

ORIGINAL ARTICLE

Antarctic shallow water benthos in an area of recent rapid glacier retreat

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Abstract

The West Antarctic Peninsula is one of the fastest warming regions on Earth. Faster glacier retreat and related calving events lead to more frequent iceberg scouring, fresh water input and higher sediment loads, which in turn affect shallow water benthic marine assemblages in coastal regions. In addition, ice retreat creates new benthic substrates for colonization. We investigated three size classes of benthic biota (microbenthos, meiofauna and macrofauna) at three sites in Potter Cove (King George Island, West Antarctic Peninsula) situated at similar water depths but experiencing different disturbance regimes related to glacier retreat. Our results revealed the presence of a patchy distribution of highly divergent benthic assemblages within a relatively small area (about 1 km²). In areas with frequent ice scouring and higher sediment accumulation rates, an assemblage mainly dominated by macrobenthic scavengers (such as the polychaete *Barrukia cristata*), vagile organisms and younger individuals of sessile species (such as the bivalve *Yoldia eightsi*) was found. Macrofauna were low in abundance and very patchily distributed in recently ice-free areas close to the glacier, whereas the pioneer nematode genus *Microlaimus* reached a higher relative abundance in these newly exposed sites. The most diverse and abundant macrofaunal assemblage was found in areas most remote from recent glacier influence. By contrast, the meiofauna showed relatively low densities in these areas. The three benthic size classes appeared to respond in different ways to disturbances likely related to ice retreat, suggesting that the capacity to adapt and colonize habitats is dependent on both body size and specific life traits. We predict that, under continued deglaciation, more diverse, but less patchy, benthic assemblages will become established in areas out of reach of glacier-related disturbance.

Introduction

The West Antarctic Peninsula (WAP) is widely known to be one of the fastest warming regions on Earth, with an increase in some regions of 1.09 °C per decade in winter

and a total increase in mean annual air temperatures of around 2.8 °C over the last half century (period 1961–2000) (Vaughan *et al.* 2003; Turner *et al.* 2005). Glaciers along the WAP have been retreating rapidly since the 1950s (Cook *et al.* 2005). Glacial retreat impacts the local

marine environment. Large amounts of ice can be released in one single calving event, potentially leading to abrupt increases in water turbidity, freshening of surface waters (Dierssen *et al.* 2002), and the formation of icebergs and coastal brash ice. In general, the impact of icebergs can be detected down to 600 m depth, and occasionally up to 1000 m, on the Antarctic continental shelf, where it represents one of the main disturbances, causing the patchy (fragmented) structure of the benthic communities (Peck *et al.* 1999; Gutt 2001; Smale & Barnes 2008; Convey *et al.* 2012 and references therein). In shallow waters and in the vicinity of the glacier fronts, frequent ice scouring events have a major structuring effect on benthic communities (Sahade *et al.* 1998, 2008; Gutt 2001; Smale *et al.* 2008a,b; Philipp *et al.* 2011). Glacier retreat also opens up newly exposed substrata for colonization (Rückamp *et al.* 2011; Quartino *et al.* 2013). In addition to enhanced glacier calving, regional changes also include enhanced snow melting, which speeds up ice and permafrost melting and can lead to sudden freshening events and increased turbidity in the marine coastal environment during warm summer periods (Dierssen *et al.* 2002; Schloss *et al.* 2002; Hass *et al.* 2010).

The present study investigates the shallow water benthos, associated with soft sediments in Potter Cove (PC, King George Island, WAP), within the context of a wider ecosystem study (ESF-PolarClimate, IMCOAST, www.imcoast.org) which aimed at assessing the complex changes affecting WAP shallow water environments. Aerial photography and satellite images document the fast retreat of the Fourcade Glacier since 1956 (Rückamp *et al.* 2011). Extrapolations from sediment core data indicate that this glacier has been retreating during at least the past 100 years, with an acceleration in the retreat rate since the 1940s (Monien *et al.* 2011; Rückamp *et al.* 2011).

By comparing the benthic biota and environmental parameters from soft sediments at three sampling sites in the cove which differ with respect to duration of ice-free

period and impact of the consequences of glacial retreat, we addressed the following specific questions:

- Are the structure and composition of benthic assemblages different between areas under different glacier retreat impact?
- Do different taxa and size classes differ in their response to differences in environmental conditions resulting from glacier retreat?

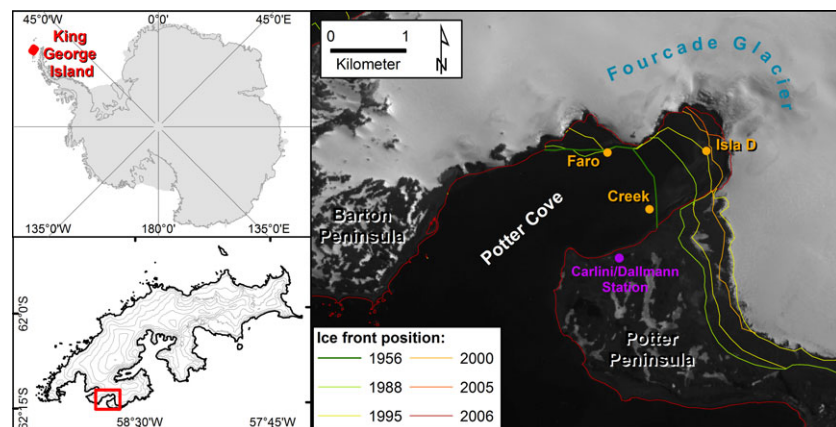
Material and methods

Study sites

Potter Cove is a small fjord-like inlet on the southern coast of King George Island (South Shetland Islands, Fig. 1). Sandy sediments predominate in exposed areas of the cove, whereas silt and clay are found in less exposed locations (Veit-Köhler 1998). The fine material is mainly deposited in the deeper basins in the inner cove and close to the glacier front (Wöfl *et al.*, 2014). The inner part of PC, with a maximum depth of 50 m, is characterized by a clockwise circulation from Maxwell Bay that enters from the north and exits in the southern coastal area (Roese & Drabble 1998; Schloss *et al.* 2012). The water that enters carries little suspended sediment. The south coast of the cove is mostly flat and meltwater streams carry sediments into the coastal areas during the summer months (Schloss *et al.* 2002; Eraso & Domínguez 2007). Although the major part of this sedimentary run-off is transported into the adjacent Maxwell Bay (Monien *et al.* 2013), sedimentation of this inorganic material also affects the newly ice-free areas within the cove.

We sampled three shallow water stations (each at a depth of 15 m) in the inner cove, which are influenced by different glacial, meltwater and water current conditions. Isla D ($62^{\circ}13'32.6''$ S, $58^{\circ}38'32''$ W) is the most recently ice-free area, being exposed since 2003, and situated about 200–215 m away from the glacier front. Faro

Fig. 1. Map of Potter Cove showing its location with respect to the Antarctic continent (top left) and within King George Island (bottom left). The retreat lines of the Fourcade Glacier are indicated; the three sampling stations are presented in orange. Background image: SPOT satellite image, 2011-01-15, (c) ESA TPM, 2011.



station (62°13'32.6" S, 58°40'03.7" W) is situated on the northern side of the cove and became ice-free between 1988 and 1995. This area is characterized by low ice disturbance and is affected by wave action (Wöflf *et al.*, 2014). The third station, 'Creek Station' was located adjacent to 'Potter Creek' (62°13'57.3" S, 58°39'25.9" W). This location has been ice-free since the early 1950s and is influenced by a meltwater river that forms during summer. It is also an area where the impact of growler ice, which can scour the benthos in PC up to a depth of 20 m (Kowalke & Abele 1998; Sahade *et al.* 1998), is high.

Benthic samples were collected over two consecutive years each time in March by SCUBA divers from the Argentinian/German Carlini (former Jubany) Station. Samples obtained in 2011 were analysed to describe meiofauna, prokaryotes and environmental factors. In 2012, further samples were obtained for macrofauna analysis. Samples for granulometry and organic content analysis from all study sites were obtained in November and December 2010.

Environmental variables

Sediment trap data

Clear cylindrical Plexiglas tubes [height (h): 25.3 cm, diameter (d): 4.19 cm, h/d: 6.04] were used as sediment traps. This type of tube is adequate due to its diameter/height ratio, which prevents sediment re-suspension within the tube (Hakanson *et al.* 1989). In summer 2011, all three locations were sampled once. In 2012, sediment traps were deployed four times during January and February (Faro, Creek). On each occasion, two replicate traps were placed at each study location. The traps were deployed without fixative for 7 days. The main particle flux in Potter Cove consists of inorganic material (average 90%, Khim *et al.* 2007), and fluxes can reach 130 g·m⁻²·day⁻¹ (Schloss *et al.* 1999). Occasionally, poor weather delayed trap recovery for up to 14 days. Location coordinates, sampling frames and raw data are available from the PANGAEA database (doi: 10.1594/PANGAEA.815209). Collected trap material was filtered over pre-weighted polycarbonate filters (Millipore, Billerica, MA, USA). After careful washing with 20 ml 18.2 MΩ water, the filters were stored at 4 °C, and subsequently dried at 60 °C for 12 h. Data were averaged by stations and extrapolated to estimate the annual flux (g·cm⁻²·year⁻¹), considering glacier activity with sediment discharge of 183 days, based on average fluvial flow on King George Island (Eraso & Domínguez 2007). Although these sediment trap data provide temporal snapshots, they provide recent sedimentation characteristics for the three investigated locations.

Sediment composition characteristics

Surface sediment samples were taken with a van Veen grab sampler. One sample was taken at each study location for measurement of grain size distribution within a sediment characterization study in Potter Cove (Wöflf *et al.* accepted). For each of these stations, organic carbon, carbonate and nitrogen contents were analysed. Prior to grain size analysis, acetic acid and hydrogen peroxide were added to the sediment samples to remove carbonate and organic matter. Samples were mixed with sodium polyphosphate on an orbital shaker to avoid aggregation of particles. The analyses were performed using a particle size analyser (CILAS 1180L; CILAS, Orleans, France), which measures particles between 0.04 and 2500 µm in volume percent. Grain size distributions were evaluated with the GRADISTAT program (Blott & Pye 2001), and graphical measures after Folk & Ward (1957) were used for further applications.

Total organic carbon (TOC; expressed as % C_{org}), total nitrogen (TN) samples (expressed as % N) and total carbon (TC) were prepared by drying and homogenization of the sediment. Additionally, the TOC samples were decalcified by adding 37% HCl (purity grade). TOC contents were determined by combustion using an ELTRA CS2000 (ELTRA, Haan, Germany), TC and TN contents were measured using an Elementar Vario ELIII, (Elementar Analysensysteme, Hanau, Germany), respectively.

Photosynthetic pigment content

Sediment cores were sliced to obtain 0–1 cm, 1–3 cm and 3–5 cm layers. The analysis of chlorophyll-*a* (Chl-*a*) and phaeopigments was carried out according to Lorenzen & Jeffrey (1980). Pigments were extracted (12 h at 4 °C in the dark) from each layer using 5 ml of 90% acetone. Extracts were analysed fluorometrically to estimate the Chl-*a* and phaeopigment concentration, the latter after acidification with 200 ml 0.1 N HCl. The concentrations of Chl-*a* and phaeopigments (expressed in µg·g⁻¹ of dry sediment) were summed to obtain the total chlorophyll concentration (Chloroplast Pigments Equivalent, CPE) (doi: 10.1594/PANGAEA.815192).

Sedimentary organic matter

Total protein concentration was determined on sediment sub-samples according to Hartree (1972). Protein concentrations (PRT) were expressed as bovine serum albumin (BSA) equivalents. Total carbohydrates were analysed according to Gerchakov & Hatcher (1972) and expressed as glucose equivalents. Total lipids were extracted from the sediment by direct elution with chloroform and methanol (1:1 v/v) according to Bligh & Dyer (1959) and then determined according to Marsh & Weinstein (1966). Analyses were performed spectrophotometrically.

Carbohydrate (CHO), protein and lipid (LIP) concentrations were converted to carbon equivalents using the conversion factors 0.40 and 0.49 and 0.75 mg C mg⁻¹, respectively, and normalized to sediment dry weight (Fabiano *et al.* 1995; Danovaro *et al.* 1999). The ratio between PRT and CHO (PRT/CHO) was considered indicative of the aging of the organic matter (Pusceddu *et al.* 1999). Biopolymeric organic C (BPC) was calculated as the sum of the C equivalents of proteins, lipids and carbohydrates (doi: 10.1594/PANGAEA.815193).

Biota

Prokaryotic abundance and biomass

Three sediment push cores (5.4 cm inner diameter, 22.89 cm² surface) per station were obtained in March 2010 and were sliced in 0–1 and 3–5 cm depth profiles. Total prokaryotic number (TPN) was obtained using a staining technique with Acridine Orange (Luna *et al.* 2002). Briefly, 0.5-g sub-samples of each replicate/layer were diluted in tetrasodium pyrophosphate and incubated for 15 min before sonication. Subsequently, samples were stained with Acridine Orange (final concentration 0.025%), filtered over 0.2-µm pore size polycarbonate filters under low vacuum and analysed as described by Fry (1990), using epifluorescence microscopy (1000 × magnification). For each filter, between 10 and 20 microscope fields were counted, corresponding to c. 400 cells.

Prokaryotic biomass (TPBM) was estimated using epifluorescence microscopy (Zeiss Axioskop 2; 1000 × magnification, Carl Zeiss SpA, Milan, Italy). Image analysis was carried out using the IMAGEJ free software (<http://rsb.info.nih.gov/ij/>). Maximum width and length of prokaryotic cells were measured and converted to bio-volumes, assuming on average C content of 310 fg C µm⁻³ (Fry 1990). TPN and TPBM were normalized to sediment dry weight after desiccation of a sediment aliquot (24 h at 60 °C).

Diatom assemblage structure

Diatoms were prepared following Renberg (1990), embedded in Naphrax[®] (Brunel Microscopes Ltd, Chippenham, UK) and counted using a Zeiss Axiophot (Carl Zeiss SpA) light microscope with immersion oil for 100 × magnification. Taxonomic identification and assessment of habitat preferences followed Cremer *et al.* (2003) and Al-Handal & Wulff (2008).

Meiofauna abundance and biomass

At each station at least three replicates were obtained on each sampling occasion. The sediment cores were sliced (0–1, 1–2, 2–5 cm depth) and stored in formaldehyde (4%, buffered with seawater) until extraction. The extrac-

tion of meiofauna followed standard procedures of centrifugation–rotation with LUDOX HS40, and sieving over 1000- and 32-µm sieves (Heip *et al.* 1985; Vincx 1996). Meiofaunal taxa identification and counting followed Higgins & Thiel (1988).

Nematodes were identified at the genus level. About 60 individuals were collected randomly from each replicate and each layer of sediment and mounted on glass slides. The identification keys for free-living marine nematodes (NeMysKey©) developed within Nemys (<http://nemys.ugent.be/>) and by Warwick *et al.* (1998) were used.

Biomass was estimated for nematodes, copepods, cumaceans and polychaetes. Biomass (µg C 10 cm⁻²) of individual nematodes, copepods and cumaceans was estimated based on the total µg C content of samples used for the analysis of the natural d¹³C signatures values of these animals (Pasotti *et al.*, in preparation), divided by the number of individuals picked out per sample. The resulting value was then multiplied by the total number of individuals (per 10 cm²) for each layer to obtain biomass estimates per taxon and layer. The carbon content of the entire samples was determined using a PDZ Europa ANCA-GSL elemental analyzer 230 (UC Davis Stable Isotope Facility). For polychaetes, the total number of individuals obtained was used for stable isotope analysis in order to estimate their biomass in each layer.

Macrofauna abundance and biomass

At each station, five replicate samples were taken for macrofauna analysis with a 16.5*16.5 cm van Veen grab operated from a zodiac. The samples were washed over a 1-mm mesh, and the total number of individuals sorted by morphotype and stored in formaldehyde (8% buffered in seawater) until counting. Deep burrowing species such as the bivalve *Laternula elliptica* or ascidians were not counted, since the sampling gear was not appropriate to evaluate their abundance or biomass. Abundances were expressed as the total number of individuals per m² (ind. m⁻²). Where possible, identification was made to species level or otherwise to family or higher taxonomic level. Biomass was estimated as ash-free dry weight of the organisms. Animals were sorted into taxonomic groups, placed into pre-weighed ceramic cups and dried at 60 °C for 48 h. The weight was measured again after drying to obtain the dry weight of the animals, and the samples were then placed in a muffle furnace at 500 °C overnight. The weight of the remaining ash was subtracted from the dry weight to calculate the ash-free dry weight (AFDW, g-m⁻²). For most taxa, an estimation of the total biomass was obtained from a subsample of individuals in order to preserve specimens for other purposes. The bivalve *Yoldia eightsi* was divided into size subclasses (big >2 cm; medium 1.5–2 cm; small 1–1.5 cm, very small <1 cm)

and individuals belonging to each subclass were removed from the shell and processed for AFDW. Tube-dwelling polychaetes were processed after removal from the tube. Specimens of *Barrukia cristata* (also known as *Gattyana cristata*) and *Aglaophamus trissophyllus* were also divided in size classes according to body length. *Barrukia cristata* individuals were weighed after removal of scales, as some individuals did not possess a complete set of scales when sampled. Similarly, for the serolid isopod *Paraserolis polita* and the pennatulid *Malacobolemnion daytoni*, length size classes were used.

Trophic composition

The trophic diversity of the nematode assemblage was determined within the upper 0–5 cm of sediment, using the classification system of Wieser (1953). The trophic guilds that characterize the nematode assemblage are: selective deposit feeders (1A), characterized by a small buccal cavity and assumed to feed selectively on bacteria; non selective-deposit feeders (1B) showing a larger unarmed buccal cavity and expected to feed on detritus and sediment particulate organic matter; epistrate feeders (2A), which usually feed on microalgae or other small organisms and have buccal cavities with one or more small teeth; predators/omnivores (2B), which are normally larger nematodes with large teeth and/or mandibles, and predate on other meiofauna organisms and/or ingest detritus particles.

Macrofauna were merged in trophic feeding groups based on the literature and stable isotope analysis (Corbier *et al.* 2004; Mac Donald *et al.* 2010; Siciński *et al.* 2011; Pasotti *et al.*, in preparation). The trophic groups are: predators (Pr) (including scavengers); Omnivores (Om); deposit feeders (De), which feed on deposited organic matter including microalgae and bacteria; suspension feeders (Su), which filter particulate organic matter in suspension in the water column; filter feeders (Ff), which feed selectively on particles suspended in the water column; and grazers (Gr), which strictly feed on micro- or macroalgae.

Statistical analysis

To test for differences in vertical profiles of meiofaunal density/biomass, prokaryotic density/biomass, and environmental variables (combined and individually), non-parametric permutational ANOVAs (PERMANOVA) with a fully crossed three-factor design were performed with random factor replicate 're' nested in the fixed factor station 'st', next to the fixed factor layer 'la'. With this design we resolve the problem of 'non independence of data' from values of contiguous layer parameters (*e.g.* nematode abundances in the first layer are linked to

abundances in the second layer etc. when considering the complete depth profiles abundance), shuffling the same layers between the replicates of each station (we nested random factor 're' in fixed factor 'st'). The interaction term 'st × la' indicates the difference in depth profiles of environmental parameters between the stations. This type of analysis is equivalent to use of univariate ANOVAs with P-values obtained by permutation (Anderson & Millar 2004) and is therefore more robust against violation of normality. An Euclidean distance-based resemblance matrix was used for the analysis of the environmental variables, and a Bray–Curtis similarity resemblance matrix was used for the abundance and biomass data. In case of significant 'st × la' interactions, pair wise tests of 'st' and 'la' within 'st × la' were performed to determine which of the layers differed significantly between stations. Because of the restricted number of possible permutations in pairwise tests, P-values were obtained from Monte Carlo samplings (Anderson & Robinson 2003). Permdisp confirmed homogeneity of multivariate dispersion for any of the tested terms in each PERMANOVA. Since the assemblages were sampled in bulk (via van Veen grab), we performed one-way non-parametric permutational ANOVAs (one-way PERMANOVAs) for macrofauna densities, biomasses and trophic structure, in which a single fixed factor station 'st' was considered during the analysis. If the factor 'st' was significant, a pairwise test was performed. Again, in the light of the restricted number of possible permutations in the pairwise tests, P-values were obtained from Monte Carlo samplings (Anderson & Robinson 2003). Similarity percentage analysis (SIMPER) was performed on the nematode genera and macrofaunal datasets, in order to identify the most important taxa contributing to the differences in biomass and abundance between the stations. Non-metric multi-dimensional scaling (nMDS) was performed on meiofauna and macrofauna abundances to better visualize the data. Abundance and biomass data were fourth root-transformed prior to each analysis to downweight the influence of the more abundant taxa (*e.g.* nematodes). Environmental data were normalized when variables with different unit measures were analysed together. For the sediment trap material, insufficient data were available to perform statistical analysis. We therefore provide the data as a box plot, to display the full variability. The results are reported as mean values ± standard deviation.

Results

Table 1 summarizes all PERMANOVA results and pairwise comparisons between the three sampling locations.

Table 1. Resumé of permutational ANOVA (PERMANOVA).

| | | | 'st × la' | | | | | | | | | | | |
|---|------|-----------|-----------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| | | | 'st' | | | 0–1 cm | | | 1–2 cm | | | 2–5 cm | | |
| | | | F | F | C | F | F | C | F | F | C | F | F | C |
| | 'st' | 'st × la' | versus | versus | versus | versus | versus | versus | versus | versus | versus | versus | versus | versus |
| | | I | C | I | I | C | I | I | C | I | I | C | I | |
| Meiofauna | | | | | | | | | | | | | | |
| Abundances | | | | | | | | | | | | | | |
| Ind. 10 cm ⁻² | * | * | | | | * | ns | ns | * | ns | ns | * | ns | ns |
| Nematodes | ns | ns | | | | | | | | | | | | |
| Copepods | ** | ** | | | | <*** | ns | <*** | <*** | ns | <* | <* | ns | ns |
| Nauplii | *** | ** | | | | <*** | | <* | <*** | | <* | <* | ns | |
| Polychaetes | * | * | | | | ns | >* | ns | ns | ns | ns | >*** | >* | ns |
| Cumaceans | ns | ns | | | | | | | | | | | | |
| Biomass | | | | | | | | | | | | | | |
| Total biomass µg C 10 cm ⁻² | ** | NA | * | ns | ** | | | | | | | | | |
| Nematodes | ns | | | | | | | | | | | | | |
| Copepods | ** | | <*** | ns | <* | | | | | | | | | |
| Cumaceans | *** | | >*** | ns | >*** | | | | | | | | | |
| Nematodes | | | | | | | | | | | | | | |
| Trophic groups | *** | | ** | ** | ns | | | | | | | | | |
| Genera rel. Ab. ^a | *** | * | *** | *** | *** | * | ns | * | * | * | * | * | ns | * |
| Macrofauna | | | | | | | | | | | | | | |
| Abundances | | | | | | | | | | | | | | |
| Total ind. m ⁻² | *** | | >*** | >*** | ns | | | | | | | | | |
| Ind. m ⁻² (diversity) | ** | | ** | ** | *** | | | | | | | | | |
| <i>Yoldia eightsi</i> | *** | | >*** | ns | >*** | | | | | | | | | |
| Cirratulidae | ** | | <* | >* | <* | | | | | | | | | |
| <i>Barrukia cristata</i> | * | | ns | ** | ns | | | | | | | | | |
| <i>Priapulid</i> sp. | *** | | >*** | >*** | ns | | | | | | | | | |
| <i>Eudorella</i> sp. | ** | | >*** | >* | >* | | | | | | | | | |
| <i>Malacobelemnion daytoni</i> | *** | | >*** | >*** | ns | | | | | | | | | |
| Biomass | | | | | | | | | | | | | | |
| Total g AFDW m ⁻² | * | | >*** | >* | ns | | | | | | | | | |
| Total g AFDW m ⁻² (diversity) | *** | | *** | *** | ** | | | | | | | | | |
| <i>Yoldia eightsi</i> | *** | | >*** | >*** | >*** | | | | | | | | | |
| Cirratulidae | ** | | ns | >*** | <* | | | | | | | | | |
| Maldanidae | * | | >*** | ns | ns | | | | | | | | | |
| <i>Barrukia cristata</i> | * | | ns | <*** | ns | | | | | | | | | |
| <i>Aglaophamus trissophyllus</i> | * | | <* | ns | <* | | | | | | | | | |
| <i>Eudorella</i> sp. | ** | | >*** | >* | >* | | | | | | | | | |
| <i>Malacobelemnion daytoni</i> | *** | | >*** | >*** | ns | | | | | | | | | |
| Trophic structure | *** | | *** | *** | ** | | | | | | | | | |
| Prokaryotes | | | | | | | | | | | | | | |
| TPN (cells g ⁻¹) ^b | *** | * | | | | <* | ns | <* | NA | NA | NA | <*** | <* | ns |
| TPBM (µg C g ⁻¹) ^b | *** | * | | | | <* | ns | <* | NA | NA | NA | <*** | <* | ns |
| Environmental | | | | | | | | | | | | | | |
| Chl-a | * | *** | | | | >* | ns | >* | <* | ns | <*** | <*** | <*** | >* |
| Phaopigments | ** | ** | | | | >*** | ns | >* | ns | ns | ns | ns | <*** | ns |
| CPE | ** | ** | | | | >*** | ns | >* | ns | ns | ns | ns | <* | ns |
| Food quality (PRT,CHO,LIP) ^a | *** | *** | | | | *** | *** | *** | * | ** | ** | ns | ** | ns |
| PRT | ** | ns | >*** | ns | >* | | | | | | | | | |
| CHO | * | ** | | | | ns | ns | ns | >* | >*** | <* | >* | ns | >* |
| LIP ^a | *** | *** | | | | >*** | <*** | >*** | >* | ns | ns | >* | >*** | ns |
| PRT/CHO | * | *** | | | | ns | ns | >* | <* | <* | >* | ns | ns | ns |
| BPC ^a | *** | *** | | | | >*** | <*** | >*** | >*** | ns | >* | >*** | ns | ns |

The signs > and < are relative to the comparative label (e.g. F versus I). Significance values: *P < 0.05, **P < 0.01, ***P < 0.0001. When Permdisp analysis gave values P > 0.05, no remarks were made. In case of P < 0.05, ^awas added beside the investigated parameter, whereas when the Permdisp was not possible because of too low a number of levels, ^bwas placed next to the investigated parameter.

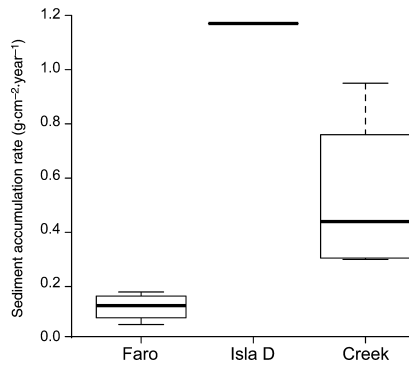


Fig. 2. Sediment accumulation rates ($\text{g}\cdot\text{cm}^{-2}\cdot\text{year}^{-1}$) are given as median, quartiles (box) and 95% confidence intervals (whiskers) for sites Faro, Isla D and Creek. Please note, site Isla D was sampled only once.

Environmental variables

Sediment deposition rate

Sediment deposition rate at the three locations showed high variability (Fig. 2). Faro station had the lowest deposition rate (median $0.12 \text{ g}\cdot\text{cm}^{-2}\cdot\text{year}^{-1}$, range $0.18\text{--}0.06 \text{ g}\cdot\text{cm}^{-2}\cdot\text{year}^{-1}$). The rate at Creek station was higher (median $0.45 \text{ g}\cdot\text{cm}^{-2}\cdot\text{year}^{-1}$, range $0.3\text{--}0.95 \text{ g}\cdot\text{cm}^{-2}\cdot\text{year}^{-1}$). The highest rate was measured at Isla D ($1.17 \text{ g}\cdot\text{cm}^{-2}\cdot\text{year}^{-1}$), but this was based on a single sediment trap deployment.

Sediment composition characteristics

Sediment composition at the three locations was clearly different (Table 2). Site-specific grain size composition ranging from sand (Creek) to mud (Isla D) dominated.

Table 2. Sediment biogeochemistry and diatom relative abundance composition of the three investigated sites.

| | Faro | Isla D | Creek |
|---------------------------|----------|----------|----------|
| % Gravel | 0.0 | 0.0 | 0.8 |
| % Sand | 63.5 | 0.9 | 95.7 |
| % Mud | 36.5 | 99.1 | 3.4 |
| % C_{org} | 0.212 | 0.119 | 0.150 |
| % Carbonate | 5.799 | 2.899 | 2.662 |
| %N | 0.042 | 0.032 | 0.039 |
| C/N | 142.044 | 95.515 | 72.013 |
| C_{org}/N | 5.002 | 3.771 | 3.833 |
| Diatoms | % | % | % |
| Planktonic/sea ice | 12.87129 | 44.35484 | 22.94118 |
| Benthic | 86.63366 | 54.83871 | 40.58824 |
| Unknown/both | 0.49505 | 0.806452 | 36.47059 |

% C_{org} = percentage organic carbon; % N = percentage total nitrogen; C/N = carbon to nitrogen ratio; C_{org}/N = organic carbon to nitrogen ratio; planktonic/sea ice = planktonic and/or sea ice algae percentage; unknown/both = unknown and or both microalgae percentage.

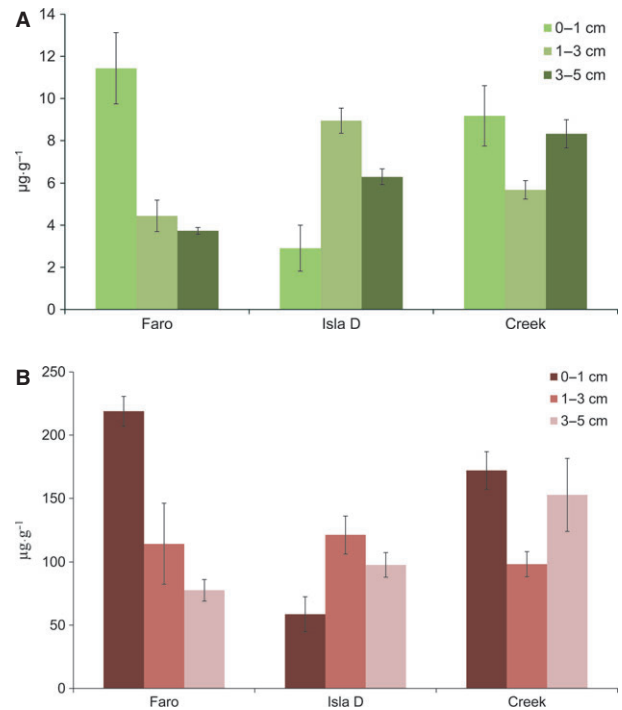


Fig. 3. Chlorophyll-*a* (a) and phaeopigment (b) concentrations expressed as $\mu\text{g}\cdot\text{g}^{-1}$ dry weight per sediment layer (mean \pm SD).

Faro station displayed a higher percentage of organic carbon (% C_{org}), carbonate (%carbonate), as a higher C:N ratio, as well as C_{org}/N ratio, compared with the two other stations.

Pigments

The concentrations of phaeopigments were two orders of magnitude higher than the Chl-*a* concentrations at all three locations (Fig. 3a,b). Chl-*a* and phaeopigment concentrations in the 0–1 cm layer were significantly higher at Faro and Creek than at Isla D. Instead, Isla D had a subsurface (1–3 cm) peak in pigment concentration. The pigment concentrations in the deeper layer (3–5 cm) were higher at Creek than at the other two locations.

Organic matter composition

At all three locations, proteins were the dominant class of biochemical organic matter (mean 57.9%), followed by lipids (mean, 31.5%) and carbohydrates (mean 10.6%) (Fig. 4a,b). The three classes showed variable vertical distribution, with significantly lower mean PRT values at Isla D than at Faro and Creek. The CHO concentration was comparable in the upper layer at all three, whereas in the 1–3 cm layer, Faro had the highest CHO concentration, followed by Isla D and Creek. In the deeper layer (3–5 cm), Faro showed the highest concentration followed by Creek and Isla D, with the only significant

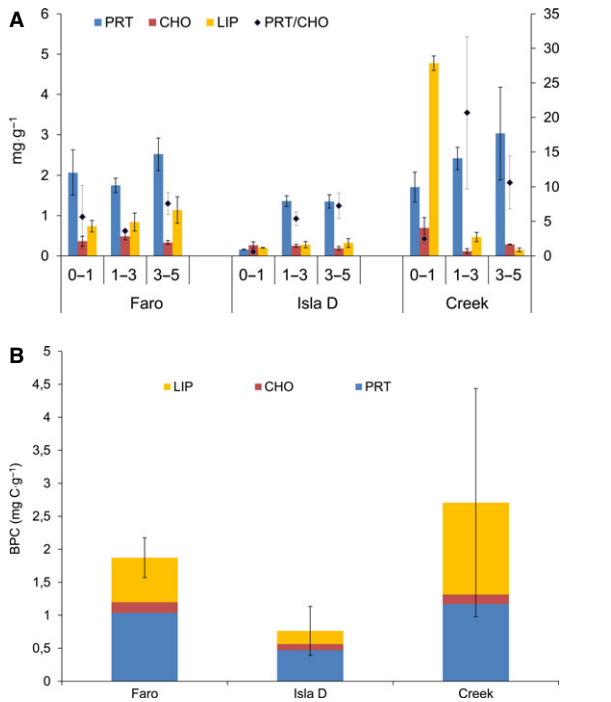


Fig. 4. (a) Proteins (PRT, blue bars), carbohydrates (CHO, dark red bars) and lipid (LIP, orange bars) concentrations ($\text{mg}\cdot\text{g}^{-1}$, left vertical axis) and PRT:CHO ratio (black rhombus, right vertical axis) in each layer (0–1 cm, 1–3 cm and 3–5 cm) of each station (mean \pm SD). (b) Biopolymeric carbon (BPC, $\text{mg}\cdot\text{g}^{-1}$) and relative contribution of PRT, CHO and LIP (expressed in carbon equivalents) in the three stations on a bulk sediment 0–5 cm profile (mean \pm SD).

difference being between Isla D and the other two stations. The PRT/CHO ratio in the surface layer of Creek was significantly higher than at Isla D. The 1–3 cm layer of Creek had the highest PRT/CHO values (although also the highest standard deviation), followed by Isla D and Faro. In the deeper layer the ratios were similar at all the stations. PERMANOVA further indicated highly significant differences of the ‘st \times la’ factor (see Table 1) for LIP and BPC between stations; however, due to a significant Permdisp value (distance among centroids grouping factor ‘st \times la’, Permdisp factor ‘st’), we do not consider these representative of real differences between stations and layers, but rather the result of natural variability. Creek had higher levels of BPC and lipids than the other two stations.

Biota

Prokaryotic abundance and biomass

Prokaryotic abundance and biomass were significantly higher in surface sediments (0–1 cm) from Isla D compared to both Faro and Creek (Fig. 5). In contrast, the deeper layer (3–5 cm) of sediment at Faro contained

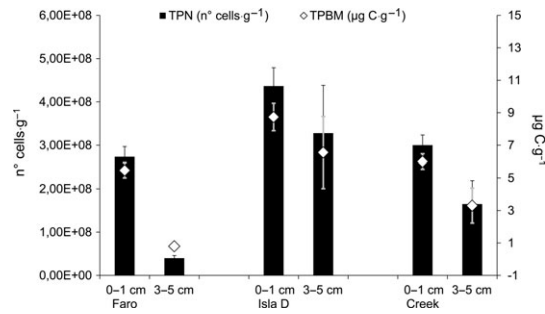


Fig. 5. Prokaryotic abundances (total prokaryotic number, TPN, number of cells per gram of sediment) and biomass (total prokaryotic biomass, TPBM, $\mu\text{g}\cdot\text{C}\cdot\text{g}^{-1}$ of sediment) for the surface (0–1 cm) and deeper (3–5 cm) layers of the three stations (mean \pm SD).

significantly lower numbers of prokaryotes and related biomass compared to the other two stations.

Diatom assemblage structure

The diatom assemblages were dominated by benthic species at Faro, whereas taxa associated with sea-ice or normally living in open waters were more abundant at Creek and particularly at Isla D (Table 1). Diatom abundance was conspicuously low at Isla D.

Meiofauna abundance and biomass

The total abundance and overall taxonomic composition of the meiofauna are illustrated in Fig. 6a,b (see Supporting Information Table S1). Nematodes were always the most abundant taxon, contributing 93.7% at Faro, 94.5% at Isla D, and 98.1% at Creek to the assemblages. Harpacticoid copepod abundance and nauplii densities were higher at Isla D. Polychaetes were the second most abundant taxon at Faro (3.28%), whereas at Creek and Isla D they contributed 0.51% and 1.08%, respectively. Cumaceans reached the highest abundance at Faro (0.4%). The upper layer (0–1 cm) contained 52% of the total 0–5 cm assemblage at Isla D, and 42% at Faro. At Creek almost half of the assemblage (43%) was concentrated in the subsurface layer (1–2 cm). Total meiofauna abundance differed between Isla D and Faro across all three depth layers (see Table 2).

Nematode biomass (Fig. 6c, Supporting Information Table S1) did not differ significantly between stations. Cumacean biomass was highest at Creek, whereas copepod biomass was significantly higher at Isla D than at Faro and Creek.

The nMDS of the meiofauna vertical distribution (Fig. 7a) revealed a relatively higher patchiness at the Isla D and Creek sites than at the Faro site. At the latter station, each replicate layer clustered more closely together in the two-dimensional space compared with the same layers at the other two sites.

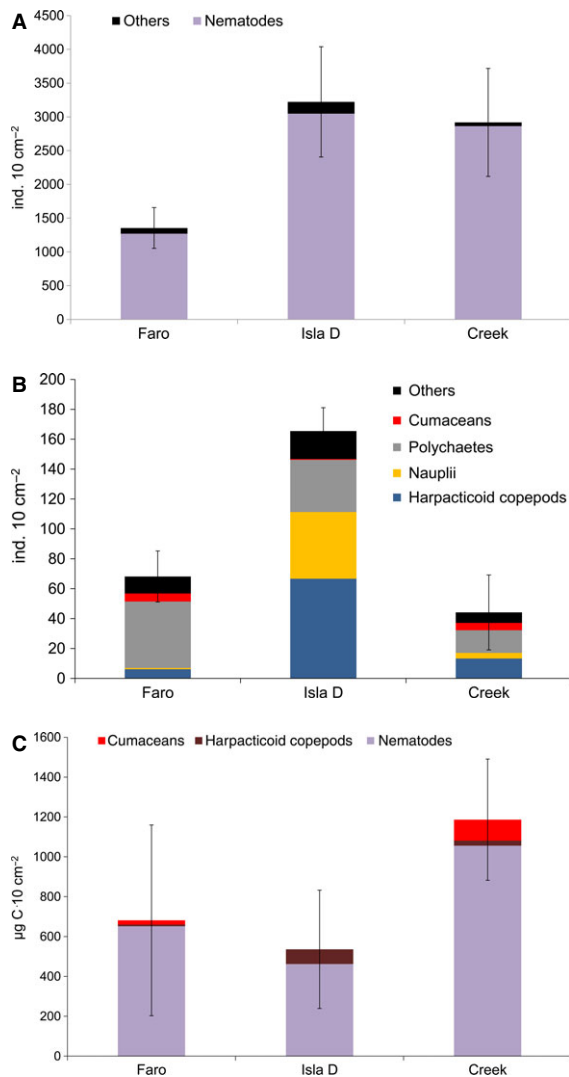


Fig. 6. (a) Meiofauna total abundances (mean number of individuals per $10 \text{ cm}^{-2} \pm \text{SD}$) with average layer contribution. (b) Abundances of meiofauna taxa with the exclusion of nematodes for the 0–5 cm profile (average number of individuals per $10 \text{ cm}^2 \pm \text{SD}$). The 'Others' class includes a total of 19 taxa, including amphipodes, priapulids ostracods and turbellarians. (c) Meiofauna biomass (mean \pm SD): taxa included are nematodes (more than 90% of biomass in each station), cumaceans and copepods.

Nematode genus composition and trophic diversity

Nematode assemblage composition on the genus level and trophic diversity are shown in Fig. 8a,b, respectively. In general, we found significant differences in nematode genus composition based on relative abundances between Isla D and the other two stations in the first layer of sediment (0–1 cm), between all the stations in the subsurface layer (1–2 cm), and between Isla D and the other two stations in the deeper layer (2–5 cm; Table 2). The SIMPER analysis of the nematode assemblage showed that Faro was dominated by *Daptonema* (40%) and *Sabatieria*

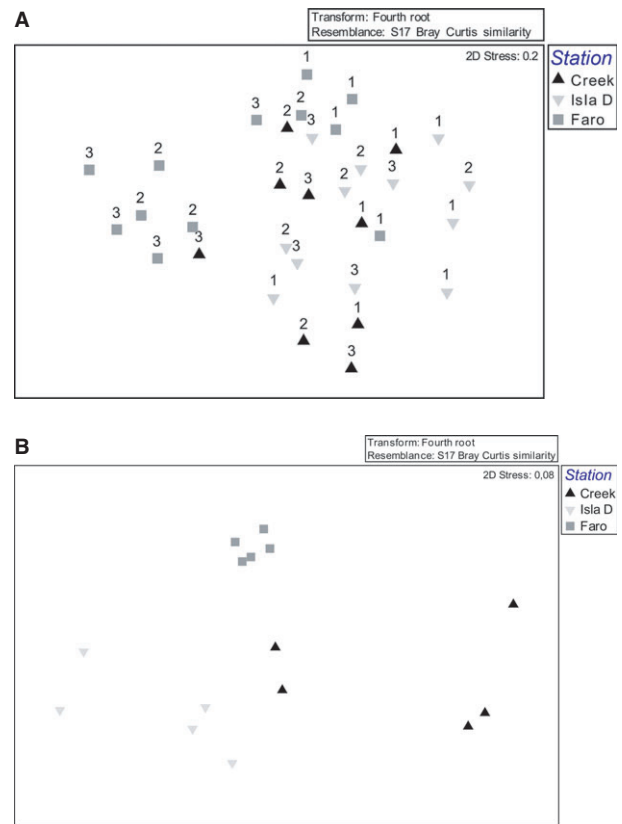


Fig. 7. Nonmetric multi-dimensional scaling (nMDS) based on (a) meiofauna abundances (three to four replicates per site) with the 1 = 0–1 cm depth, 2 = 1–2 cm depth and 3 = 2–5 cm depth profiles and (b) macrofauna abundances with the five replicate samples for each site. The more scattered labels of Creek and Isla D compared with Faro may point at a higher patchiness, possibly related to disturbance due to the glacier and creek discharge.

(20%), which are both non-selective deposit feeders (1B). Creek was characterized by a more even nematode assemblage, with *Daptonema* still being the most abundant taxon (20%) followed by *Aponema* (12%) and *Acantholaimus* (10%). These last two genera are epistrate feeders (2A). The nematode assemblage at Isla D was dominated by *Daptonema* (29%) and *Microilaimus* (27%); the latter belongs to the trophic guild 2A.

The three stations showed significant differences in trophic guild composition. Faro was strongly dominated (76%) by non-selective deposit feeders (1B), 53% of Isla D nematode assemblage belonged to the epistrate feeder 2A group, and Creek showed a more even nematode assemblage composed of non-selective deposit feeders (46%) and epistrate feeders (39%).

Macrofauna abundance and biomass

Macrofauna abundances and biomass are summarized in Fig. 9a,b (values reported in Supporting Information

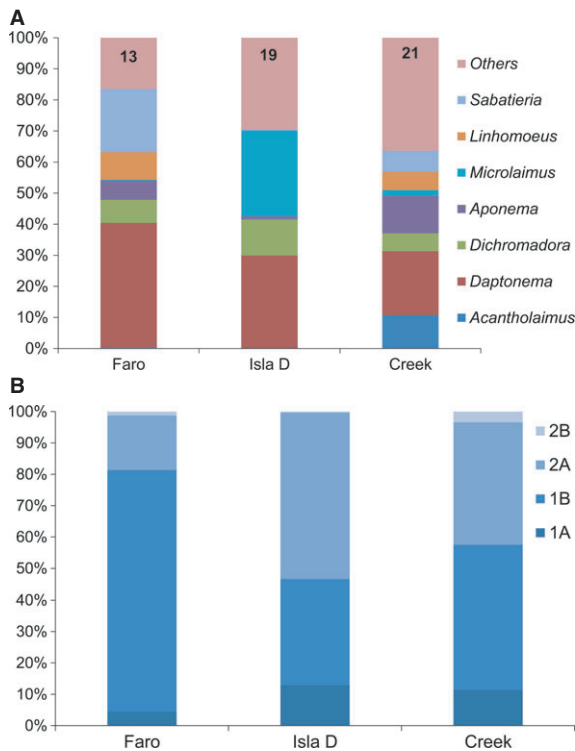


Fig. 8. (a) Nematode genus composition of the 0–5 cm profile. The most important genera are presented with their Latin names and the other genera are lumped in 'Others' and their number reported. (b) Nematode community trophic diversity of the 0–5 cm profile based on abundances (Philipp *et al.* 2011). 1A, selective deposit feeders; 1B, nonselective deposit feeders; 2A, epistrate feeders; 2B, predators/omnivores.

Tables S2 and S3, and SIMPER results are reported in Table 3a,b). Macrofauna densities differed significantly between all three stations (Table 2). In general, the highest total abundance was found at Faro followed by Isla D and Creek (Fig. 9a). Differences were also significant for the major taxa between all stations. The nMDS (Fig. 7b) based on abundances was more scattered in samples from Isla D and Creek than Faro. The latter formed a well defined group. *Malacobelemnnon daytoni* (Cnidaria, Pennatulacea) and *Priapulius charchoti* (Priapulida) were only found at Faro, whereas *B. cristata* (Polychaeta, Polynoidae) was only present at Isla D. Bivalves were more abundant at Creek, where *Mysella charchoti* (Bivalvia, Galeommataidae), *Genaxinius* sp. (Bivalvia, Thyasiridae) and *Yoldia eightsi* (Bivalvia, Nuculanidae) made up about 41.8% of the whole assemblage. *Yoldia eightsi* was also present at Faro but at a low relative abundance (0.68%) and was absent at Isla D. Polychaetes were also abundant, with little differences in relative abundance between the stations, namely 23% of the total assemblage at Creek, 27% at Isla D and 28% at Faro. Cirratulidae (Polychaeta)

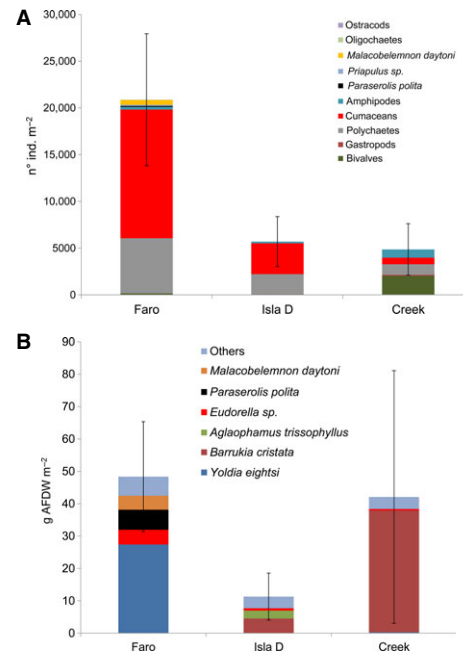


Fig. 9. (a) Macrofauna abundances (average number of individuals \pm SD) of the main taxonomic groups. Bivalves include *Yoldia eightsi*, *Mysella charchoti* and *Genaxinius* sp. Cumaceans include *Eudorella* sp. for three stations and *Dyastylis* sp. and *Vaunthompsonia* sp. only for Isla D. Polychaetes include the families Cirratulidae, Orbinidae, Terebellidae, Capitellidae, Ophaelidae, Maldanidae, Spionidae, Polynoidae and Nephyidae. (b) Macrofauna biomass expressed in grams of ash-free dry weight per meter square (g AFDW m^{-2} \pm SD) with the contribution of the most important species at the three stations.

were the most abundant family found in higher numbers at Faro, followed by Isla D and Creek. Maldanidae (Polychaeta) were also present only at Faro. The peracarid crustaceans were mainly represented by the cumaceans, although the tanaidaceans were also present in very low numbers at Faro. Cumaceans made up more than 50% of total abundance at both Faro and Isla D, and only 14% at Creek. The cumacean macrofauna assemblage at Isla D was composed of three different genera (*Eudorella* sp., *Diastylis* sp. and *Vaunthompsonia* sp.), whereas only *Eudorella* sp. was found at the other two stations. The abundance of amphipods was only significantly different between Faro and Creek, with Creek being characterized by the highest density of these crustaceans (Table S7).

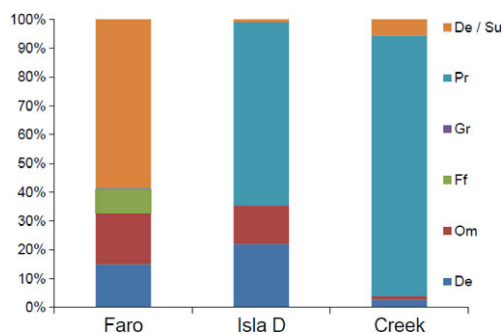
Total macrofauna biomass was significantly higher at Faro than at either Creek or Isla D (Table S6). SIMPER analysis revealed that differences in the biomass of larger organisms differ between stations (Table 3b). The assemblage at Faro was composed of *Y. eightsi* (56.6% of the total biomass), *Paraserolis polita* (12.8%) (Crustacea, Serolidae) *Malacobelemnnon daytoni* (8.9%) and *Eudorella* sp. (9.4%). The biomass at Creek was dominated by the

Table 3. Similarity percentages analysis (SIMPER) results based on (a) nematode genera (b) macrofauna abundances and (c) macrofauna biomasses.

| (a) Nematode genera | | | | | |
|--------------------------------|----------|-------------------------------|----------|-------------------------------|----------|
| Groups Faro & Isla D | | Groups Faro & Creek | | Groups Isla D & Creek | |
| Average dissimilarity = 70.66% | Contrib% | Average dissimilarity = 65.96 | Contrib% | Average dissimilarity = 67.26 | Contrib% |
| <i>Daptonema</i> | 20.75 | <i>Daptonema</i> | 24.33 | <i>Microloaimus</i> | 14.62 |
| <i>Microloaimus</i> | 14.86 | <i>Sabatieria</i> | 15.6 | <i>Daptonema</i> | 14.09 |
| <i>Sabatieria</i> | 13.26 | <i>Aponema</i> | 8.25 | <i>Dichromadora</i> | 9.71 |
| <i>Dichromadora</i> | 10.2 | <i>Linhomoeus</i> | 7.98 | <i>Aponema</i> | 8.45 |

| (b) Macrofauna abundances | | | | | |
|--------------------------------|----------|------------------------------------|----------|------------------------------------|----------|
| Groups Creek & Isla D | | Groups Creek & Faro | | Groups Isla D & Faro | |
| Average dissimilarity = 66.16% | Contrib% | Average dissimilarity = 58.72% | Contrib% | Average dissimilarity = 54.57 | Contrib% |
| <i>Eudorella</i> sp. | 11.98 | <i>Eudorella</i> sp. | 18.17 | <i>Malacobelemn</i> <i>daytoni</i> | 10.81 |
| <i>Yoldia eightsi</i> | 10.03 | Cirratulidae | 13.96 | <i>Dyastilis</i> sp. | 8.7 |
| Cirratulidae | 9.89 | <i>Malacobelemn</i> <i>daytoni</i> | 10.08 | <i>Eudorella</i> sp. | 8.29 |
| <i>Mysella charcoti</i> | 9.35 | <i>Mysella charcoti</i> | 8.41 | <i>Yoldia eightsi</i> | 8.15 |
| <i>Dyastilis</i> sp. | 8.96 | <i>Barrukia cristata</i> | 7.28 | Maldanidae | 7.28 |
| <i>Barrukia cristata</i> | 6.7 | <i>Priapul</i> sp. | 6.79 | <i>Priapul</i> sp. | 7.28 |

| (c) Macrofauna biomass | | | | | |
|----------------------------------|----------|------------------------------------|----------|------------------------------------|----------|
| Groups Creek & Isla D | | Groups Creek & Faro | | Groups Isla D & Faro | |
| Average dissimilarity = 83.35% | Contrib% | Average dissimilarity = 94.73% | Contrib% | Average dissimilarity = 92.51% | Contrib% |
| <i>Barrukia cristata</i> | 63.65 | <i>Barrukia cristata</i> | 35.61 | <i>Yoldia eightsi</i> | 48.41 |
| <i>Aglaophamus trissophyllus</i> | 12.42 | <i>Yoldia eightsi</i> | 35.42 | <i>Paraserolis polita</i> | 9.72 |
| Terebellidae | 5.86 | <i>Paraserolis polita</i> | 7.33 | <i>Malacobelemn</i> <i>daytoni</i> | 8.64 |
| <i>Mysella charcoti</i> | 4.96 | <i>Malacobelemn</i> <i>daytoni</i> | 6.28 | <i>Eudorella</i> sp. | 7.84 |

**Fig. 10.** Macrofauna trophic structure based on biomass. De/Su = deposit/suspension feeders; Pr = predators; Gr = grazers; Om = omnivores; Ff = filter feeders; De = deposit feeders.

polynoidae *B. cristata* (89% of the total biomass). The biomass at Isla D was more evenly divided between *B. cristata* (40% of the total biomass) and *Aglaophamus trissophyllus* (22%) (Polychaeta, Nephtyidae); *Eudorella* sp. was scant (6% of the total biomass).

Macrofauna trophic structure

The trophic diversity based on biomass data was significantly different between the three stations (Fig. 10, Table 4). Three different assemblages could be defined. At Faro the assemblage was characterized by a high bio-

mass and composed of deposit/suspension feeders (59%), predators (13.09%), omnivores (17.64%), depositivores (14.93%) and filter feeders (8.49%). At Isla D biomass was low, and the assemblage (63%) was dominated by predators/scavengers followed by deposit feeders (21.9%) and omnivores (13%). At Creek, an assemblage with an intermediate biomass was present, dominated (90%) by predators/scavengers.

Discussion

Coastal ecosystems in the Western Antarctic Peninsula have experienced glacial advance and retreat during the Holocene. However, the rapid retreat of the Fourcade tidewater glacier on King George Island during the last 100 years can be considered an extreme event driven by the regional climate warming in the WAP (Monien *et al.* 2011). A trough is present in the middle of the cove and now accumulates erosive sediments, and iceberg scouring has led to ice furrows visible in sonar images of Potter Cove (PC). These features are mainly detected in deeper waters, most likely due to better preservation than in nearshore and shallower areas (A.-C. Wöfl, unpubl.data). The dynamics related to glacier retreat in combination with the oceanographic characteristics (*e.g.* bathymetry, waves and currents) of the cove have resulted in a

Table 4. Macrofauna species and taxon names with corresponding feeding groups.

| Species/taxon | Feeding group | Species/taxon | Feeding group |
|---|---------------|--|---------------|
| Ophaelidae | De | Gasteropoda | Gr |
| Spionidae | De | <i>Mysella charcoti</i> (Lamy, 1906) | Ff |
| Orbinidae | De | <i>Malacobelemnion daytoni</i> (López González <i>et al.</i> 2009) | Ff |
| Terebellidae | De | <i>Yoldia eightsi</i> | De/Su |
| <i>Eudorella</i> sp. | De | <i>Barrukia cristata</i> (Willey, 1902) | Pr |
| <i>Dyastilis</i> sp. | De | Polynoidae | Pr |
| <i>Vauthompsonia</i> sp. | De | <i>Aglaophamus trissophyllus</i> (Grube, 1887) | Pr |
| Tanaidacea <i>Pseudotanaia</i> sp. | De | <i>Priapulius</i> sp. | Pr |
| Maldanidae | Om | | |
| Cirratulidae | Om | | |
| Oligochaetes | Om | | |
| Amphipodes | Om | | |
| <i>Paraserolis polita</i> (Pfeffer, 1987) | Pr | | |

De = deposit feeder; Om = comprises omnivores which behave like scavengers, detritus feeders, grazers *non stricto sensu*; Gr = grazers *stricto sensu*; Ff = filter feeders intending organisms feeding selectively on certain component of the particulate organic matter in the water column; De/Su = deposit/suspension feeders feeding on deposited/suspended particulate matter unselectively; Pr = predators and scavengers supposed to occupy the higher level of the food web.

gradual maturation of the ecosystems away from the glacier front and towards the patchy structure in the benthic assemblages present at the different sites under study. Recently emerged ice-free areas, such as Faro or Isla D, are subject to colonization and biological succession by macroalgae and organisms directly depending on them. The spread of macroalgal beds on the newly ice-free areas in Potter Cove, and their decay and decomposition enhance the transport of material (both organic carbon and nutrients) and thus available energy in deeper benthic habitats (Quartino & Boraso de Zaixso 2008; Quartino *et al.* 2013 and references therein). Here we highlight the possible drivers for each benthic assemblage identified at the three sites, including the environmental parameters measured and the possible interactions between the different biotic and abiotic components, in order to place these in a context of recent glacial change events.

Faro

The Faro site became ice-free between 1988 and 1995 (Rückamp *et al.* 2011) and ice growler action is absent (Philipp *et al.* 2011). Instead, bottom communities at this station are affected by high bed shear stress and wave action (Wöfl *et al.*, 2014). The large grain sizes found at Faro indicate that this site does not experience high deposition and fine sediments are eroded as seen in the analysis of the sediment trap data. Recently, macroalgae have colonized the hard substrates of this newly ice-free area (Quartino *et al.* 2013). At this station, we found higher macrofaunal biomass and a more homogeneous assemblage than at the other two stations. Large mobile predators, such as nephtyidae or polynoidae polychaetes,

were absent at the time of sampling. The presence of the brooder *Paraserolis polita* and the high abundances of small polychaetes are indicative of low disturbance and relatively clear waters (Kowalke & Abele 1998; Smale 2008). This is corroborated by the dominance of benthic diatom taxa over planktonic and sea-ice species in the sediment biofilm. The influence of previous glacial-related disturbances on these communities is reflected by the presence of pennatulids and larger individuals of the bivalve *Yoldia eightsi*. These organisms are of low motility but have pelagic larvae with high dispersal capacities, and are known to be able rapidly to colonize previously disturbed areas of the Antarctic seabed (Smale 2008). *Yoldia eightsi* is typically found in glacial coves and is potentially capable of outcompeting the larger *Laternula elliptica* when the latter is present at low abundance (Siciński *et al.* 2012). At Faro only large *Y. eightsi* of shell width > 1.5 cm were found. Under icebergs impact, smaller and younger individuals are abundant (Brown *et al.* 2004). In spite of being inferior competitors, pennatulids exhibit high growth rates and are often found in high abundance on bare substrata after physical disturbance, reflecting their high colonization capacity (Sahade *et al.* 1998; Momo *et al.* 2008). The dominance of particular suspension and filter-feeders in combination with subdominant deposit feeders points to frequent re-suspension events, which support an environment for a specific macrobenthic assemblage, feeding at the sediment-water interface.

In contrast, both the meiofaunal and the prokaryote assemblages were characterized by the lowest biomass among the three stations. This is surprising given the higher food availability (Chl-*a* and high BPC) compared with the other sites. Unsurprisingly for soft sediments,

the meiofaunal assemblage was dominated by nematodes. Polychaetes and cumaceans were also present, but harpacticoid copepods and their larvae were virtually absent. A dominance of nematodes and meiobenthic polychaetes with a lower abundance/frequency of other common taxa (e.g. harpacticoids and nauplii) was also found in the inner part of Hornsund Fjord in the High Arctic, a location similarly impacted by rapid glacial retreat (Grzelak & Kotwicki 2012), whereas cumaceans were absent. The nematode assemblage at Faro station was dominated by two genera of non-selective deposit feeders (*Sabatieria* in the deeper layers and *Daptonema* in the surface layer), which thrive in low oxygen, organically enriched environments worldwide (Soetaert & Heip 1995; Steyaert 2003; Moreno *et al.* 2008). *Daptonema* is opportunistic and easily switches between different food sources such as microalgae and bacteria (Vanhove *et al.* 2000; Pasotti *et al.* 2012). These findings point to a detritus-based assemblage, which is often associated with hypoxic bottom conditions. Macroalgal debris is accumulating in this part of the cove and may cause anoxia in the sediments, explaining lower endobenthic densities and dominance of *Sabatieria* and *Daptonema* (Wetzel *et al.* 2002). The low copepod abundance might also relate to the low oxygen concentrations in the surface layer (Coull 1970; Giere 2009).

Isla D

The upper sediment layers at this location were muddy and soft, and the sediment accumulation rates relatively high compared with the other two stations. BPC was the lowest compared with the other stations and the organic matter in the surface layer appeared to be old (high CHO %, low BPC, low PRT/CHO) (Pusceddu *et al.* 1999). Low organic carbon content, BPC, diatom and Chl-*a* concentrations at Isla D are likely to be a consequence of the local high sedimentation of inorganic sub-glacial derived material. Moreover, the low primary production is probably related to the typically high turbidity and low light conditions, caused by the combination of brash ice movements and glacial discharge. Isla D is located in an area of the inner cove where wave action is negligible and therefore represents a low energy environment, which is also reflected in the occurrence of fine sediments.

The macrofaunal assemblage at Isla D was relatively poor in terms of both density and biomass when compared with the other two sites. It also showed a highly patchy distribution, as revealed in the nMDS analysis. It is likely that the assemblage at this site represents a recent colonization stage in a high sedimentation (low energy)/glacier calving-related disturbance environment. This is confirmed by the dominance of cumaceans

and relatively large polychaete species such as the vagile predator *Aglaophamus trissophyllus* and the motile scavenger *B. cristata*. Cumaceans are successful organisms in areas with high sediment accumulation rates, whereas small infaunal polychaetes typically arrive at a later successional stage when physical disturbance is lower (Kowalke & Abele 1998). Vagile secondary consumers are generally observational and indicative of locations affected by ice disturbance (Smale 2007, 2008; Siciński *et al.* 2012). Devastating as it is for many sessile species, ice-scouring events also produce dead animal material for scavengers such as *B. cristata*. Compared with Faro, filter and suspension feeders were lacking at Isla D. This may be due to the presence of high sediment loads in the waters, which can exert a negative effect on filter-feeding activity through dilution or clogging of the filter apparatus.

Contrasting with the macrofauna, prokaryotic biomass and abundance at Isla D were the highest of all three stations. The meiofauna showed the highest number of individuals, and only at Isla D were copepods and nauplii relatively abundant, in spite of their general preference for coarser sediments (Vanhove *et al.* 2000; Pasotti *et al.* 2012). This might be counteracted by their ability to colonize barren substrates such as sites after iceberg scouring (Lee *et al.* 2001; Veit-Köhler *et al.* 2008). The presence of copepods and a richer meiofaunal assemblage indicates relatively well oxygenated conditions. The nematode assemblage was dominated by epistrate feeders (50%, e.g. *Dichromadora* and *Microlaimus*), followed by non-selective deposit feeders. The high proportion of non-selective deposit-feeding nematodes reflects the important role of the benthic microbial assemblage in their diet (Wieser, 1953) and indicates that they play an important role in the benthic food web. The latter is truncated of smaller organisms, as evidenced by the relatively high number and biomass of prokaryotes and dominance of meiofauna over macrofauna. The lower transfer of organic matter to the macrofauna level suggests that this system may act as a carbon sink. The subsurface Chl-*a* peak may support the high abundance of epistrate feeders such as *Dichromadora* in the deeper layers, and the higher abundance of prokaryotes in the surface layer may be the cause of the dominance of *Daptonema*. Furthermore, the second dominant genus, *Microlaimus*, is known to be a relatively rapid colonizer (Wetzel *et al.* 2002) and has been reported to be the dominant taxon after iceberg scouring (Lee *et al.* 2001). These observations are consistent with a hypothesis that the sediments at Isla D are at an early stage of meiofaunal colonization, during which the organisms benefit from the less disturbed sedimentary conditions and need to be tolerant of high sediment deposition rates. Nonetheless, the nMDS of meiofauna for this site

shows a relatively more scattered distribution of the replicate layers compared to Faro, highlighting a higher micropatchiness at this site.

Creek

Of the three stations, Creek has the longest ice-free history in more than 50 years. The creek flows during the summer months and is fed by glacier- and snowmelt as well as by groundwater drainage through moraines (Varela 1998; Eraso & Domínguez 2007). The location experiences the discharge of highly suspended particle laden meltwater, although our measured sediment accumulation rates are lower than at Isla D. High meltwater discharge can also result in sediment re-suspension, in spite of usually low bed shear stress (Wölfl *et al.*, 2014). Moreover, the area receives a lot of brash ice and ice flow from the glacier. It is therefore likely that the assemblages at Creek station are influenced by both intermediate levels of terrestrial inorganic sedimentation and ice disturbance.

Macrofaunal abundances were lowest at Creek with a patchy distribution (Fig. 9b), possibly related to the diverse impact of both meltwater and ice. Thus, relatively younger and smaller individuals of *Yoldia eightsi* (shell length < 1–1.5 cm) were present at Creek than at Faro

(>2 cm). Despite the high abundance of *Y. eightsi*, the scavenger/predator *B. cristata* was the dominant biomass component at Creek. Likewise, a shift towards smaller/younger *Y. eightsi* was observed at Signy Island after an iceberg scour event (Peck & Bullough 1993). The authors suggested that the removal of adults, which inhibit the settlements of larvae, facilitates recruitment in this bivalve species. The higher presence of vagile scavengers such as amphipods or the scale worm *B. cristata* are also indicative of ice growler impact, as they feed on decaying animal material (Smale 2007, 2008). Although the level of disturbance at Creek station is very high, a low number of small-sized filter and suspension feeders were observed, indicative of sufficient near bottom currents with intermediate turbidity caused by meltwater and wave action.

Prokaryotes at Creek were relatively abundant, probably taking advantage of the high BPC and primary producers, as inferred from Chl-*a* concentrations. The meiofaunal densities were similar to those found at Isla D and higher than at Faro. The distribution of meiofauna, as deduced from the nMDS, shows similarities with Isla D, and is more scattered than in Faro, probably indicating a higher micropatchiness within these sediments. At Creek and, to a lesser extent, at Faro macrofaunal biomass was relatively higher than that of prokaryotes and meiofauna, which suggests that C_{org} was more efficiently

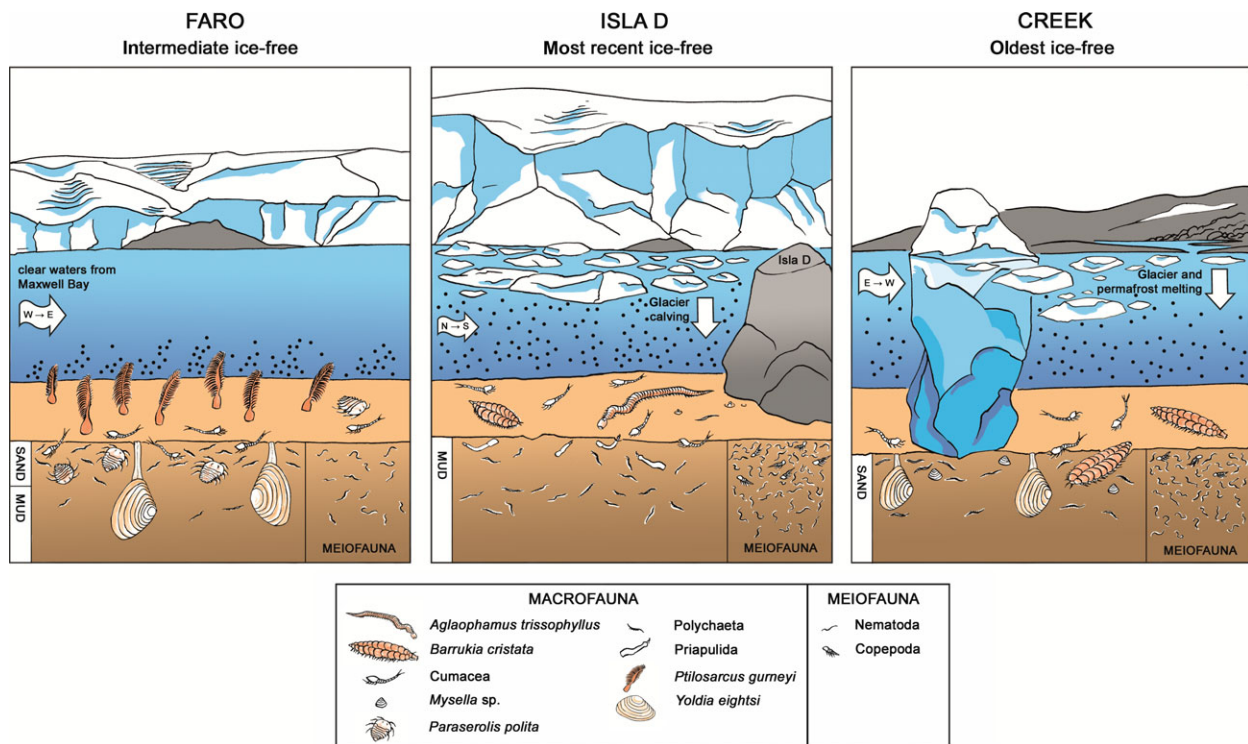


Fig. 11. Conceptual scheme of the coves' processes. For details see legend on Figure.

transferred to higher trophic levels here, probably through a shorter food chain dominated by scavengers/predators. The nematode assemblage at Creek was relatively diverse and was characterized by the highest number of genera (21). The trophic diversity was evenly structured, with non-selective deposit feeders being dominant, closely followed by epistrate feeders and a higher proportional presence of predators. No genus dominated at this site, which indicates that this assemblage is well adapted to the local disturbance regime.

Conclusions

A summarizing conceptual scheme of the processes in the cove is presented in Fig. 11. The distribution of the different components involved in the benthic system (microbiota, meio- and macrofauna) varies in response to a complex array of variables. In general, it is clear that different assemblages (in terms of abundance, biomass and trophic structure) exist at the same depth over a relatively small spatial scale (about 1 km²) within the same cove water body. Moreover, our results suggest that the size-class specific life history traits of organisms may allow them to respond in diverse ways to glacier-related disturbance. Where the glacier influence is generally low (Faro station), a macrofauna assemblage with an even biomass distribution of different trophic groups was found, whereas higher organic matter concentrations can accumulate in the sediments with consequences for hypoxia-sensitive meio- and microbiota (e.g. hypoxic sediment conditions). Ice growler action is likely reflected in the high patchiness of the soft bottom benthos at stations Creek and Isla D, with dominance of a motile fauna and a virtual lack of sediment sessile species, together with the higher relative abundance of fast-spreading nematode colonizers such as *Microlaimus*. It is likely that, with time, the glacier will redraw completely onto the land, ice disturbance will cease and the re-establishment of more diverse and less patchy distributed macrobenthic assemblages can be expected. Anyhow, future repeated samplings are needed to confirm these conclusions and substantiate our present observations and predictions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Meiofauna (0–5 cm) abundance (n° ind. 10 cm⁻²) and biomass (µg C 10 cm⁻²).

Table S2. Macrofauna biomass (mg AFDW m⁻²).

Table S3. Macrofauna abundances (ind. m⁻²).