



The impacts of climate change on Antarctic nearshore mega-epifaunal benthic assemblages in a glacial fjord on King George Island: Responses and implications



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ABSTRACT

We examined the impacts of climate change on Antarctic nearshore marine benthic communities on the West Antarctic Peninsula, one of the most rapidly warming regions on earth. We surveyed the epibenthic megafaunal assemblages of Marian Cove, a representative fjord on King George Island. We collected specimens by SCUBA diving at varying distances from the retreating glacier front during the 2013/2014 austral summer. Based on presence/absence data from the collected taxa, we determined species richness (S), taxonomic distinctness (TD) and functional diversity (FD) and further analyzed differences in assemblages in relation to environmental characteristics. Faunal assemblages in the inner cove (ice-proximal zone) were compositionally distinct from those in the outer cove. Species number and FD were also lower in the inner cove and tended to increase toward the outer cove. Nonetheless, TD values were similar among sites, indicating that all sites were distinct taxonomically. This may be because glacier retreat affected organisms of lower taxonomic levels the most. Multivariate and univariate analyses demonstrated that these differences were significantly related to distance from the glacier, substrate grain size, and organic content. The high correlation ($R=0.909$, $P<0.01$) of assemblages with distance from the glacier front suggests that physical disturbance by ice is a major process shaping benthic communities. Thus, we provide evidence that glacier retreat and its consequent processes impact the structure and function of communities. With their spatial pattern significantly associated with environmental suites, nearshore megabenthic communities respond sensitively and measurably to climate-induced impacts, suggesting their utility as long-term biomonitors. As a small but confined glacial cove with very distinct environmental gradients related to climate-induced processes, Marian Cove could serve as a model ecosystem for assessing climate impacts on Antarctic nearshore benthic communities.

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1. Introduction

King George Island (KGI) is the largest of the South Shetland Islands, which are located at the northern tip of the West Antarctic Peninsula (WAP), one of the regions where warming and ice retreat is proceeding most rapidly on earth (Clarke et al., 2007; Turner et al., 2013). The Islands have relatively warm temperatures and high humidity with summer air temperatures well above freezing

(reviewed by Griffith and Anderson, 1989; Rückamp et al., 2011). These climatic conditions produce a temperate to sub-polar glacial setting, which in turn makes the region vulnerable to climate-induced ice sheet changes (Hoskin and Burrell, 1972; Griffith and Anderson, 1989). Approximately 90% of KGI is glaciated, but ice cover has been decreasing (by 7% over 1956–1995 and by 1.6% over 2000–2008), and marine-terminating glaciers have been retreating rapidly in many coastal areas (Rückamp et al., 2011).

The retreat of marine-terminating glaciers (tidewater glaciers) and the resulting melt-water introduction has been reported in some coastal waters off KGI during the austral summer (Pęcherzewski, 1980; Yoon et al., 1998; Yoo et al., 1999, 2002; Ahn et al., 2004; Tatián et al., 2008). Introduction of glacial melt-water loaded with terrestrial sediment is significantly changing seawater

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and seabed properties and impacting marine organisms as well (Yoo et al., 1999, 2002; Ahn et al., 2004; Sahade et al., 2008; Tatián et al., 2008). Added to turbid melt-water inflow, physical disturbance by grounded or floating icebergs generated by ice break-up likely also affects the spatial distribution and diversity of benthic communities, particularly those in shallow nearshore habitats (Sahade et al., 1998a; Pabis et al., 2011) and on the continental shelves (Gutt and Piepenburg, 2003; Teixidó et al., 2007). Slow-moving or sedentary benthic organisms in shallow waters are likely most vulnerable, making them suitable as indicators of climate-induced perturbations (Cook et al., 2005; Barnes and Conlan, 2007; Clarke et al., 2007; Smale et al., 2008; Barnes and Souster, 2011; Siciński et al., 2011).

Antarctic benthic communities show richer assemblages than might be expected (White, 1984; Knox, 2006; Brey and Gerdes, 1997; Peck, 2005; Brandt et al., 2007a,b; Gutt et al., 2010; De Broyer and Danis, 2011; Grange and Smith, 2013), contributing significantly to world biodiversity. Macrobenthic fauna are key components of food webs in shallow Antarctic coastal waters, serving as the main food of sea birds, fish, and mammals, and playing key roles in benthic–pelagic coupling and energy transfer among various trophic levels (Ahn, 1993; Gili and Coma, 1998). Nonetheless, there have been relatively few studies on shallow subtidal communities, apparently due to sampling difficulties and limited access to the harsh nearshore environment (Barnes et al., 2006; Kowalke and Abele, 1998; Sahade et al., 1998b; Siciński et al., 2011, 2012), as compared with deeper water communities, which have been studied mostly via floating laboratories.

We investigated epibenthic megafaunal communities in a representative nearshore glacial fjord in Maxwell Bay, KGI, and determined the communities' characteristics in terms of species richness (S), taxonomic distinctness (TD) and functional diversity

(FD). We then analyzed variation in relation to environmental characteristics, such as distance from the glacier front and sediment properties, and assessed faunal responses to climate-induced processes in the glacial fjord. The TD and FD indices were used to complement S and as alternatives to conventional indices of species diversity. Conventional methods in analyzing species diversity (i.e., S) rely heavily on sampling effort, and are thus not always realistic in Antarctic nearshore waters, where divers collecting specimens are impeded by floating ice and freezing water and by aggressive leopard seals. Furthermore, bulk sampling is not recommended in the Antarctic, as it may damage slow growing populations. Therefore, more recent indices that do not rely on sampling intensity may provide a better alternative. Using these approaches, we provide several perspectives in assessing the responses of Antarctic nearshore marine benthic communities to climate-induced changes.

2. Materials and methods

2.1. Study area

We chose Maxwell Bay as our study area (Fig. 1). Surrounded by King George and Nelson Islands, the bay is rimmed by ice cliffs descending from the islands' low-profile ice caps (Yoon et al., 1998; Rückamp et al., 2011). Glacier retreat has been proceeding continuously for the past few decades in several tributary embayments within the bay, including Marian Cove (MC) (Park et al., 1998; Lee et al., 2008; Rückamp et al., 2011). MC is a small glacial fjord (~4.5 km long and ~1.5 km wide) located in the northeastern part of Maxwell Bay. It consists of three basins (outer, central and inner) with a maximum depth of ca. 120 m in the ice-proximal zone and is separated bathymetrically from Maxwell Bay by a shallow (ca. 70 m deep) sill at its mouth (Yoo et al., in press). Tidewater glaciers

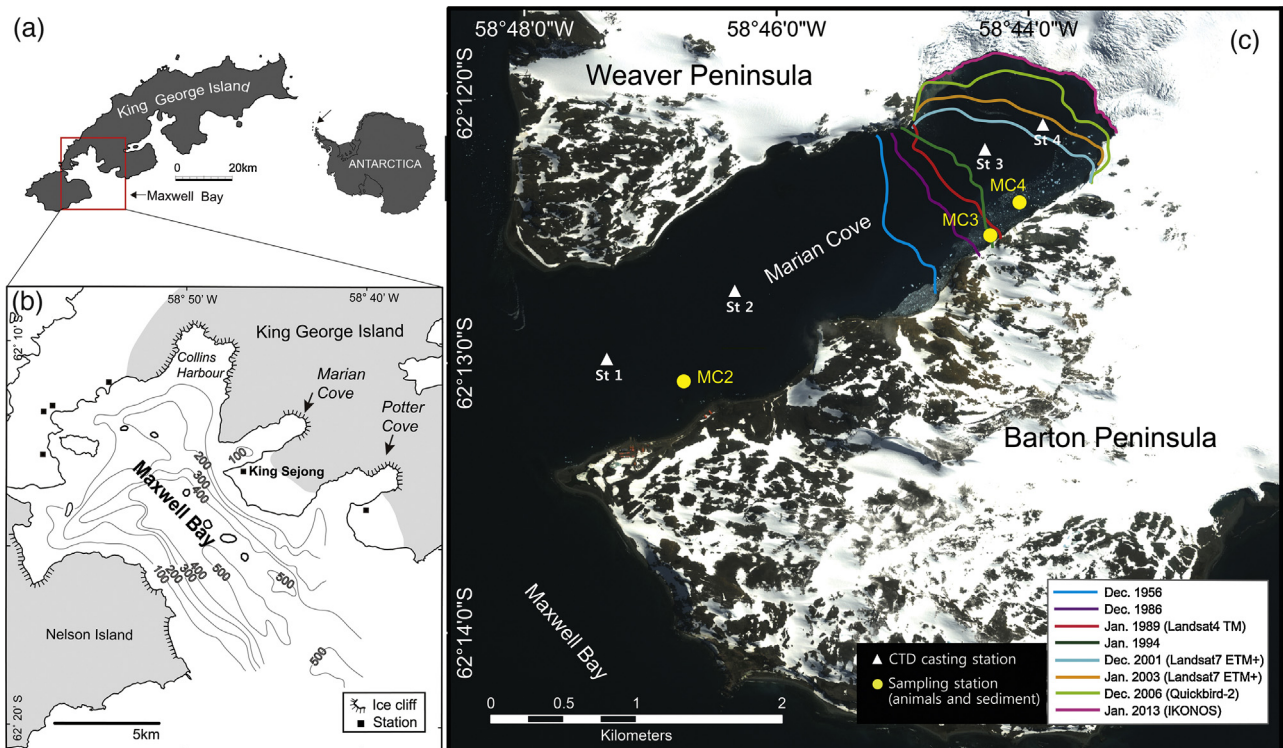


Fig. 1. (a) Location of King George Island and Maxwell Bay. (b) Bathymetry of Maxwell Bay and its tributary embayment. Bathymetric contours are drawn based on information from the Atlas Hidrografico Chileno Antarctica from the Instituto Hidrografico de la Armada, Chile (1982). The gray area denotes glacier cover. (c) Sampling sites in Marian Cove (MC). Glacier lines are drawn based on information from satellite images and aerial photographs (1956 by the Royal Navy, UK; 1986 by the Chilean Air Force; 1994 by the Korea Ocean Research and Development Institute).

(20–30 m high) are well developed in the inner cove, and these glaciers begin to break off in early summer time. The glacier carving occurs almost every day until late March, introducing large volumes of meltwater and icebergs into the cove throughout the summer months (Yoon et al., 1998; Yoo et al., 1999, 2002; Ahn et al., 2004). Meltwater brings a substantial influx of terrigenous particles, produced by erosion and weathering processes (Yoon et al., 1997, 1998). Overall, the glaciers have retreated approximately 1.7 km from 1956 to 2012 (Park et al., 1998; Lee et al., 2008; Rückamp et al., 2011), although their retreat has slowed slightly in recent years (2006–2012) (Fig. 1c). The seabed sediment in Marian Cove consists mostly of poorly sorted muddy sediment mixed with sand, gravel, and clastic rock fragments transported by melt-water and ice rafting (Yoon et al., 2004).

Previous surveys revealed that the overall faunal assemblage in the cove is very similar to those of other Antarctic nearshore communities, with distinct vertical variation (KOPRI, 2012a, 2013, 2014). Intertidal and shallow subtidal (~15 m) bottom substrates were devoid of large animals except limpets and amphipods due to frequent ice disruption and anchor ice formation. By contrast, in deeper water down to 35 m, representative Antarctic shallow benthic fauna such as *Laternula elliptica*, *Nacella concinna*, *Odonotaster validus*, *O. meridionalis*, *Sterechinus* sp., *Ophionotus victoriae*, *Parborlasia corrugatus*, *Molgula pedunculata*, and *Waldeckia obesa*, were common, indicating that the study area is a representative Antarctic nearshore habitat.

Meteorological data from the King Sejong Station over recent decades (1988–2013) show an average relative humidity of 88.7%, an average annual air temperature of -1.8°C (with a minimum value of -5.7°C in July and a maximum of 2.0°C in January) and an average precipitation of 524.1 mm (KOPRI, 2014). Air temperatures are mostly $>0^{\circ}\text{C}$ from December through March; snow melting and tidewater glacier carving occur throughout the summer months, introducing meltwater and icebergs into the cove (Yoon et al., 1998). Surface water freezes in winter and melts in summer, but a variable cover of drifting ice occurs throughout much of the year. Seawater temperature varies seasonally, from a maximum of ca. 1.8°C in February to a minimum of ca. -1.8°C in August; salinity ranges from 32.6 to 34.3 psu (Ahn et al., 2003; KOPRI, 2012b). Marked summer-time blooms in primary production have been reported, wherein benthic diatoms dominate the water column biomass (Ahn et al., 1997; Kang et al., 2002). Further details of the hydrographic features and other environmental conditions of the area have been described elsewhere (Chang et al., 1990; Kang et al., 1997; Yoo et al., in press).

2.2. Sample collection and analysis

We conducted field surveys from Dec. 9, 2013 through Jan. 29, 2014. Based on previous studies (KOPRI, 2012a, 2013, 2014), we selected three sampling stations in Marian cove, two in the inner cove (MC 3 and MC 4) and one in the outer cove (MC 2), to reflect high- and low-intensity physical disturbance and melt-water influence, respectively (Ahn et al., 2004; Yoo et al., in press). The bottom substrate of MC 2 in the outer cove has been exposed following glacier retreat for more than 60 years, while those of MC 3 and MC 4 have been exposed for ~20 years and 13–20 years, respectively. In summer, we observed that the surface water around MC 4 was almost always covered by floating and/or grounded ice produced by occasional glacier break-up. MC 3 was just outside the ice-covered water and closer to MC 4 than to MC 2. We chose this site as a third sampling location, because it displayed a relatively rich species assemblage despite its proximity to MC 4.

For quantitative sampling, we deployed three 30 m transect lines that spanned the depths of 15–30 m at each site, as we found relatively few large animals in intertidal and shallow (~15 m)

subtidal substrates (KOPRI, 2014). The transect lines were separated by at least 5 m. Divers collected all specimens observed within 50 cm of either side of the transect line as they descended along it. We also took photographs of the specimens which were difficult to be collected by hand, such as bryozoans. The number of taxa at each transect line was determined from both directly collected and photographed specimens. Three divers worked together and dove twice for each transect line.

Only epibenthic megafauna were considered. We defined epibenthic megafauna as benthic invertebrates visible to the naked eye or discernable from photographs (Starmans et al., 1999), generally >20 mm, with the exception of small epibiotic bivalves and amphipods. Burrowing infauna that could be recognized from the visible portions of their bodies (e.g., burrowing bivalves such as *Laternula elliptica* and some polychaetes such as Terebellidae) were also included. Collected specimens were fixed with 4–5% seawater-buffered formalin and preserved in 70% or 100% ethanol. Each specimen was identified morphologically to the lowest possible taxon, following identification characteristics described in the literature (Schultz, 1981; Brueggeman, 1998; Barnes, 2007; Hibberd and Moore, 2009; Danis, 2013) and online (<http://invertebrates.si.edu/antiz/index.cfm>, <http://www.marinespecies.org/rams/>, <http://www.marinebarcoding.org/checklists>, <http://species-identification.org/index.php>) (accessed on August 5, 2014).

Sediment samples were also taken by SCUBA divers from the depth of ca. 30 m within the area where transect lines were placed. For grain size analysis, four to five core samples were collected at each station using a hand-held plastic corer (7.5 cm in diameter \times 10 cm in length). The top 5 cm of the core samples were sectioned into 0–1, 1–2 and 2–5 cm and then used for analysis. Sediment grain size was analyzed using a Ro-Tap[®] sieve shaker for sediment particles larger than 4 phi after removing organic matter by soaking in 35% H₂O₂, followed by removal of calcium carbonate with 35% HCl. Finer fractions (>4 phi) were analyzed using a sediment particle size analyzer (SediGraph[®] 5120, Micrometrics Inc.). Sediment organic carbon and nitrogen were determined

Table 1

Trait variables and categories used to construct a species-by-traits matrix describing functional diversity (FD) for the assemblages at the sampling stations.

Trait	No.	Category
Feeding type	1	Filter feeder
	2	Deposit feeder
	3	Omnivore
	4	Canivore
	5	Browser
Mobility	1	Mobile
	2	Slow-moving
	3	Sessile
	4	Burrowing
	5	Tube-building
Body form	1	Cylindrical
	2	Flattened-lateral
	3	Flattened-dorsal
	4	Ball-shaped
	5	Long thin threadlike
	6	Dendritic
	7	Fan-shaped
	8	Irregular
Association with same species	1	Solitary
	2	Colonial
Association with others	1	0
	2	0–2
	3	>2
Substrate type	1	Soft
	2	Hard
	3	Mixed

in the surface flocculent layer, which was sampled by a diver using a 50-ml Falcon® tube. Total organic carbon (TOC) and total nitrogen (TN) were analyzed using a FlashEA® 1112 NC Analyzer (Thermo Fisher Scientific Inc.) after removing calcium carbonate with 8% sulfurous acid. Seawater temperature and salinity were determined along the longitudinal axis of the central cove using conductivity–temperature–depth (CTD) data logger (RBR XR-620) casting to reveal variations by distance or depth over the period of investigation.

2.3. Determination of species richness (*S*), taxonomic distinctness (*TD*) and functional diversity (*FD*)

We determined *S*, *TD*, and *FD* from the presence/absence list developed from our transect sampling at three stations (MC 2, MC 3, and MC 4). *S* is simply the number of species present in the samples and indicates the structural diversity of the benthic communities. In addition to the commonly used *S*, we also used two other indices that calculate diversity independently. *TD* measures average taxonomic distance, which is the path length between two randomly chosen species, traced through the taxonomic

classification in an assemblage. *TD* is a robust index of diversity as it is not affected by sampling effort (Clarke and Warwick, 2001; Magurran, 2004). The *TD* value is obtained by dividing the path length of every pair of species in the list by the total number of paths. Calculations were performed using the preset in PRIMER version 6 (Clarke and Gorley, 2006). Meanwhile, a third index, *FD*, measures diversity by incorporating the number, type, and distribution of traits (or functions) performed by organisms (Díaz and Cabido, 2001; Petchey and Gaston, 2007). This makes *FD* a suitable index for measuring ecosystem functions (Díaz et al., 2007). *FD* measures the extent of differences among species' traits (i.e., complementarity among species) (Petchey and Gaston, 2002). *FD* values among samples are influenced by the number of species and functional traits, and by community composition and species identity (Petchey and Gaston, 2002, 2006).

We produced a species-by-traits matrix based on six traits: feeding type, mobility, body form, intraspecific associations, inter-specific associations, and substrate type (Table 1). Each of these traits contained several different categories. For example, 'feeding type' was classified into five categories, including 'filter feeder', 'deposit feeder', 'omnivore', 'carnivore,' and 'browser'. Each taxon

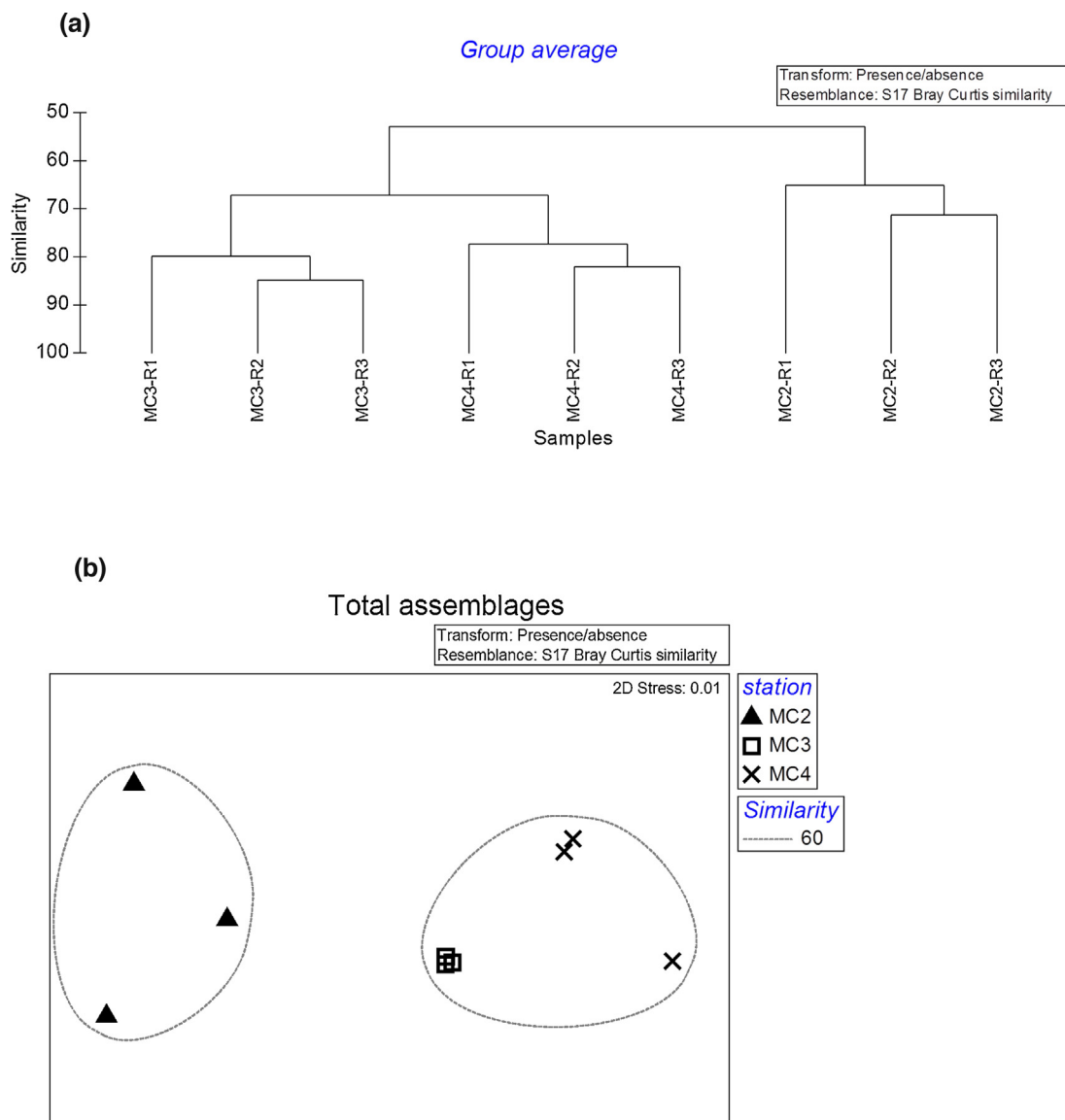


Fig. 2. Multivariate analyses of spatial variations in the benthic assemblages of Marian Cove (MC): (a) dendrogram and (b) non-metric multidimensional scaling (MDS) ordination plot of all assemblages based on the Bray–Curtis similarity matrix for presence/absence data of the benthic communities in Table 2.

was assigned a value from 0 to 1 in each category, for a total sum of '1' for each trait, based on feeding habit. For example, if a taxon is an exclusive filter feeder, it would be coded as '1' for 'filter feeder' and '0' for all other categories. We calculated FD using code freely available from <http://owenpetchey.staff.shef.ac.uk/Code/code.html> (Petchey and Gaston, 2002, 2006). Calculations were carried out using R version 3.0 software (R Development Core Team, 2008).

2.4. Statistical analysis

We performed non-parametric univariate analyses (Mann–Whitney *U*-test, Kruskal–Wallis test) using MINITAB 13 (MINITAB Inc.) to assess differences in biotic and abiotic data among stations. Meanwhile, all multivariate measures were performed using PRIMER version 6 software (Clarke and Gorley, 2006) for both biotic and abiotic data. We also performed non-metric multi-dimensional scaling (MDS) based on the Bray–Curtis similarity to produce a two-dimensional ordination plot representing similarity in the assemblages among stations. Occasionally, similarity among samples in terms of biological data was also presented in a dendrogram using cluster analysis based on Bray–Curtis similarity. We tested for statistical differences between samples using analyses of similarity (ANOSIM). The nature of community groupings identified in the MDS ordinations was further explored using the similarity percentages program (SIMPER) to determine the contribution of individual species to the average dissimilarity between samples. A principle component analysis (PCA) based on Euclidean distance was used to identify groups of samples with similar environmental characteristics. Correlations between benthic assemblages and environmental variables were analyzed using BIO-ENV to determine which parameters best explained the distribution of the faunal community. All abiotic variables were standardized prior to analysis.

3. Results

3.1. Taxonomic composition of the benthic assemblage in the cove

Taxonomic compositions of the mega-epibenthic communities in each replicate sample from the three stations are summarized in Table 2. A total of 117 taxa were described. The most dominant group was molluscs, which in average accounted for 18.0% of all species collected, followed by echinoderms (15.4%), sponges (13.7%), arthropoda (12.8%), and cnidaria (9.4%). Together, these major groups comprised ~70% of all taxa collected. However, the relative compositions of major taxa varied among stations. Molluscs (21.5%), echinoderms (17%) and ascidians (10.9%) dominated the outer cove, while bryozoans (18.3%), ascidians (16.3%) and molluscs (15%) dominated the inner cove. Filter feeders were common across all stations, with higher proportions (~56%) in the inner cove than in the outer cove (44%). Most (~60%) of these filter feeders in the inner cove were bryozoans and ascidians.

Based on the Bray–Curtis similarity matrix for the presence/absence data given in Table 2, we constructed dendrogram and MDS plots to represent the similarity among stations (Fig. 2). Benthic assemblages were clearly discriminated from each other, and MC 3 and MC 4, the two stations in the inner cove, were clustered more closely than was MC 2 (outer cove). An ANOSIM test revealed significant differences among stations (global $R=0.877$, $P=0.004$), as well as between MC 2 and the pooled data for MC 3 and MC 4 ($R=0.963$, $P=0.012$). We found that differences in the MDS analysis for all assemblages were primarily from molluscs ($R=0.77$, $P=0.004$) and bryozoans ($R=0.568$, $P=0.014$) (Fig. 3).

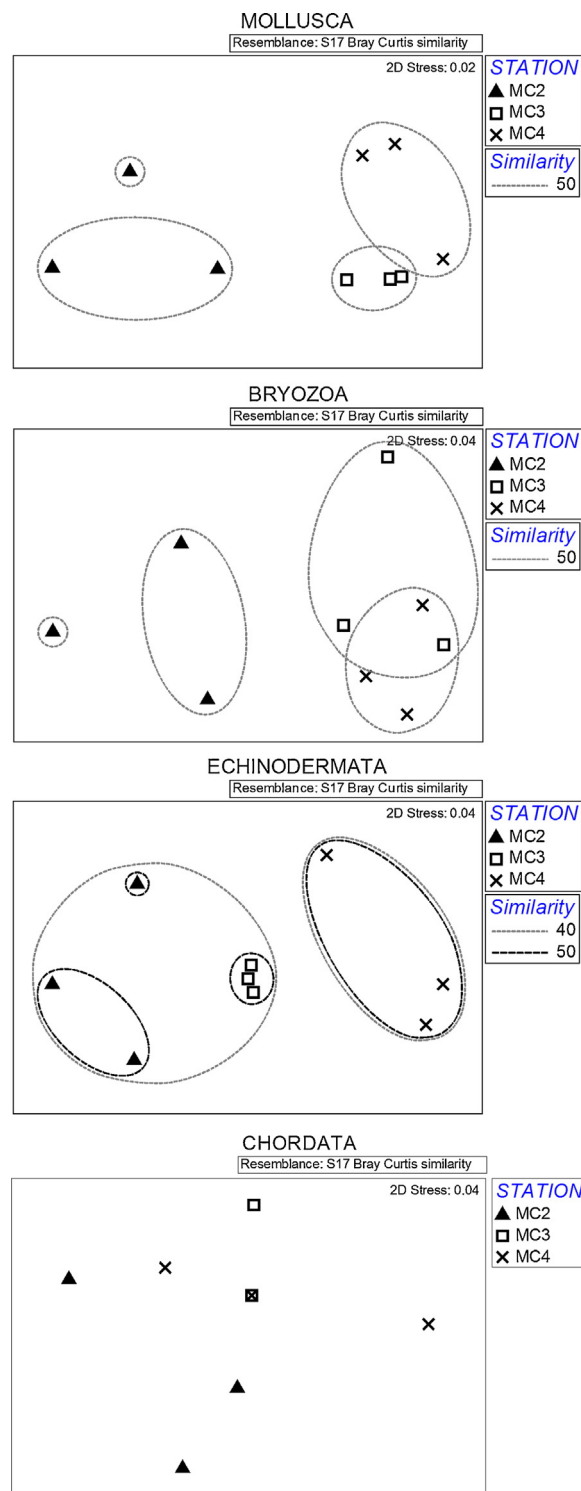


Fig. 3. Non-metric multidimensional scaling (MDS) plots for the major taxa molluscs, bryozoa, echinoderms and chordata based on the Bray–Curtis similarity matrix for the presence/absence data of benthic communities at all three stations in Marian Cove (MC) (see Table 2).

In particular, the MDS plot for molluscs was very similar to that of all assemblages combined. The total number of mollusc species present at MC 2 (13.7 ± 0.6 , $n=3$) was almost twice that at MC 3 (7.7 ± 0.6) and MC 4 (6.3 ± 0.6), and 11 of 21 total species were present only at MC 2. Most of these were small gastropods and bivalves (e.g., *Limatula* sp.,

Table 2 (Continued)

Taxon	MC2			MC3			MC4			Morphological description
	tr1	tr2	tr3	tr1	tr2	tr3	tr1	tr2	tr3	
<i>Amauropsis</i> sp.	+	+	–	–	–	–	–	–	–	Brownish olive, convex whorls with fine growth lines and eroded spire
<i>Laevilitorina</i> sp.	+	–	–	–	–	–	–	–	–	Dark brown
Gastropoda sp. 1	+	–	–	–	–	–	–	–	–	Brown
Gastropoda sp. 4	+	+	+	–	–	–	+	–	+	Dark brown to black
Gastropoda sp. 5	–	–	+	+	+	+	+	+	+	Gray, spiral and sharp tip
<i>Austrodroris kerguelensis</i>	+	+	+	+	+	+	–	–	–	
Nudibranchia sp.	–	–	+	+	+	+	–	+	–	Translucent to white or light orange, with white pigment on cerata tips
Nudibranchia 5	–	+	–	–	–	–	–	–	–	Translucent to white, with conical papillae scattered on mantle surface
<i>Marseniopsis</i> sp. 1	–	–	+	–	–	–	–	–	–	Translucent lemon yellow, with soft and smooth mantle
<i>Marseniopsis</i> sp. 3	–	+	+	–	–	–	–	–	–	Peach- or pink-colored, red spots on dorsal part with bumplike structures
<i>Laternula elliptica</i>	+	+	+	+	+	+	+	+	+	
<i>Limatula</i> sp.	+	+	+	–	–	–	–	–	–	
<i>Philobrya</i> sp.	+	+	+	–	–	–	–	–	–	
<i>Yoldia eightsi</i>	+	+	+	+	–	–	–	–	–	
bivalves sp. 2	–	+	–	–	–	–	–	–	–	Olive green, associated with pencil urchin spines
bivalves sp. 3	+	–	–	–	–	–	–	–	–	Brown
Polyplacophora sp. 1	+	+	+	–	–	–	–	–	–	White to reddish, armor-like with eight overlapping valves (<1 cm)
Polyplacophora sp. 2	–	–	–	–	–	+	–	–	+	Brown, relatively large (a few cm) and wide
Annelida										
<i>Flabelligera</i> sp.	+	+	+	+	+	+	+	+	+	Light yellow to transparent, with thick and gelatinous sheath
Terebellidae sp.	+	+	+	+	+	+	+	+	+	Pinkish to white, burrowing, with long extended tentacles and spines in the middle body part
Polynoidae sp. 1	+	+	+	+	+	+	+	+	+	Dull-brown, with large scales on the dorsal surface
Polynoidae sp. 2	–	+	–	–	–	–	–	–	–	Black, found attached on <i>Abatus</i> sp.
Sabellidae sp. 1	–	+	+	+	+	+	–	+	–	Red to white tentaculate crown, tube (strawlike) dwelling
Sabellidae sp. 2	+	–	+	+	+	+	+	+	+	White, tube (calcareous) dwelling
Polychaeta sp. 2	+	+	+	–	–	–	–	–	–	Red-brown to black with a large number of segments
Clitellata sp.	–	–	+	–	–	–	–	–	–	Red-brown, with distinctive suckers
Arthropoda										
<i>Glyptonotus antarcticus</i>	–	–	–	+	–	–	–	–	–	
<i>Serolis</i> sp.	+	+	+	+	+	+	+	+	+	
Isopoda sp. 3	–	+	+	–	+	+	+	–	+	
Isopoda sp. 4	–	–	–	–	+	+	–	–	–	
<i>Waldeckia obesa</i>	–	+	+	+	–	+	–	+	+	
Amphipoda sp. 1	+	+	+	–	+	+	–	–	–	
Amphipoda sp. 2	+	+	+	–	–	–	–	–	–	
Amphipoda sp. 7	–	+	–	–	–	–	+	–	–	
Amphipoda sp. 8	–	+	–	–	–	–	–	–	–	
Amphipoda sp. 9	–	+	+	–	–	–	–	–	–	
Amphipoda sp. 10	–	–	–	–	–	–	+	–	–	
Amphipoda sp. 11	–	–	–	–	–	–	–	+	+	
Amphipoda sp. 12	–	+	+	+	+	+	–	–	–	
Pycnogonida sp. 1	–	+	–	–	–	–	–	–	–	Red or yellow, large hook-shaped dorsal appendages with large proboscis
Pycnogonida sp. 3	–	+	–	–	+	+	–	–	–	Pinkish or brown, long thin legs
Echinodermata										
<i>Odontaster meridionalis</i>	–	+	+	+	+	+	–	+	–	
<i>Odontaster validus</i>	+	+	+	+	+	+	+	+	+	
<i>Porania antarctica</i>	–	+	–	–	–	–	–	–	–	
<i>Psilaster</i> sp.	–	–	+	+	+	+	–	–	+	
<i>Perknaster</i> sp.	–	+	+	+	–	–	+	–	+	
<i>Acodontaster</i> sp.	–	–	+	–	–	–	–	–	–	
<i>Diplasterias</i> sp.	+	+	+	+	+	+	–	–	–	
<i>Cryptasterias</i> sp.	+	+	+	–	–	–	–	–	–	
<i>Labidiaster</i> sp.	–	+	–	–	–	–	–	–	–	
Asteroidea sp. 1	+	+	+	–	–	–	–	–	–	Vivid orange
Asteroidea sp. 2	–	+	+	+	–	–	–	–	–	
<i>Ctenocidaris</i> sp.	–	+	–	–	–	–	–	–	–	Yellowish brown with long stout spines
<i>Sterechinus</i> sp.	+	+	+	+	+	+	–	–	–	Dull purple, with short and densely packed spines
<i>Abatus</i> sp.	–	+	–	–	–	–	–	–	–	Dark brown, heart-shaped test with radial pattern
Echinoidea sp.	–	–	+	–	–	–	–	–	–	Olive green, ball-shaped test with radial pattern
Holothuroidea sp. 1	+	–	+	–	–	–	–	–	–	Gray to brown, leathery body
Ophiuroidea sp. 1	+	+	+	+	+	+	–	+	–	
Crinoidea sp.	–	+	–	+	+	+	+	+	+	Red-brown to whitish, with long and fragile feathery arms
Chordata										
<i>Molgula pedunculata</i>	+	+	+	+	+	+	+	+	+	Fairly translucent, with long stalk or peduncle, solitary
<i>Cnemidocarpa verrucosa</i>	+	+	+	+	+	+	+	+	+	Brown, yellow to white and translucent, cylindrical and covered with protuberances
<i>Ascidia challengerii</i>	+	+	+	+	+	+	–	+	+	Yellowish and translucent, body lying flat on the bottom without stalk, distinct siphons
Ascidacea sp. 2	+	+	+	–	–	+	+	–	+	Grayish, with its surface completely covered in flexible bristles
Ascidacea sp. 3	+	–	–	+	+	+	–	+	+	Pinkish, bean-shaped with long stalk

Table 2 (Continued)

Taxon	MC2			MC3			MC4			Morphological description
	tr1	tr2	tr3	tr1	tr2	tr3	tr1	tr2	tr3	
Asciacea sp. 4	–	+	+	+	+	+	+	+	+	Translucent, flat and smooth surface
Asciacea sp. 10	–	–	–	+	+	+	+	+	+	Pinkish and translucent, cotton ball-shaped, colonial
Asciacea sp. 12	+	+	+	+	+	+	–	+	+	Translucent, rounded or club-shaped, colonial
Asciacea sp. 14	–	+	+	+	+	–	+	+	–	Orange and translucent, shoe-shaped with a tough leathery outer layer
Asciacea sp. 15	–	–	+	–	–	–	–	–	–	Orange and translucent, cylindrical with distinct siphons

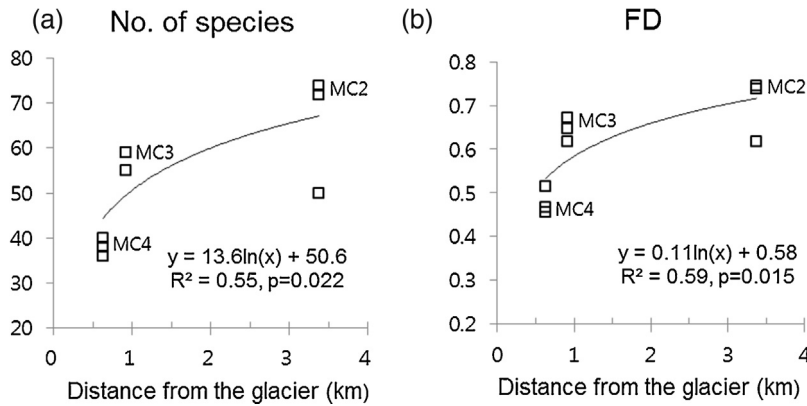


Fig. 4. Spatial variations in faunal assemblages: (a) species richness (S) and (b) functional diversity (FD) showing a significant increase with distance from the glacier front in Marian Cove.

Philobrya sp., *Amauropsis* sp., *Laevilitorina* sp.), which were associated with seaweed or other animals. For the bryozoa, 10 of 11 species occurred in the inner cove (MC 3 and MC 4), while 8 species were collected at MC 2. Conversely, MC 2 and MC 3 were clustered closely with respect to arthropoda, echinodermata, and porifera, while ascidians showed no spatial pattern and occurred at all stations.

3.2. Comparisons of S, TD and FD among stations

Species numbers differed significantly among stations (65 ± 13 at MC 2, 58 ± 10 at MC 3, 38 ± 2 at MC 4, $n=3$) (Kruskal–Wallis test, $P=0.02$) and generally decreased from the outer to inner cove (regression analysis, $r^2 = 0.55, P=0.02$) (Fig. 4a). FD values also differed among stations (0.70 ± 0.07 at MC 2, 0.64 ± 0.03 at MC 3, 0.48 ± 0.03 at MC 4, $n=3$) (Kruskal–Wallis test, $P=0.05$) with a similar increase from the inner to outer cove (Fig. 4b). By contrast, TD values showed no differences among stations. Despite a lower value at MC 4, TD values at MC 4 did not differ significantly from those expected (Fig. 5).

3.3. Environmental characteristics of the cove

Sediment properties at each station are summarized in Table 3. All stations were characterized by poorly sorted heterogeneous sediment with sorting values of 3.78–4.82 ϕ . In particular, the sediment at the outer cove (MC 2) was sorted extremely poorly (4.62–4.82 ϕ). Sediments at MC 3 and MC 4 consisted of silt and clay (~75%) with small percentages of gravel (~7%) and sand (~20%). By contrast, MC 2 sediments had higher percentages of gravel and sand particles (~55%) and less silt and clay (~45%) (Mann–Whitney U-test, $P<0.001$). TOC and TN contents were significantly higher in the outer cove than at the two stations of the inner cove (Mann–Whitney U-test, $P<0.01$). There were no significant differences in core depth within the depth ranges (0–5 cm) analyzed. The overall characteristics were confirmed by the PCA plots in Fig. 6, which showed that the two stations at the inner cove were relatively closer to each other in terms of sediment properties than to MC 2.

Fig. 7 shows the vertical profiles of water column temperature and salinity recorded by CTD along the longitudinal axis of the cove during the study period in early and late December 2013 and

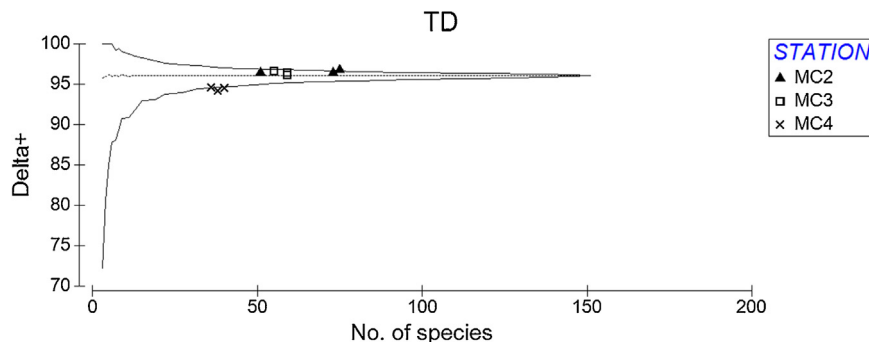


Fig. 5. Comparison of taxonomic diversity among stations. Funnel plot showing differences in taxonomic distinctness (TD) among faunal assemblages collected from the three stations in Marian Cove (MC). All values are within expectations, indicating that all assemblages are similar taxonomically.

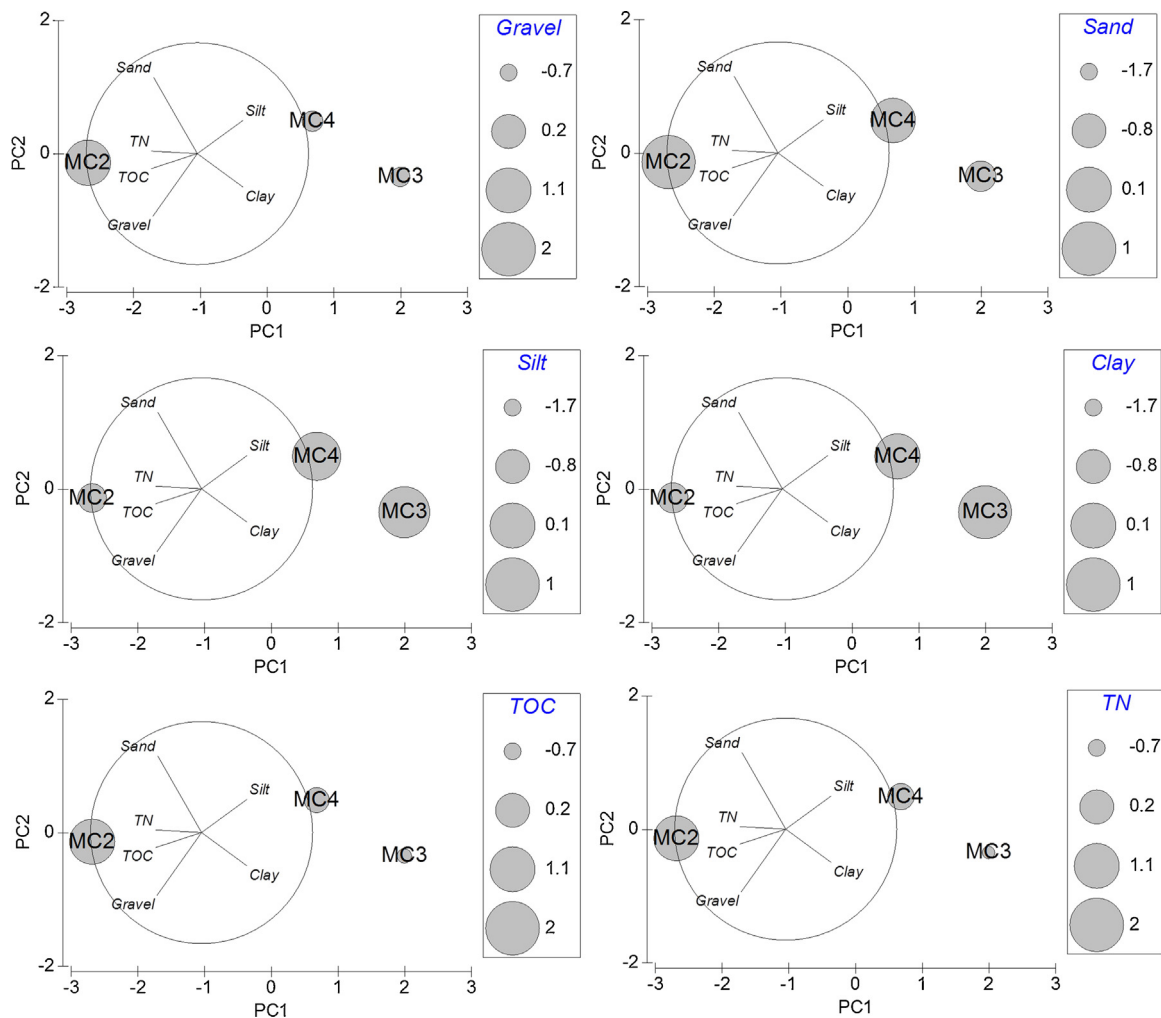


Fig. 6. Principle component analysis (PCA) plots showing spatial variation in sediment properties among the stations. The upper 0–2 cm of the sediment cores were used for analysis. Data from 0–1 cm and 1–2 cm sediment depths were similar statistically and were pooled before analysis. Total organic carbon (TOC) and nitrogen (TN) values were obtained from the topmost surface layers at each station. All data were normalized before analysis.

Table 3
Summary of sediment properties of the sampling stations in Marian Cove (MC). Sediment samples were collected by SCUBA divers from January 3 to 29, 2014 from the depth of ca. 30 m. For grain size analysis, four to five core samples (inches 7.5 cm in diameter \times 10 cm in length) were collected at each station. The top 5 cm of the core samples were sectioned into 0–1, 1–2 and 2–5 cm and then used for analysis. Values represent means \pm standard deviations ($n=5$ for MC 2 and MC 3 and $n=4$ for MC 4, except where indicated). Sediment organic carbon and nitrogen were determined in the surface flocculent layer which was also collected by SCUBA divers. TOC: total organic carbon, TN: total nitrogen.

Station	Distance (km) from glacier front	TOC (%) ($n=6$)	TN (%) ($n=6$)	Core depth (cm)	Composition (%)				Mean size (\emptyset)	Sorting* (\emptyset)	Skewness (\emptyset)
					Gravel	Sand	Silt	Clay			
MC2	3.38	0.75 ± 0.21	0.100 ± 0.04	0–1	24.9 ± 15.8	30.7 ± 8.7	20.2 ± 4.9	24.3 ± 6.6	3.68 ± 1.5	4.73 ± 0.5	0.20
				1–2	21.2 ± 6.4	33.4 ± 8.2	20.5 ± 5.2	24.9 ± 7.1	3.83 ± 1.2	4.82 ± 0.3	0.08
				2–5	18.6 ± 8.1	33.5 ± 12.2	21.3 ± 6.1	26.6 ± 7.8	4.26 ± 1.3	4.62 ± 0.5	0.11
MC3	0.92	0.41 ± 0.08	0.041 ± 0.02	0–1	6.8 ± 4.1	17.3 ± 3.6	35.0 ± 2.3	41.0 ± 4.2	6.55 ± 0.7	3.87 ± 0.5	–0.28
				1–2 ($n=4$)	6.6 ± 3.5	16.3 ± 3.8	36.5 ± 2.2	40.6 ± 3.6	6.67 ± 0.6	3.78 ± 0.4	–0.25
				2–5	14.1 ± 7.6	17.8 ± 6.4	32.8 ± 3.6	35.3 ± 4.2	5.51 ± 0.8	4.55 ± 0.6	–0.26
MC4	0.64	0.49 ± 0.10	0.060 ± 0.01	0–1	6.2 ± 5.5	25.5 ± 11.5	33.7 ± 5.8	34.6 ± 7.1	6.11 ± 0.9	3.84 ± 0.6	–0.10
				1–2 ($n=3$)	8.5 ± 6.1	24.8 ± 4.7	32.8 ± 5.1	34.0 ± 5.1	5.90 ± 0.8	4.07 ± 0.6	–0.14
				2–5	6.8 ± 4.7	24.3 ± 3.9	33.6 ± 0.7	35.3 ± 1.9	6.07 ± 0.4	4.01 ± 0.4	–0.17

Mean size, sorting and skewness were calculated following the statistics by Fork and Ward (1957).

* 2.00–4.00 \emptyset very poorly sorted, >4.00 \emptyset extremely poorly sorted.

mid-January 2014. Although the ranges of variation were small, seawater temperature and salinity varied distinctly with depth, horizontal distance, and time. The water mass was generally much colder and saltier with increasing depth for the first 10 m but

stabilized at depths >30 m. In particular, seawater temperature and salinity varied widely and erratically down to a depth of 30 m in the inner ice-proximal zone, compared with the mid- and outer cove. Temperature and salinity also tended to increase from the inner

Table 4

Summary of the results from biota–environment (BIOENV) analysis of the relationships between environmental variables and the benthic assemblages in Marian Cove (refer to Table 1). *R*: Spearman correlation coefficient.

No. of variables	<i>R</i>	Environmental variables	<i>P</i>
1	0.909	Distance	0.01
2	0.909	Distance, gravel	0.01
1	0.72	Silt	0.02
1	0.72	Clay	0.01
1	0.72	Gravel	0.01
1	0.72	TOC	0.03
2	0.72	Distance, sand	0.01
2	0.72	Distance, silt	0.01
2	0.72	Distance, clay	0.01
2	0.72	Distance, TOC	0.03

to the outer cove. A distinct salinity gradient was observed at the surface 20 m depth in Dec. 9.

On Jan. 17, seawater temperature across all depths and stations were above 0 °C, with a maximum of 2.2 °C at the surface of the outer cove. Even in January, however, a large mass of colder water was detected at the surface and at depths of 10–30 m at the inner cove. Salinity also showed a distinct gradient from the inner to outer cove, particularly within 10 m of the surface. During our study (Dec. 9, 2013 through Jan. 29, 2014), seawater temperature and salinity in the cove varied over ranges of 0.14–2.2 °C and 32.67–33.86 psu at 0–10 m, –0.49 to 1.2 °C and 33.60–33.89 psu at 10–20 m, and –0.68 to 1.1 °C and 33.76–33.92 psu at 20–30 m, respectively.

3.4. Relationship between benthic assemblages and environmental parameters

Table 4 shows the results of BIOENV analysis used to determine which parameters best explain the distribution of faunal assemblages. The single variable that best determined the ordination of faunal assemblages in Marian Cove was distance from the glacier front ($R=0.909$, $P=0.01$), followed by % clay, % gravel, TOC, and % silt, all of which had a similar Spearman rank correlation value ($R=0.720$). The combined variable showed that distance from the glacier front, together with gravel, were most influential in shaping the faunal assemblage ($R=0.909$, $P=0.01$). The second best combinations were between distance and clay, silt, and TOC, all of which had *R*-value of 0.720. These results imply that among all sediment types and sizes, gravel was the most influential in shaping the faunal assemblage, while sand was the least.

4. Discussion

4.1. Spatial variations in taxonomic and trophic compositions among the benthic assemblages

The epibenthic megafaunal assemblages in Marian Cove showed distinct spatial variation among the three stations in terms of species number and composition and FD. At all sites, we observed common species that occur throughout the Antarctic, such as the clam *Laternula elliptica*, limpet *Nacella concinna*, starfish *Odontaster validus*, *O. meridionalis*, *Perknaster* sp., nemertean worm *Parborlasia corrugates*, ascidian *Molgula pedunculata*, and amphipod *Waldeckia obesa*. However, sponges, small gastropods and bivalves (mostly associated with macroalgae), and gorgonians were very rare in the inner cove. The gorgonian *Arntzia gracilis* was reported recently at MC 2, the first such Antarctic observation in waters shallower than 40 m (Song et al., 2012).

Filter feeders comprised the largest trophic group at all stations, with the higher proportions in the inner cove (~60%), particularly ascidians and bryozoans. Tube-building sabellid polychaetes were

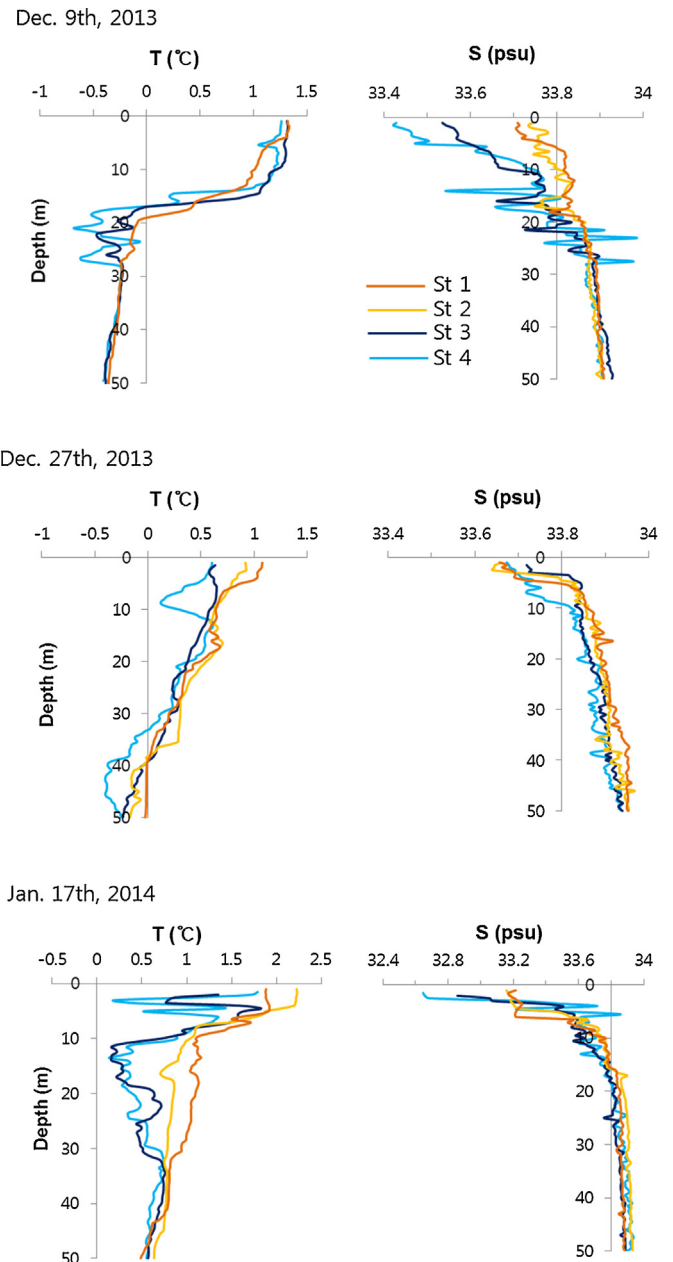


Fig. 7. Comparison of the vertical profiles of temperature (T) and salinity (S) recorded by conductivity–temperature–depth (CTD) data logger along the longitudinal axis of Marian Cove in early and late December 2013 and mid-January 2014. See Fig. 1 for CTD casting stations (Sts 1–4).

also observed frequently in the inner cove. Most of these sabellid polychaetes were affixed to the surfaces of rock fragments and other animals, such as ascidians. A burrowing bivalve (*Laternula elliptica*) and terebellid polychaetes were also common filter feeders in the inner cove, indicating that burrowing is likely an adaptive strategy developed to avoid ice impacts (Ahn, 1994). These burrowing species are apparently able to avoid ice impacts by retracting their bodies into the sediment. The bivalve *L. elliptica* and ascidians flourish and contribute greatly to the biomass in nearby Potter Cove, where summer sedimentation is intense (Sahade et al., 1998a; Tatián et al., 2008). The prevalence of filter-feeders in ice-impacted and unstable habitats seems to be very common in the Antarctic. In particular, bryozoans, sponges and ascidians dominate many Antarctic shelf benthic communities (Orejas et al., 2000; Gutt et al., 2010). In this study, however, sponges rarely occurred in highly

disturbed shallow waters (>30 m), implying that nearshore assemblages differ somewhat from deeper shelf communities.

We found that many ascidians in the inner cove were covered with other animals, such as bryozoans, sabellid polychaetes, and even with the same or other ascidian species (adults and/or juveniles), while those at MC 2 were relatively free from such epifauna. This implies that ascidians provide settlement substrates for their own and other species, thereby facilitating the colonization of benthic communities, particularly in highly disturbed areas. Almost all bryozoans were found attached to ascidians, other animals, or rock fragments, suggesting that this is a suitable strategy for colonizing highly disturbed habitats. At any rate, the higher proportion of filter feeders, many of which seem to be opportunistic species that colonize disturbed substrates through rapid growth and reproduction, indicates that the benthic assemblage in the inner cove remains in an early successional stage.

4.2. Comparison of *S*, *TD*, and *FD* among the stations

Both species number and *FD* differed significantly among stations, with a general increasing trend toward the outer cove. This shows that trait diversity and species number are correlated strongly. Such strong correlation shows that the functions of benthic fauna in Marian Cove were equally complementary to the functions of other species; that is, the increase in *FD* resulting from the addition of any one species to the site was similar to that from the addition of any other species (Sala et al., 1996; Tilman et al., 1997; Díaz and Cabido, 2001; Petchey and Gaston, 2002). We expected that the use of multiple traits would decrease the influence of *S*. However, our results did not support this. This might be because the number of rare species, which differ functionally from one another, was relatively high in Marian Cove. Adding these species to the system proportionally increases *FD* without reaching asymptote that would reduce the importance of *S*. However, in hindsight, the asymptote would likely be reached if samples were collected from a larger pool.

By contrast, *TD* values were similar among sites, indicating that all sites were equally distinct taxonomically. This may be because the impact of glacier retreat would be most apparent among the lower taxonomic levels. For example, the number of molluscs present at MC 2 was almost twice that at MC 4, but all of these molluscs were small gastropods and bivalves that are very similar taxonomically, apparently contributing little to the increase in *TD* values. Most of the major orders and even families were well represented at all stations, contributing to the similar *TD* values.

4.3. Primary mechanisms structuring benthic assemblages in a glacial cove

In general, the break-up of marine-terminating glaciers (tide-water glaciers) is accompanied by the formation of hundreds of floating ice pieces along with turbid melt-water (Yoon et al., 1998). These ice pieces often disturb the substrate through scouring and/or ice grounding, affecting the organisms that live there. Floating ice tends to occur at a much higher density in the inner cove, indicating that physical disturbance by ice is inversely proportional to distance from the glacier front. During our study, we observed that the surface water in the inner cove was almost always covered by floating and/or grounded ice that dispersed rapidly toward the outer cove. In the inner cove, divers frequently observed bottom substrates that were pressed flat or dented, and shell fragments of bivalves that were apparently crushed by ice. Thus, the high correlation ($R = 0.909, P < 0.01$) between faunal assemblages and distance from the glacier front strongly suggests that the low species number and *FD* at MC 4, the site closest to the glacier front, are due to physical disturbances by drifting or grounded ice. Physical disturbance

from grounding and scouring of icebergs is regarded as a major factor structuring the Antarctic benthos and affecting substrates in shallow, nearshore waters (Sahade et al., 1998a) and on continental shelves (Gutt and Piepenburg, 2003; Teixidó et al., 2007).

The CTD profiles (Fig. 7) in this study also indicated massive intrusion of melt-water into the inner cove. We found colder and less saline water masses in the inner cove, with distinct gradients toward the outer cove. Notably, temperature and salinity in the inner cove varied widely and erratically at the top 10 m depth, apparently due to the introduction of haphazard melt-water. As shown in Fig. 7, melt-water tended to increase in volume from December to January, apparently due to higher air temperatures in January (KOPRI, 2014).

The BIOENV analysis (Table 4) demonstrated that sediment grain size also influences the benthic assemblages in this glacial cove. This study found out that high silt-clay content (~75%) is associated with lower species and functional diversity, while the lower silt-clay content (~45%) is associated with more diverse assemblage. Similar results were reported in the glacial coves of Admiralty Bay on KGI, where lower diversity and *S* were associated with higher silt-clay content and where sandy sediment had higher *S* and diversity (Siciński et al., 2012).

The higher percentages of silt and clay in the bottom sediment at the sites near to the glaciers indicate higher rates of sedimentation of these fine-grained particles from the overlying water. Higher rates of sedimentation could take place in more sheltered area like the inner cove than in exposed area. However, the sediment properties in the cove are more likely determined by melt-water processes. Fine-grained sediment such as silt and clay in the cove was originated from terrestrial rocks and introduced into the coastal water by melt-water processes (Yoon et al., 1998). It has been reported that the concentrations of these fine-grained particles were notably elevated in the inner cove near the melt-water sources, and sharply decreased with increasing distance from the meltwater sources (Yoon et al., 1998; Ahn et al., 2004).

The sedimentation process of terrigenous particles loaded in melt-water has been well described by Yoo et al. (in press). Yoo et al. (in press) also demonstrated that the main influences on melt-water processes in the cove are tidal cycles coupled with wind stress, and suggested that northwestern and western winds coupled with flood tide promote the settling and sedimentation of suspended particles from turbid melt-water in the ice-proximal zone of the inner cove. The sedimentation of fine lithogenic particles associated with melt-water likely aggravated the unstable physical environment of the inner cove, affecting benthic communities. Torre et al. (2012) showed experimentally that different sensitivities to sedimentation among several filter-feeding species caused species compositional changes, and that the sea pen *Malacobelemnion daytoni* was more resistant to increasing turbidity than were ascidian species, which rapidly colonize disturbed areas.

We found relatively high *S* and *FD* values at MC 3 despite its high silt-clay content in the substrate and its proximity to MC 4. As shown in Fig. 4, species number and *FD* values increased non-linearly with increasing distance from the glacier front. This strongly suggests that physical impact by ice is more influential than sedimentation in shaping benthic assemblages, and that the highly detrimental impact of ice scouring is limited to the area near the glacier front even within the inner cove.

To this end, our results demonstrate that lower *S* and *FD* close to the glaciers are primarily due to habitat instability caused by physical disturbance from ice scouring and partially due to the sedimentation of fine lithogenic particles. The high proportion of opportunistic ascidian species (e.g., *Molgula pedunculata*, *Cnemidocarpa verrucosa*, *Ascidia challengerii*) in the inner cove also supports the idea that habitat instability is a major factor structuring benthic

communities in glacial coves. However, the widespread occurrence of these opportunistic ascidians across all stations suggests that most of the area is influenced, at least to some degree, by physical perturbation following glacier retreat, although physical instability likely decreases sharply with distance from the glacier front.

4.4. Other possible factors affecting faunal assemblages

Highly heterogeneous substrates at MC 2 likely contribute to the higher S at this site. In particular, higher percentages (~25%) of gravel substrates at MC 2 seem to provide substrates for diverse sessile fauna that were absent from the ice-proximal sites (Table 3). The BIOENV analysis confirmed that of all the sediment grains, gravel, both singly and combined, was the most influential in shaping the faunal assemblage, while sand was the least influential. Thus, habitat heterogeneity along with reduced ice impact in the outer cove apparently increased S and FD.

The BIOENV analysis (Table 4) also showed that organic carbon content can affect the benthic faunal assemblage significantly. The organic carbon content of the surface sediment was significantly higher in the outer cove, suggesting that more food is available for benthic fauna here. Although we did not collect abundance or biomass data, it was clear that biomass was much higher in the outer cove than in the inner cove. For example, in a previous study, we found that the common ascidian *Molgula pedunculata* occurred at very high densities (~148 individuals/m²) in the outer cove (KOPRI, 2014). The dominance of *M. pedunculata* was also reported in nearby Potter Cove (Sahade et al., 1998a; Tatián et al., 2008). Similarly, the photographic images from this study also showed that *M. pedunculata* was greater at the outer cove in terms of biomass. This opportunistic species is likely to colonize disturbed substrates rapidly by growing and reproducing whenever food is sufficient.

5. Conclusions

- We provide evidence that glacier retreat and its consequent processes impact the structure and function of nearshore benthic communities in an Antarctic fjord.
- The nearshore epibenthic megafaunal communities responded to this climate-induced process sensitively and measurably even over relatively short distances (<3 km), suggesting their utility as biomonitors for long-term monitoring. The bottom substrate at MC 2 has been exposed following glacier retreat for >60 years, while those of MC 3 and MC 4 have been exposed for ~20 years and 13–20 years, respectively. Thus, we can infer temporal changes from the present pattern of distribution from the inner to outer cove after many years, adding to the communities' value as biomonitors.
- As a small but confined glacial cove with very distinct environmental gradients, Marian Cove can serve as a model ecosystem in assessing and monitoring climate-induced impacts.

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