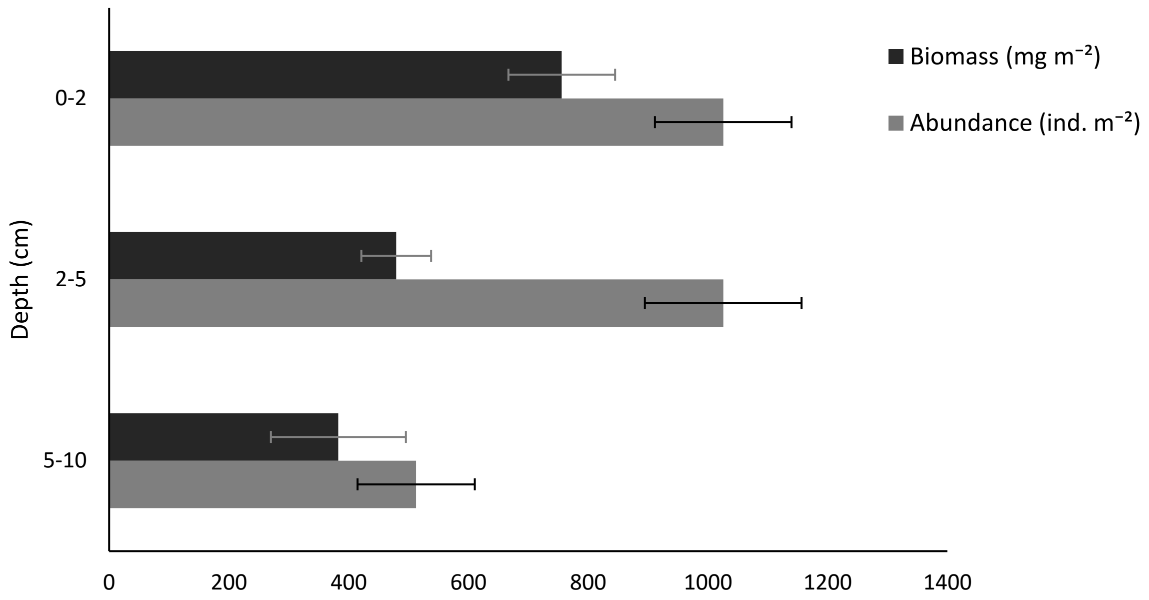

Figure 5. Mean abundance (ind. m^{-2}) ±SE and biomass (mg m^{-2}) ±SE of macrofauna by sediment depth (cm).

The majority of Polychaeta species were distributed between the lower layers, with the 2-5 cm layer holding 45.45% of all identified polychaetes and the 0-2 cm sediment column containing only 13.64% of counted polychaetes. Overall, biodiversity decreased from the uppermost to the lower layers, whereby the classes Gastropoda, Ophiuroidea and Malacostraca were only present in cores of the 0-2 cm sediment column (Fig. 6). Within the shallow 0-2 cm layer, malacostracans (37.50%) were most abundant (Fig. 6). Bivalve abundance was highest in the 2-5 cm sediment column, accounting for 54.17% of all macrofauna in the middle layer. The deepest sediment column was dominated by polychaetes, representing 75% of total abundance in the layer.

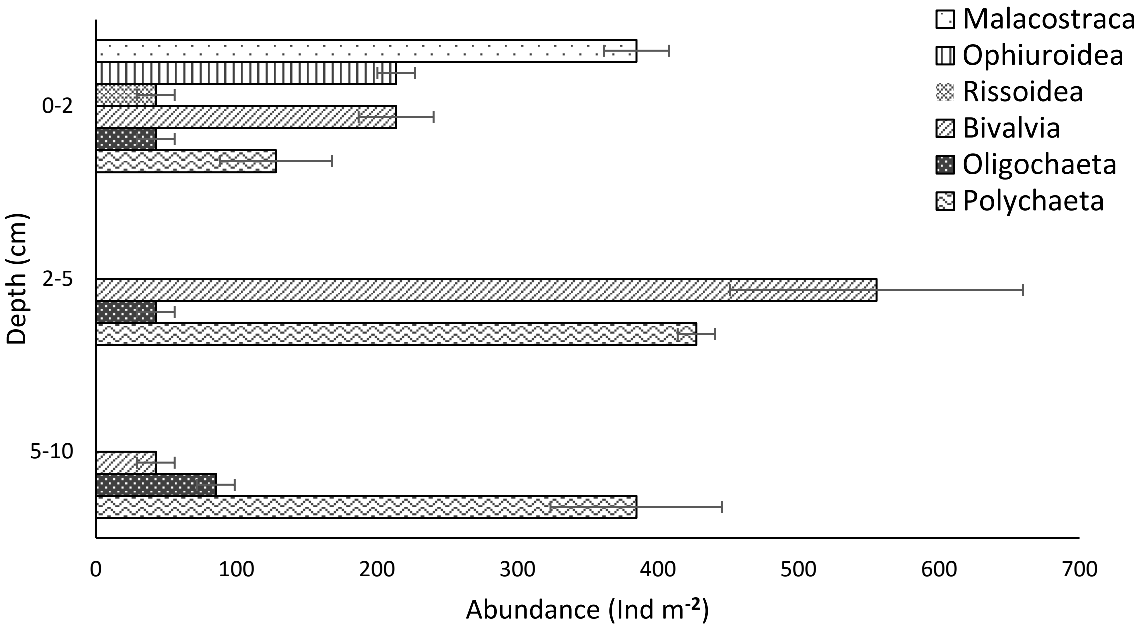

Figure 6. Mean abundance (ind. m^{-2}) ±SE of macrofauna classes by sediment depth (cm)

Bivalve biomass was concentrated (>90%) and approximately evenly split between the upper two sediment layers. Within the 2-5 cm layer macrofauna biomass was dominated by bivalves (51.43%) and polychaetes (43.58%). Polychaete biomass gradually increased from the highest to the lowest layer, with 59.40% of polychaete biomass encountered in the lowest column and just under 3% present in the surface layer. Oligochaeta biomass decreased from the highest to lowest layer, contrasting the increased abundance at the 5-10 sediment column (Fig. 6 & 7). Over 86% of the biomass in the deepest layer was comprised of polychaetes.

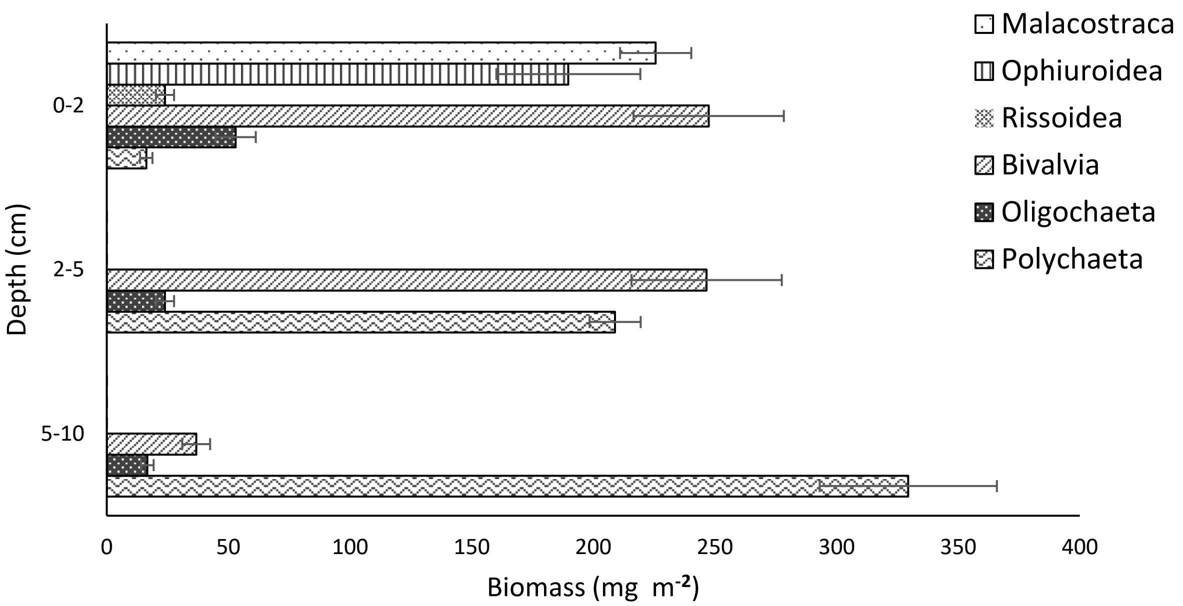

Figure 7. Mean biomass (mg m^{-2}) ±SE of macrofauna classes by sediment depth (cm)

The mid-layer (2-5 cm) was the most abundant and diverse column in terms of polychaete families present (45.45% of all polychaetes) (Fig. 8). Opheliidae was the only polychaete family sampled in all layers and the single polychaete in the 0-2 cm sediment column of station 6, whereby half of the family's abundance was present in the uppermost layer and abundance was reduced towards the deepest layer (Fig. 8). Cirratulidae specimens increased their abundance from representing 20% of all polychaete families in the 2-5 cm column to 44.44% and thus, the most dominant polychaete family in the deepest column.

The calculated mean macrofauna polychaete biomass increased from the shallow to the deepest sediment column, whereby approximately 60% of all Polychaeta biomass was contained in the 5-10 cm layer. Opheliidae represented the only polychaete biomass contribution to the uppermost layer and the highest polychaete biomass found in the 2-5 cm column (Fig. 9). Paraonidae made up the highest biomass polychaete family of the lowest layer, representing 32.04% of all polychaete biomass. Over 80% of Cirratulidae species were found in the deepest layer, accounting for 14.27% of polychaete biomass. Although only one third of Orbiniidae specimens were present in the deeper layer, 53.97% of their biomass constituted the sediment column (Fig. 8 & 9).

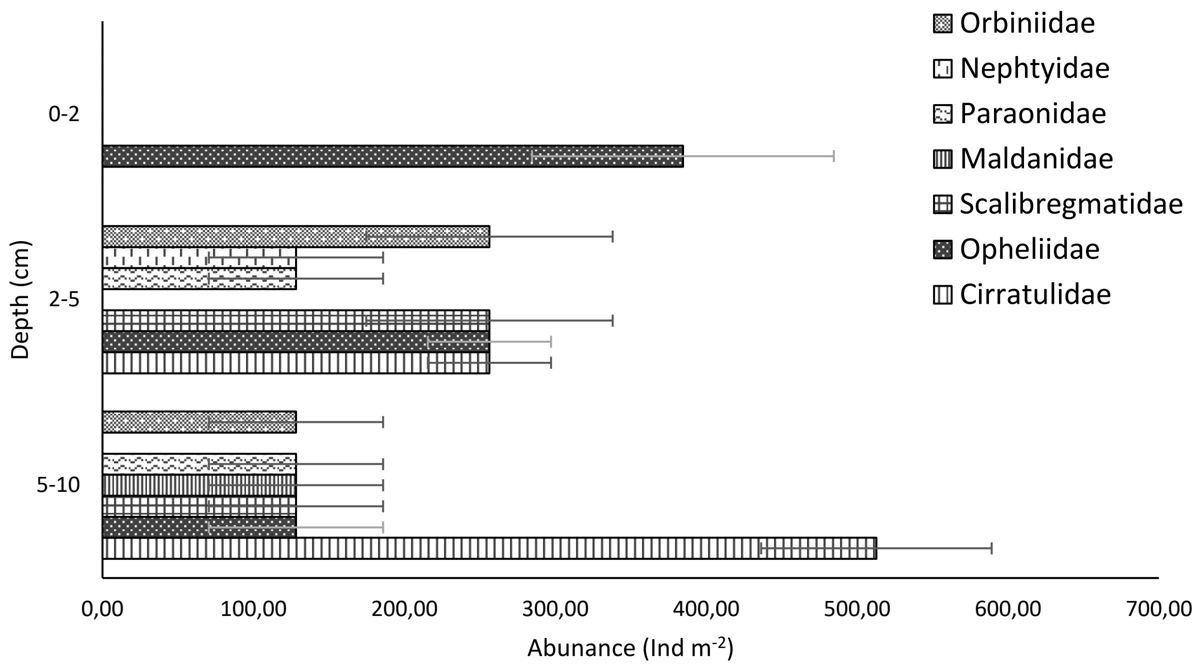

Figure 8. Mean abundance (ind. m^{-2}) ±SE of polychaete families by sediment depth (cm)

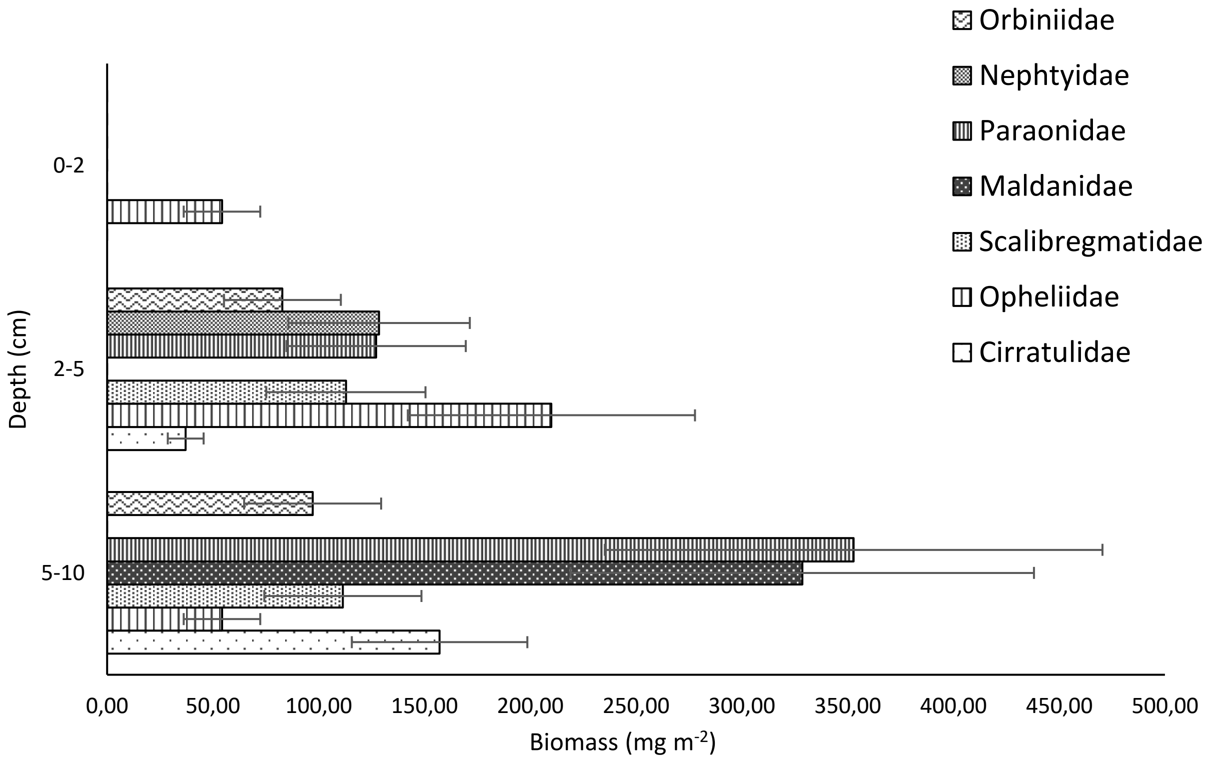

Figure 9. Mean biomass (mg m^{-2}) ±SE of polychaete families by sediment depth (cm)

Natural stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of sedimentary macrofauna

The mean macrofaunal natural $\delta^{13}C$ signature for all benthic metazoa was -21.55‰ ± 0.96 SD (ranging from −23.33‰ to −20.12 ‰), showing little variation. Ophiuroidea represented the class with the lowest $\delta^{13}C$ signature of -22.69 (Table 2). The highest $\delta^{13}C$ signature was given by malcostracans at -20.92‰. No significant differences were identified of $\delta^{13}C$ signatures between the 0-5 and 5-10 cm layers (Mann Whitney U; p=1.00, W=48).

The mean macrofaunal $\delta^{15}N$ signature was 9.23‰ ± 2.58 SD (ranging from 3.23‰ to 13.32‰), therefore detailing significant differences between classes (representing > 2 trophic levels). The lowest $\delta^{15}N$ signature was found in the class Ophiuroidea (Table 2). Oligochaetes were found to have the highest $\delta^{15}N$ signature at 11.29‰. In addition, $\delta^{15}N$ signatures were not significantly different between the two layers (Mann Whitney U; p=0.610, W=51).

Table 2. Mean natural $\delta^{13}C$ and $\delta^{15}N$ isotope signatures of all macrofaunal classes

Class	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Polychaeta	-21.56	9.95
Oligochaeta	-21.48	11.29
Bivalvia	-21.57	8.72
Ophiuroidea	-22.69	3.23
Malacostraca	-20.92	9.06

Within polychaete family's stable isotope signatures concurred with the mean macrofauna results, describing no significant difference for $\delta^{13}C$ and $\delta^{15}N$ between the layers (Mann Whitney U, p > 0.05). The mean background $\delta^{13}C$ signatures of polychaete families were -21.63‰ ± 0.50 SD and -21.96‰ ± 0.84 SD for the upper and lower layer respectively. Polychaete ^{15}N stable isotope values were 10.55‰ ± 2.63 SD in the upper and 8.31‰ ± 1.91 SD in the lower column. The average stable isotope signature of polychaetes in the upper layer was 0.33‰ and 2.24‰ higher for ^{13}C and ^{15}N signatures respectively. Therefore, when present in both layers, the ^{13}C and ^{15}N signatures of polychaete families were higher in the upper column (Fig. 10).

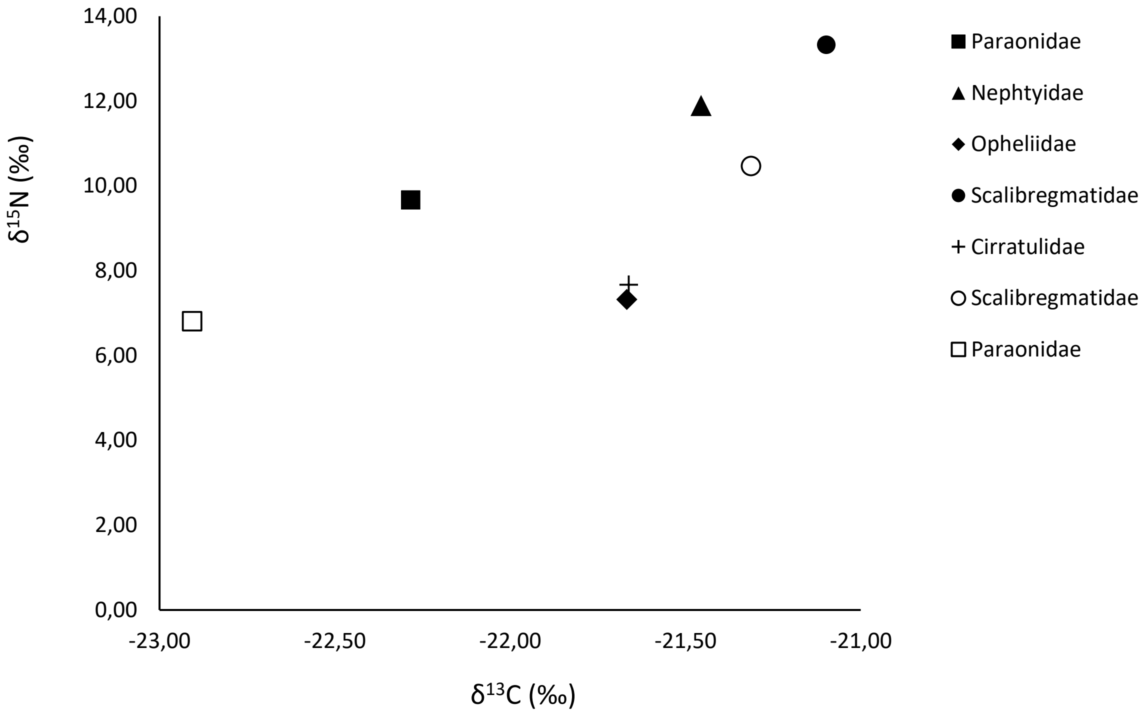

Figure 10. Mean background $\delta^{13}C$ and $\delta^{15}N$ signatures of polychaete families in the 0-5 cm (black) and 5-10 cm column (open, +)

Discussion

Benthic community structure

Altogether, macrofauna at station 6 was composed of typical benthic groups, however, abundance and biomass were relatively low. There is little comparable data available, with most studies from the west of the Antarctic Peninsula. Given the proximity to station 6, results of station 38 and the Prince Gustav Channel have been used for comparison. The datasets for station 38 and the PGC were prepared by another honours student and the results are therefore presented within this section.

Whereas abundance at station 6 was higher than at the PGC, biomass was over 3 times higher at the channel (Fig. 11). As a consequence of the shorter period of sea ice cover at the PGC, benthic nutrient availability is expected to be higher compared to station 6. The large polychaete specimens found at the PGC seem to benefit most from available nutrients, a pattern also identified in the Arctic (Vedenin et al. 2018).

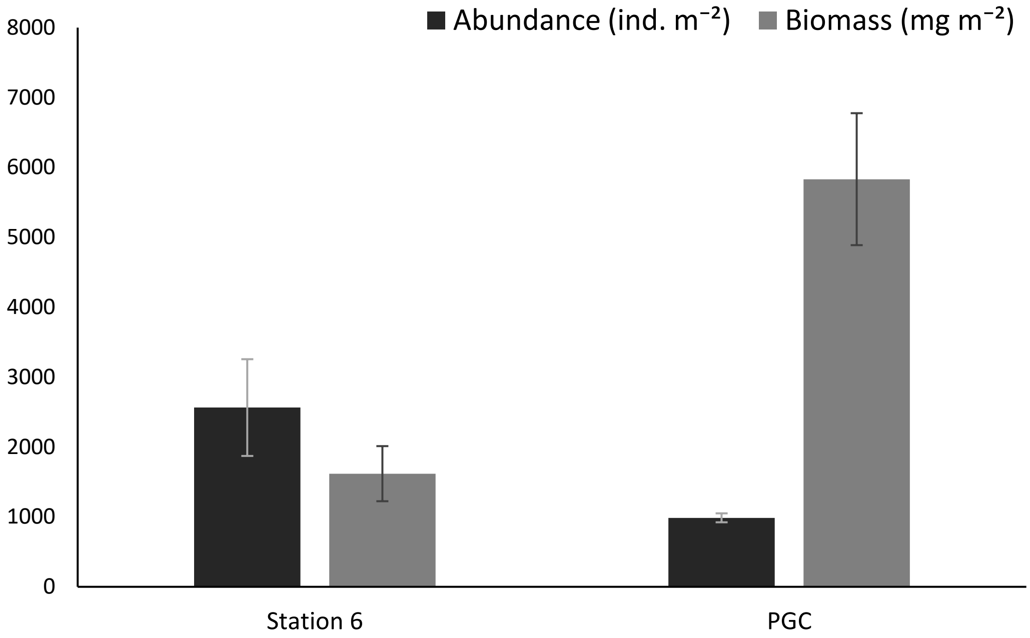

Figure 11. Mean abundance (ind. m^{-2}) ±SE and biomass (mg m-^{2}) ±SE of benthic macrofauna from station 6 and the Prince Gustav Channel (PGC)

The high dominance of polychaetes at the PGC is contrasted by station 6. Polychaetes represented 84% of biomass at the PGC compared to only 33% at station 6 (Fig. 12). In addition, bivalves at station 6 contributed to 33% of biomass, whereas at the PGC this was less than 5%. A similar picture was given for polychaete abundance, figured at 69% and 32% at the PGC and station 6 respectively (Fig. 12). Malacostraca at station 6 represented the third highest contributor to abundance and biomass, whereas at the PGC malacostracans represented significantly lower contributions (<3%). This dominance of polychaetes in terms of abundance and biomass resembles the higher nutrient input at the PGC (Rosenzweig & Abramsky 1993). Terrestrial nutrient inputs are expected to support the benthos at the PGC, given the land proximity within the channel. No particular polychaete family was found to overly dominate abundance or biomass at station 6, as no family contributed more than 30% to either. At the PGC, however, over half of the polychaete biomass consisted of Maldanidae species. Polychaetes dominate Antarctic marine macrofauna and with higher productivity levels within the PGC certain polychaete species, such as Maldanidae, appear to benefit and dominate the benthic community (Hilbig et al. 2006, Glover et al. 2008, Dimitriou et al. 2017).

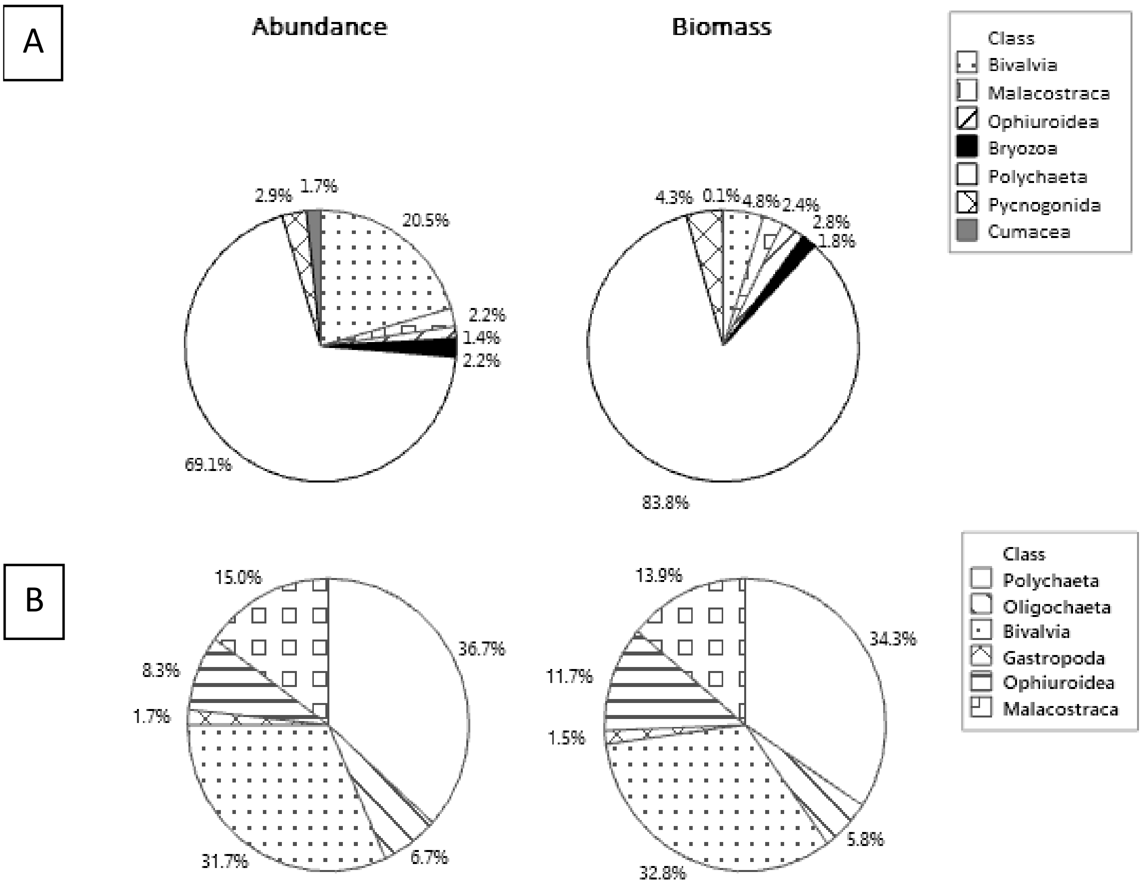

Figure 12. Relative abundance (ind. m^{-2}) and biomass (mg m^{-2}) of macrofauna classes at the PGC (A) and station 6 (B)

Seasonal ice cover differs most significantly between station 6 and station 38 and thus, differences in community structure parameters are expected to be present between the two stations. This hypothesis is confirmed, given the significant increase in mean macrofauna biomass and abundance at station 38 (Fig. 13). The abundance estimated at station 38 was 4658.30 ± 1169.84 (SE) ind. m^{-2} and therefore 1.82 times higher than the total macrofauna density encountered at station 6 (Fig. 13). In addition, mean biomass at station 38 was over 5 times higher compared to biomass at station 6. The increase in macrofauna abundance and biomass can be elucidated by looking at the median sea ice extents at both stations. Whereas station 6 has a median sea ice extent >50% from November to March, station 38 is covered >50% by sea ice only from November to December. The longer period of light availability in the water column of station 38, along with increased rates of primary productivity and available benthic chlorophyll, are expected to contribute to the significantly higher macrofauna biomass at the station (Cochrane et al. 2009). Degen et al. (2015) found a significant reduction in abundance and biomass of macrobenthic communities under increasing sea-ice extent, relating to the results described above.

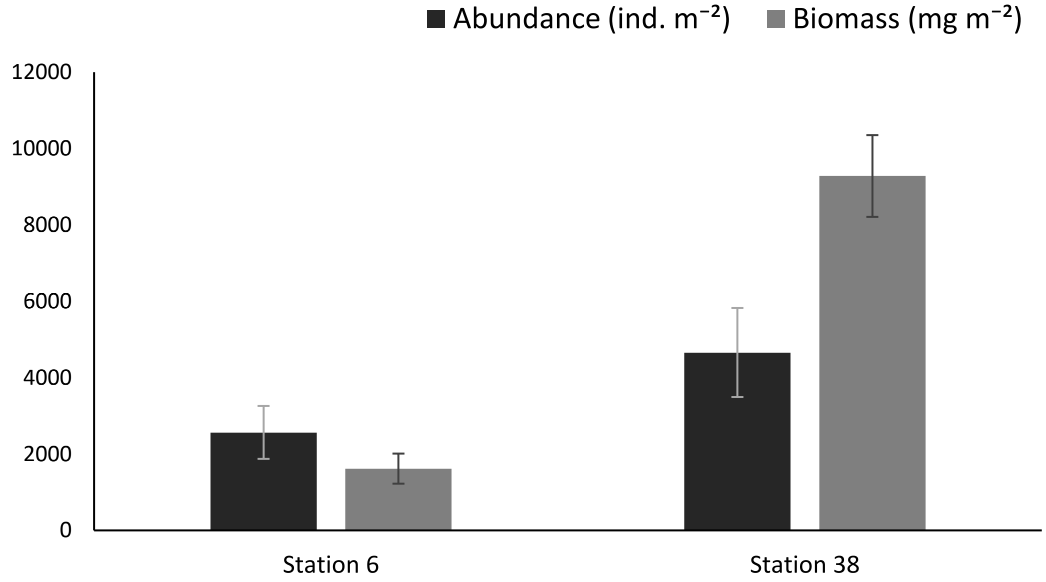

Figure 13. Mean abundance (ind. m^{-2}) ±SE and biomass (mg m^{-2}) ±SE of benthic macrofauna from station 6 and 38

The pattern of taxonomic contributions to total abundance estimates was similar between station 6 and 38, in that polychaetes covered the majority of seabed density (Fig. 14). In contrast, polychaetes sampled at station 38 comprised 72.47% of total macrofauna abundance, whereas polychaete abundance was estimated at only 36.67% at station 6. This resembles the higher contributions of bivalves (31. 67%) and malacostracans (15%) towards density at station 6, compared to 17.43% and 3.67% percent coverage for both classes at station 38 respectively.

Total macrofauna biomass between the stations showed a similar pattern as for density, given the lower abundance of polychaetes in station 6 compared to station 38 (Fig. 15). Oligochaetes, gastropods and malacostracans contributed <1% towards macrofauna biomass, followed by ophiuroids (<6%) at station 38, whereas, for example, malcostracans and ophiuroids attributed to 13.94% and 11.72% of biomass at station 6 respectively. However, bivalves represented around 30% of biomass at both stations.

In sum, although total mean macrofauna biomass and abundance were significantly higher at station 38, this is attributed to the higher abundance and biomass of polychaetes (polychaete biomass was over 10 times higher in station 38) and bivalves. Polychaetes and bivalves in station 38 were more abundant and larger in size and consequently contained a higher biomass. Contrary to the higher polychaete and bivalve abundance, station 6 had a more diverse pattern of contributions, with gastropods, ophiuroids and malacostracans comprising higher total mean abundance and biomass values (Fig. 14 & 15).

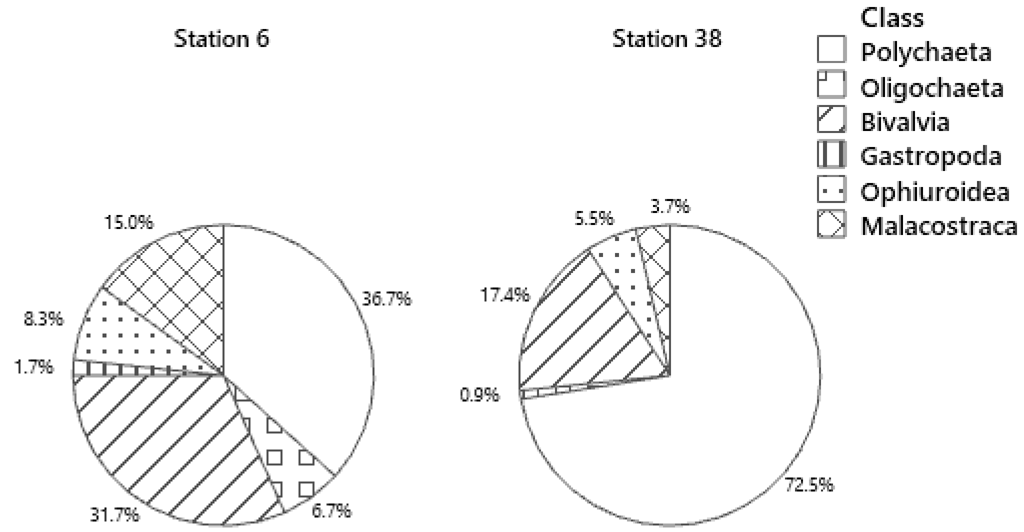

Figure 14. Relative abundance (ind. m^{-2}) of macrofauna classes at station 6 and 38

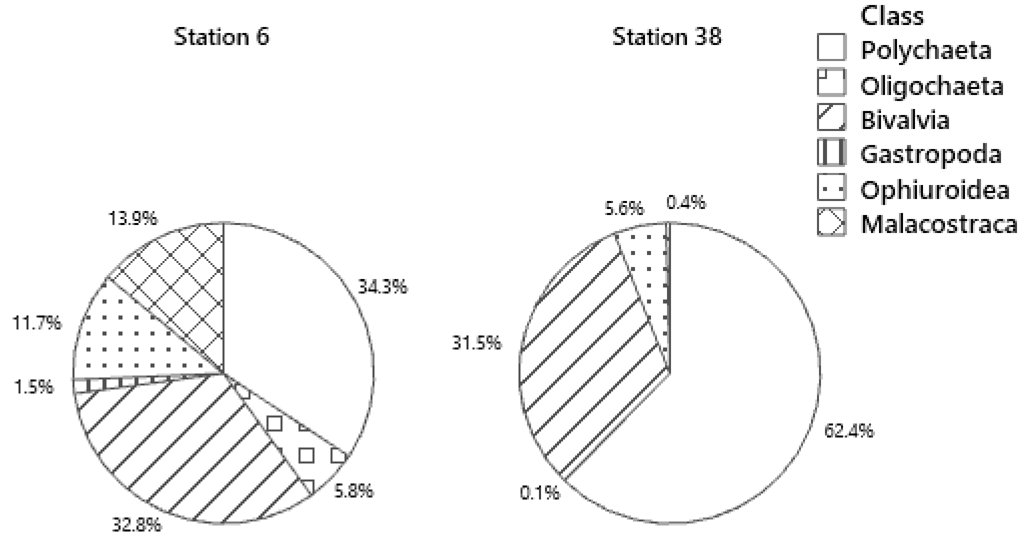

Figure 15. Relative biomass (mg m^{-2}) of macrofauna classes at station 6 and 38

The comparison of vertical distributions was limited to a single core in station 38 and thus, the total macrofauna contributions may not be representative of the sampled location. Macrofauna abundance was over 4 times higher in the 0-2 cm layer at station 38, despite station 6 comprising higher total abundances at the two lower layers (Fig. 16). Both the 0-2 and 5-10 cm layers at station 38 showed significantly higher biomass values compared to station 6, however, total macrofauna biomass at the 2-5 cm sediment column was higher at station 6 (Fig. 17).

The two deeper columns at station 38 consisted exclusively of polychaetes, indicative of a reduction in diversity in areas of increased primary productivity and organic matter transport to the benthos. Dimitriou et al. (2017) discovered a reduction in diversity and increases in the dominance of certain species in high nutrient treatment benthic macrofauna. The increased temporal availability of nutrients on the seabed at station 38 may provide polychaete species with a competitive advantage over other macrofaunal classes.

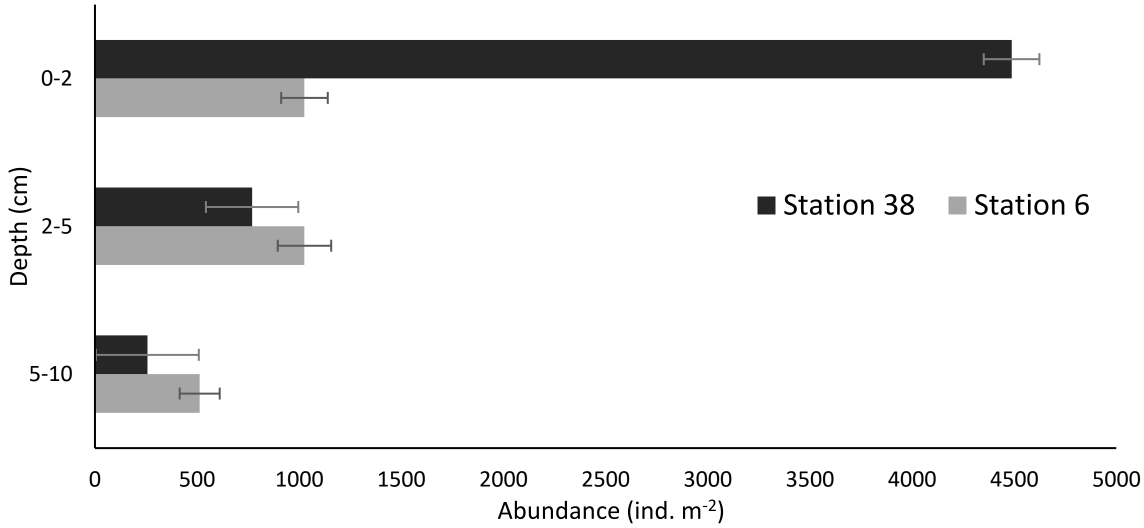

Figure 16. Mean abundance (ind. m^{-2}) ±SE of macrofauna by sediment depth (cm) at station 6 and 38

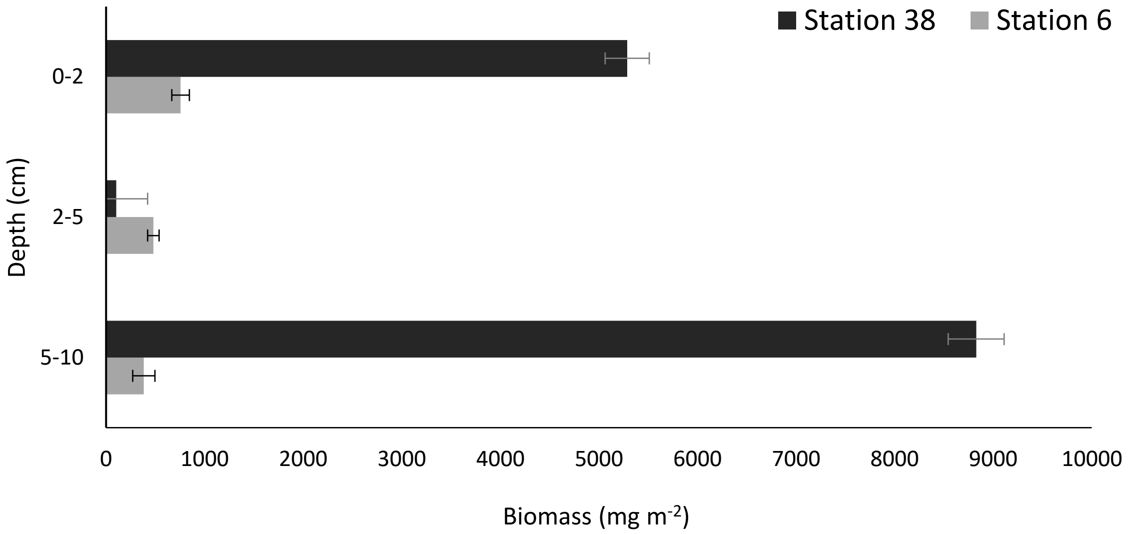

Figure 17. Mean biomass (ind. m^{-2}) ±SE of macrofauna by sediment depth (cm) at station 6 and 38

The total macrofauna abundance estimate at station 6 was substantially lower than abundance estimates identified in the Arctic climate of the western Baffin Bay region (Mäkelä et al. 2017). Abundance at the North Water Polynya area, for example, was estimated to be over 4 times higher (7974 individuals per m^{-2} more). This reduction in abundance at station 6 is in agreement with other observations where persistent sea ice cover was linked to a reduction in the overall density of benthic communities (Clark et al. 2017). Similar observations were made for overall macrofauna biomass, which was 1.5 times higher at the western Baffin Bay (Mäkelä et al. 2017). Sea ice cover has been identified as a good predictor of benthic community biomass, related to higher primary productivity in open water conditions and subsequent higher nutrient input to the benthos (Wlodarska-Kowalczuk et al. 2004, Cochrane et al. 2009).

Polychaeta was the dominating taxon of abundance and biomass at station 6, underlined by similar observations of benthic metazoan macrofaunal community structure in the Arctic (Mäkelä et al. 2017). There was no clear dominance of a particular polychaete family, however, Cirratulidae and Ophelliidae represented over half of total polychaete abundance. A single large Paraonidae specimen is responsible for the family representing the overall highest biomass. Within the Baffin Bay region crustaceans had a much higher abundance of 57% compared to only 14% at station 6, yet crustaceans represented the class with the highest density in the uppermost layer, not present in the 2-10 cm depth (Mäkelä et al. 2017). The dominant bivalve family Yoldiidae at station 6 (85% of bivalves) in terms of abundance and biomass is in general accordance with other observations of high Yoldiidae density and biomass contributions in the Antarctic (Peck & Bullough 1993, Pasotti et al. 2015).

The identified pattern of higher macrofauna abundance and biomass in the upper sediment layer is underlined by metazoan macrofauna community vertical distribution in a range of similar observations (Kornijów & Pawlikowski 2016, Mäkelä et al. 2017). Malacostracan and bivalve distribution is generally constrained to the benthic surface, whereas polychaetes and oligochaetes can thrive at lower depths (Shirayama & Horikoshi 1982). This pattern of vertical distribution is resembled within station 6, whereby malacostracans represented the most abundant class in the surface layer (37%) and polychaetes made up 75% of total macrofauna abundance in the deepest layer (5-10 cm). Biomass parameters showed a similar picture with polychaete biomass gradually increasing from the higher to the lower layers. Although polychaete diversity was higher in the 2-5 cm layer, biomass was largely concentrated in the lowest layer (> 60%).

Natural stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of sedimentary macrofauna

At station 6 the mean macrofaunal $\delta^{13}C$ signature of -21.55‰ was higher compared to available literature from similar marine ecosystems. Previous research by Bravo (2018) identified average macrofaunal $\delta^{13}C$ values of -24.06‰, -23.43‰ and -22.14‰ in the Beaufort Sea, Amundsen Gulf and Baffin Bay respectively. Variation within $\delta^{13}C$ was negligible from −23.33 ‰ to −20.12 ‰, representing a 3-step tropic level variation and a certain extent of different food sources utilised (Hobson & Welch 1992). The majority of specimens studied were deposit feeders, relating to the comparably low variation of ^{13}C signatures (Le Loc'h et al. 2008).

The mean $\delta^{15}N$ isotopic value of 9.23‰ (ranging from 3.23‰ to 13.32‰) was higher than reported nitrogen signatures in the Arctic Archipelago polynyas, reported at 2.00‰ (Mäkelä et al. 2017). The considerable $\delta^{15}N$ variation points to the presence of more than two sampled trophic levels. In addition, the degree of enrichment identified supports findings made by Aberle & Witte (2003) that benthic macrofauna do not represent a single taxonomic group.

Total mean macrofaunal $\delta^{13}C$ and $\delta^{15}N$ signatures were higher at the Prince Gustav Channel compared to station 6 (Table 3). There was considerable variation of $\delta^{13}C$ at the PGC (ranging from -46.5‰ to -6.3‰) compared to station 6 (ranging from -23.33‰ to -20.12‰). These results point towards different food sources utilised in the two sites, elucidating mixed aquatic and terrestrial inputs at the PGC. Additionally, the encountered variation may be a result of distinct lipid content of macrofauna species and subsequent varying rates of $\delta^{13}C$ depletion in the samples. Mateo et al. (2008), for example, identified a 4.9‰ $\delta^{13}C$ depletion in polychaetes post acid-treatment. The dominant feeding strategy for most species sampled at both sites was deposit feeding, therefore shifting predatory strategies in terms of particulate OM uptake is unlikely (Fry 2006, Gillies et al. 2012). Gillies et al. (2011) identified a misalignment between $\delta^{13}C$ signatures and potential food source signatures, possibly explaining the low values identified in some polychaete families at the PGC.

In accordance with the significant variation of $\delta^{13}C$ at the PGC, $\delta^{15}N$ values ranged from -0.7‰ to 21.1‰, in suggestion of more than one trophic level identified at the site. Although $\delta^{15}N$

ratios at station 6 also indicated the identification of more than one trophic level, the variation was less significant (ranging from 3.23‰ to 13.32‰), indicating more varied food sources at the PGC. The maximum $\delta^{15}N$ value of 21.1‰ could be explained by nutritional stress and sustained periods of starvation in the PGC area, resulting in continuous ^{15}N organismal tissue enrichment (Adams & Sterner 2000, Tibbets et al. 2008, Mayor et al. 2011, Gontikaki et al. 2011). Gontikati et al. (2011) identified a significant ^{15}N-enrichment pattern in the polychaete families Capitellidae and Scalibregmatidae most likely as a result of starvation cycles.

Table 3. Mean background $\delta^{13}C$ and $\delta^{15}N$ signatures ± SD by location

Stable isotope signatures [location]	Carbon and nitrogen stable isotope values ±SD
$\delta^{13}C$ [St. 6]	**-21.55‰ ± 0.96 SD**
$\delta^{13}C$ [PGC]	**-19.7‰ ± 0.8 SD**
$\delta^{15}N$ [St. 6]	**9.23‰ ± 2.58 SD**
$\delta^{15}N$ [PGC]	**10.3‰ ± 1.6 SD**

Polychaete families sampled at both sites showed higher $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures at the PGC (Fig. 18). The $\delta^{13}C$ isotopic signature of Cirratulidae polychaetes in particular was significantly different from the isotope ratios of the same family at station 6. A maximum normalized residual test (Grubbs test) confirmed the $\delta^{13}C$ signature of Cirratulidae at the PGC as an outlier ($p=0.005$, $G=1.99$). The depleted $\delta^{13}C$ signature of Cirratulidae is indicative of different food sources utilised at the PGC site. Previous work by the Larsen C Benthos research programme has identified a chemosynthetic input within the vicinity of the PGC, possibly explaining the identified depleted signature (Linse 2018). In addition, the depleted signature is expected to be connected to a terrestrial input at that site. The distance between the mid-PGC and the Antarctic land mass is approximately 7 km, whereas the nearest land mass to station 6 is well over 60 km.

Further tests for significant differences in polychaete signatures between the PGC and station 6 did not return positive results for the $\delta^{13}C$ ($p=0.651$, $DF=2$, $T=0.53$) or $\delta^{15}N$ ($p=0.072$, $DF=2$, $T=3.51$) signatures. These results are confirmed visually, as isotope signatures of polychaete families were slightly higher at the PGC, however, the differences averaged merely -2.59‰

and 4.06‰ for $\delta^{13}C$ and $\delta^{15}N$ respectively. The average Cirratulid*ae* $\delta^{13}C$ signature of -34.4‰ implies a lack of ice algae (around -15‰) or phytoplankton (around -19‰) utilisation by the polychaete family, further promoting the likeliness of a terrestrial input supporting the food web at the PGC (Mäkelä et al. 2017b).

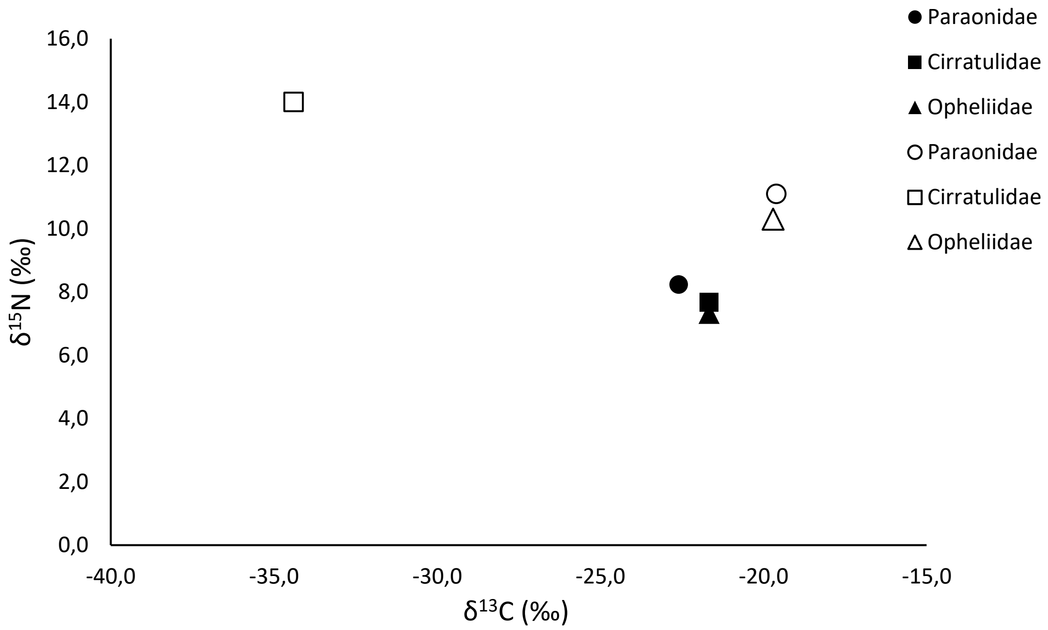

Figure 18. Mean background $\delta^{13}C$ and $\delta^{15}N$ signatures of polychaete families at station 6 (black) and Prince Gustav Channel (open)

Conclusions

The identified decreasing levels of biomass and abundance with increasing sediment depth at station 6 confirm the hypothesis (H2). The results show a variation in community structure between station 6 and station 38, detailing significantly higher biomass and abundance at station 38 (H1). Furthermore, the taxonomic distribution between the stations differ, with large polychaete specimens representing the vast majority of species identified at station 38. This shift in community structure can be attributed to the reduced period of sea ice cover at station 38 and, consequently, higher levels of light absorption, primary production and available benthic chlorophyll for the benthos.

The greater biomass at the Prince Gustav Channel (PGC) can be attributed to the higher nutrient availability in the area. Specifically, the dominance of Polychaeta as the most abundant family, representing over 80% of biomass in the channel, is contrasted by more varied taxonomic abundances and biomass contributions at station 6. The higher mean $\delta^{13}C$

and $\delta^{15}N$ signatures at the PGC elucidate different food sources utilised at the two sites of varying periods of sea ice cover. The considerable variation of $\delta^{13}C$ at the PGC, in contrast to station 6, further highlights these signature differences. The depleted natural isotope signature is indicative of increased variation in food sources utilised. Possible explanations for this observation are a chemosynthetic input at the PGC as identified in previous work in the area and/or a terrestrial input based on the land proximity of the channel.

With rapid Antarctic sea ice extent decreases identified in the recent past, culminating in a 40 year low in 2017, benthic communities will be subject to ongoing ecological changes. This study provides a first-order comparison of benthic community structure and natural stable isotope signatures between areas of varying sea ice coverage. By means of further research into the C and N uptake rates through ongoing isotope tracing experiments and with the inclusion of additional sampling areas, a more conclusive picture of the changes identified is expected.

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