Estuarine, Coastal and Shelf Science 218 (2019) 258–267

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Tight trophic association between benthic diatom blooms and shallow-water megabenthic communities in a rapidly deglaciated Antarctic fjord

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ARTICLE INFO

Keywords:
Glacial retreat
Fjords
Marine benthic diatoms
Paralia sp.
Filter feeders
C and N stable isotopes
Antarctic
King George island
Marian cove (62° 13′ S
58° 47′ W)

ABSTRACT

This study reports isotopic evidence of a unique and highly efficient trophic structure based on a rarely reported benthic diatom species in a rapidly warming Antarctic fjord (Marian Cove; MC). Recent surveys of MC revealed a very conspicuous feature, an *intense, persistent benthic diatom bloom ('benthic diatom bush') overgrowing a variety of common megabenthic fauna, primarily filter feeders* (bivalves, ascidians, and demosponges), which occurred widely at shallow depths. To ascertain if the benthic diatom bloom is consumed as a primary food source, $\delta^{13}C$ and $\delta^{15}N$ were analyzed in the associated filter feeders and other herbivores, as well as in the diatom bush and other potential food sources (microphytobenthos, sedimentary organic matter and macroalgae). The analysis showed that the $\delta^{13}C$ values of all filter feeders (−23.5 to −25.2‰) were very similar to those of the diatom bush (−23.1 to −23.6‰), strongly suggesting that these benthic diatoms are the principal diet of the associated filter feeders. The isotopic signatures of the other food sources were very close to those of the diatom bush, indicating that the organic matter had the same origin, namely benthic diatoms. Given its quality, quantity and availability, the diatom bush could be regarded as the primary food source. The benthic diatom bush was predominated by the chain-forming centric diatom *Paralia* sp., which occurs in shallow coastal waters with a wide range of salinity in various geographic localities. Thus, the *Paralia* sp. bloom in this rapidly warming fjord also indicates its potential utility as an indicator of climate-induced environmental changes. Additional isotopic analysis of other common fauna showed that the benthic food web in this fjord comprised up to four trophic levels of consumers, with starfish and isopods at the apex. Given that filter feeders comprise the largest trophic group in the cove and many other Antarctic coastal waters, the results of this study strongly suggest that benthic diatoms are of prime importance in supporting the benthic food web in MC, and possibly other nearshore Antarctic waters. Further studies on the mechanism underlying benthic diatom blooms and their relevance to climate-induced processes would provide better project future scenarios for rapidly warming fjord ecosystems.

1. Introduction

Antarctic nearshore waters are likely among the most unstable habitats on earth for marine organisms due to ice-related impacts, particularly on sedentary benthic organisms in shallow habitats (Cook et al., 2005; Barnes and Conlan, 2007; Clarke et al., 2007; Smale et al., 2008; Barnes and Souster, 2011). Except in intertidal and very shallow subtidal waters (< 10 m), however, the benthic communities in this area possess relatively high diversity and biomass (White, 1984; Picken, 1985; Brey and Gerdes, 1997a,b; Barnes et al., 2006; Pabis et al., 2011; Siciński et al., 2011, 2012; Moon et al., 2015; Lagger et al., 2017). These benthic communities likely serve as the principal diet for key organisms at higher trophic levels, such as seabirds (Favero et al., 1997) and demersal fish (Barrera-Oro, 2002), and play a key role in benthic–pelagic coupling and energy transfer among trophic levels (Ahn, 1993; Gili and Coma, 1998). To date, relatively few studies have investigated the food web structure and dynamics of Antarctic nearshore benthic communities (Dunton, 2001; Corbisier et al., 2004; Pasotti et al., 2015; Marina et al., 2018).

Marian Cove (MC) is a fjord-like embayment (~4.5 km long, ~1.5 km wide, water depth ~120 m) within Maxwell Bay in King George Island. King George Island is part of the Antarctic Peninsula, one of the most rapidly warming regions on earth. Approximately 90% of the island is glaciated, but the ice sheet has been shrinking quickly, and marine-terminating glaciers (tidewater glaciers) have retreated considerably in many coastal areas, including MC (Rückamp et al., 2011).

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https://doi.org/10.1016/j.ecss.2018.12.020
Received 10 August 2018; Received in revised form 19 November 2018; Accepted 27 December 2018
Available online 28 December 2018
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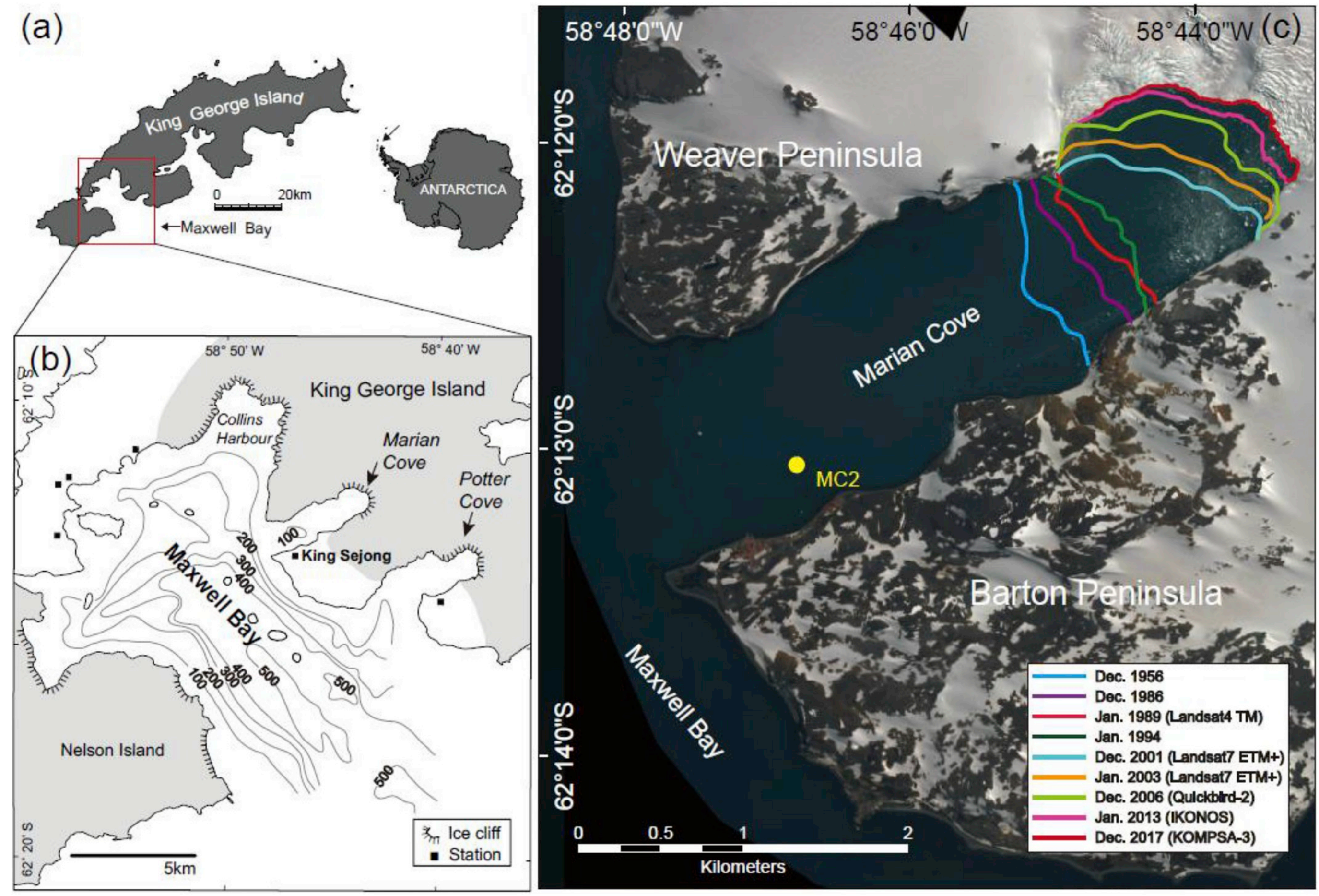

Fig. 1. (a) Location of King George Island and Maxwell Bay. (b) Bathymetry of Maxwell Bay and its tributary embayments. Bathymetric contours are drawn based on information from the Atlas Hidrografico Chileno Antarctica from the Instituto Hidrografico de la Armada, Chile (1982). The gray area indicates glacier cover. (c) The sampling site in Marian Cove (MC2). The figure was adapted from Moon et al. (2015) and the glacier lines were updated to December 2017.

In MC, tidewater glaciers retreated approximately 1.7 km from 1956 to 2013 (Moon et al., 2015). Moon et al. (2015) demonstrated that the spatial distribution of megabenthic communities was significantly associated with the glacier retreat and its subsequent processes. Consequently, Moon et al. suggested that MC may be useful as a model ecosystem for assessing and predicting climate impacts. Further analysis of recent satellite images showed that these glaciers are continuously retreating (Fig. 1).

The epibenthic megafauna in the shallow subtidal water (~35 m) of MC are representative of those of Antarctic nearshore waters (Moon et al., 2015), but their trophic structures are poorly understood. A recent survey reported a striking phenomenon in this glacial cove: *thick and massive growth of benthic diatoms on the shallow sea floor* (Ahn et al., 2016). This phenomenon is distinct from previous reports of benthic diatom blooms in the water column due to its large-scale coverage of benthic substrates, especially on a variety of common megabenthic fauna, mostly filter feeders such as ascidians, demosponges, bryozoans, tube-dwelling polychaetes and bivalves. Images obtained by an underwater remotely operated vehicle (ROV) (VideoRay Pro 4; Atlantas Marine, Yeovil, UK) during the 2017–2018 season confirmed that diatom blooms covering various megabenthic fauna were widespread in shallow waters (> 20–50 m, with a peak occurrence around 30 m) within the cove. This striking feature raised some questions, starting with whether these diatoms are consumed by the associated animals, what the drivers of benthic diatom blooms are, and whether this is a localized or widespread phenomenon in nearshore Antarctic fjords. No reasonable explanation for this phenomenon has been postulated in the existing literature.

Knowledge of the origin and availability of food sources, particularly primary producers that support benthic communities is essential to understanding the structure and function of benthic communities. In this study, we tested the hypothesis that the benthic diatom blooms (referred to as the 'benthic diatom bush' in this study) are consumed as the primary food source of the associated fauna, mostly megabenthic filter feeders. We analyzed the carbon isotope ($\delta^{13}C$) and nitrogen isotope ($\delta^{15}N$) ratios of the associated herbivorous consumers (filter feeders, deposit feeders, omnivores etc.) and their potential food sources (benthic diatom bush, microphytobenthos, sedimentary organic matter [SOM] and macroalgae). We also analyzed the fauna at higher trophic levels to delineate the basic trophic structure of the benthic communities in this fjord.

2. Materials and methods

2.1. Study area

MC is a small tributary embayment of Maxwell Bay in King George Island, within the maritime Antarctic region (Fig. 1). Meteorological data from the King Sejong Station (62° 13′ S, 58° 47′ W) during 1988–2015 indicated an annual average air temperature of approximately −1.8 °C, with a minimum of −5.7 °C in July and a maximum of 1.9 °C in January (KOPRI, 2016). From December through March, air temperatures are generally above 0 °C, and therefore snow melt and tidewater glacier calving occur throughout the summer months, introducing meltwater and icebergs into the cove (Yoon et al., 1998). Meltwater brings a substantial influx of terrigenous particles produced by erosion and weathering processes (Yoon et al., 1997, 1998), leading to distinct gradients in seawater temperature, salinity and suspended particulate matter content (Ahn et al., 2004; Moon et al., 2015; Yoo et al., 2015). Aside from the summer months, salinity and temperature are stable throughout the entire water column in the cove without detectable variations during the year (KOPRI, 2012a, 2012b, 2013, 2014). Water circulation appears to be very limited, except during the summer months, and exchange of water masses with Maxwell Bay is restricted by a shallow sill (~70 m) at the entrance of the cove that bathymetrically separates MC from Maxwell Bay (Yoo et al., 2015). The sea surface freezes frequently in winter (July to September) but does not freeze every year, and a variable cover of drifting ice occurs during most of the year. Seawater temperature varies from a maximum of 1.8 °C in February to a minimum of −1.8 °C in August (Moon et al., 2015 and therein). The hydrographic features and environmental conditions of MC have been described previously (Moon et al., 2015; Yoo et al., 2015).

2.2. Sample collection

Samples were collected by SCUBA divers at depths of 15–30 m at a distant site from the retreating glaciers (MC2 in Moon et al., 2015) during the 2013–2014 season (Fig. 1). This site appears to offer a relatively stable habitat for benthos, exhibiting the highest species richness and functional diversity within the cove (Moon et al., 2015). The epibenthic megafaunal assemblage at this location, dominated by filter feeders, is similar to those in other Antarctic nearshore waters (Sahade et al., 1998; Barnes et al., 2006; Siciński et al., 2011, 2012). In addition, intense blooming of benthic diatoms was observed at this site (Ahn et al., 2016). Among the collected samples, we selected a total of 20 taxa belonging to 10 species, four genera, four families, and two phyla for isotopic analysis. These taxa were reported as the most common benthic megafauna in this area and represent quite common Antarctic fauna (Moon et al., 2015).

In addition to the benthic diatoms overgrowing the megabenthic animals ('benthic diatom bush'), we analyzed three other potential food sources (microphytobenthos, SOM and macroalgae). We defined the brownish flocculent matter atop the uppermost sediment layer as microphytobenthos (MPB). The benthic diatom bush was retrieved from collected animals, mostly from ascidians and demosponges, while MPB was scraped from the sediment surface by a diver using a 50-ml Falcon tube. The SOM was defined as subsurface sediment (top 0–2 cm), which was collected using a handheld corer (7.5 cm in diameter, 10 cm in height).

Macroalgae are extremely abundant along the Antarctic Peninsula and provide an important food source for herbivorous grazers, such as gastropods (Iken, 1999), sea urchins (Norkko et al., 2007) and omnivorous fishes (Iken et al., 1997, 1999), thus contributing to the organic carbon (C) pool (Fischer and Wiencke, 1992). However, almost all brown algae and most common red algae are unpalatable to grazers due to their chemical defenses or stiff textures (Amsler et al., 2005; Aumack et al., 2010). Therefore, among the various macroalgae found in the study area (Chung et al., 1994; Kim et al., 2001a and 2001b), we selected three red algae (*Palmaria decipiens*, *Gigartina skottsbergii*, and *Curdiea racovitzae*) known to be palatable to many herbivores, detritivores and omnivores (Iken et al., 1997, 1999; Amsler et al., 2005; Huang et al., 2006; Bucolo et al., 2011).

Suspended particulate organic matter (SPOM), the most important form of organic particulate matter in the water column, was not included in our analysis, as SPOM in the shallow nearshore waters of MC is derived mostly from benthic sources, such as benthic diatoms detached from their biotic and abiotic substrates (Ahn et al., 1997; Kang et al., 1997, 2002). Marked summer blooms have frequently been reported in water columns dominated by benthic diatoms (Ahn et al., 1997; Kang et al., 2002). The reported δ^{13}C range of SPOM, which is derived from phytoplankton, is −28.0 to −30.4‰ (Dunton, 2001). In comparison, the SPOM of MC during the summer shows greater δ^{13}C enrichment (−24.1 ± 0.2, n = 6 in Feb 2009 [Choy et al., 2011]), similar to those of benthic sources, supporting reports that the SPOM in MC was derived mostly from benthic sources.

2.3. Sample preparation and stable isotope analysis (SIA)

Animals and potential food sources were frozen and kept in a deep freezer (−80 °C) at the King Sejong Station after collection, transported to KOPRI and maintained at −20 °C until analysis. For isotopic analysis, half-frozen specimens were dissected to excise the gut-free soft tissues. For large animals like mollusks, echinoderms, and ascidians, part of the muscle tissue was used after the shell or outer skin was removed. For small individuals, such as the gastropod *Margarella antarctica*, excised tissues were pooled to obtain sufficient tissue for analysis after the shell and gut were removed.

The soft tissues were then freeze-dried for at least 24 h, finely ground with a mortar and pestle and stored in glass vials at −80 °C until analysis. Each animal sample was placed in a glass vial, inorganic C was removed via treatment with 1 M HCl, and lipid compounds were extracted using a mixture of methanol and chloroform (1:2, v/v) before measuring the stable organic δ^{13}C ratio. The food sources were not lipid-extracted. Samples for the analysis of δ^{15}N ratios were used without pre-treatment, as the δ^{15}N ratio in tissues can be altered by pretreatment procedures such as inorganic C removal and lipid extraction (Bunn et al., 1995; Søreide et al., 2006). The C/N ratios of the food sources were determined from the % organic C and N values obtained from the isotopic analysis.

The δ^{13}C and δ^{15}N ratios were determined using an isotope ratio mass spectrometer (Isoprime 100; Elementar, Manchester, UK) coupled with an elemental analyzer (Euro EA3028; EuroVector, Milan, Italy). CH–6 and N–1 (IAEA) were used as running standards, with reported δ^{13}C and δ^{15}N values of −10.45 ± 0.03‰, relative to V-PDB, and 0.4 ± 0.2‰, relative to air, respectively. These standards were analyzed after every 10 sample runs, and the standard deviation was 0.2‰ for the SIA of both C and N.

2.4. Data analysis and statistics

The trophic level is the position of an organism within a food web, with the lowest level, 1, representing primary producers, level 2 representing herbivores and level 3 or above representing predators and other consumers. Thus, the trophic level can be used as a good estimate of the basic food web structure in a given community. In this study, the trophic position of a particular consumer ($TP_{consumer}$) was determined from δ^{15}N values according to the following formula:

$TP_{consumer} = ((\delta^{15}N_{consumer} - \delta^{15}N_{base})/TDF) + \lambda$ (2 for primary consumer)

Where TDF (trophic discrimination factor) is the average isotopic fractionation between successive trophic levels (Minagawa and Wada, 1984; Post, 2002). In this study, we used 2.3‰ as the average TDF value, as suggested by McCutchan et al. (2003), although TDFs in the Southern Ocean need further study (Jia et al., 2016; Servetto et al., 2017). We also used $\delta^{15}N_{base}$ as the lowest δ^{15}N value of the filter-feeding bivalve *Limatula* sp., as large spatial and temporal variations of δ^{15}N in primary producers sometime leads to over- or underestimation of the trophic level in marine ecosystems (Rolff, 2000; Hannides et al., 2009).

We categorized consumers into several trophic groups based on the literature and the $TP_{consumer}$ values determined in this study, including filter feeder, grazer, browser, deposit feeder, omnivore, scavenger, or predator. We defined omnivore as feeding on both plant and animal matter, and scavenger as necrophagous (Gillies et al., 2012). Browsers were defined as eating both plant and animal tissues, and grazers as

Table 1
The δ^{13}C and δ^{15}N values of common megabenthic fauna and potential basal food sources in their diet in Marian Cove. All samples were collected during the summer of 2013–2014 from 15 to 30 m * Refer to Moon et al. (2015) for descriptions of taxa. MPB: microphytobenthos; SOM: sedimentary organic matter. Values are means ± standard deviation.

Taxa*	n	δ^{13}C	n	δ^{15}N
Mollusca				
Limatula sp. (bivalves)	5	−23.68 ± 0.65	5	3.31 ± 0.2
Laternula elliptica (bivalves)	3	−23.49 ± 0.33	3	3.54 ± 0.19
Neobuccinum eatoni (gastropod)	2	−19.92 ± 0.77	2	9.49 ± 0.73
Austrodoris kerguelenensis (nudibranch)	2	−22.56 ± 0.42	2	6.34 ± 0.79
Margarella antarctica (gastropod)	2	−14.67 ± 1.36	2	7.79 ± 0.01
Porifera				
Porifera sp. 15	3	−24.76 ± 1.17	3	4.23 ± 0.94
Porifera sp. 4	3	−25.11 ± 1.65	3	6.43 ± 2.34
Chordata				
Molgula pedunculata	3	−25.16 ± 0.81	4	4.5 ± 1.18
Ascidia challengeri	3	−24.44 ± 1.27	3	5.49 ± 0.52
Cnemidocarpa verrucosa	2	−24.86 ± 0	2	5.49 ± 0.01
Annelida				
Flabelligera sp. (polychaete)	2	−18.38 ± 0.76	2	5.64 ± 0.04
Terebellidae sp. 1 (polychaete)	2	−20.56 ± 0.41	2	6.34 ± 0.04
Polynoidae sp.1	3	−18.98 ± 0.57	3	7.74 ± 0.49
Echinodermata				
Sterechinus sp. (sea urchin)	2	−18.16 ± 0.46	2	4.97 ± 0.75
Cryptasterias sp.(starfish)	3	−18.3 ± 0.66	3	7.53 ± 0.53
Ophiuroidea sp.1	2	−19.51 ± 0.91	2	8.73 ± 0.76
Odontaster validus (starfish)	2	−16.35 ± 1.43	2	9.76 ± 0.69
Cnidaria				
Actiniidae sp.1	2	−16.07 ± 0.15	2	8.44 ± 0.23
Nemertea				
Parborlasia corrugatus	2	−19.73 ± 0.31	2	8.55 ± 0.39
Arthropoda				
Glyptonotus antarcticus (isopod)	1	−17.32		10.74
Rhodophyta				
Palmaria decipiens	2	−23.06 ± 0.94	2	e ± 0.75
Gigartina skottsbergii	2	−23.09 ± 1.32	2	3.26 ± 0.36
Curdiea racovitzae	2	−14.21 ± 0.63	2	4.46 ± 0.44
Benthic diatom bush	3	−23.25 ± 0.26	3	3.55 ± 0.3
MPB	5	−23.07 ± 0.48	5	3.67 ± 0.14
SOM	4	−24.38 ± 0.39	4	4.34 ± 0.56

Table 2
Comparison of organic carbon (C) and nitrogen (N) contents and C/N ratios among the benthic diatom bush (BDB), microphytobenthos (MPB) and sedimentary organic matter (SOM) collected from megabenthos habitats in Marian Cove. Values are means ± standard deviation. The non-parametric Kruskal–Wallis test and Mann–Whitney *U* test were used to test the significance of differences among the values. * $0.01 < p < 0.05$.

Food source	N	% organic C	%N	C/N ratio
BDB	3	3.72 ± 1.14*	0.58 ± 0.12*	6.32 ± 0.58
MPB	5	0.60 ± 0.28	0.082 ± 0.047	7.60 ± 0.67
SOM	4	0.44 ± 0.04	0.045 ± 0.007	9.77 ± 1.47*

herbivorous.

The contributions of the potential food sources to the diets of primary consumers (filter feeders, deposit feeders and grazers) were estimated by SIA using Bayesian inference in the statistical package R (SIAR; Parnell et al., 2010). For SIAR modeling, we used plant-based isotopic fractionation determined from a δ^{13}C value of 0.4 (± 0.2)‰ and δ^{15}N value of 2.3 (± 0.3)‰ (McCutchan et al., 2003). We plotted the proportion of each source in the diet of primary consumers using a simple graphical method with the Bayesian model. The metrics calculated from the data must lie inside the 95%, 75% and 50% intervals calculated from Bayesian analysis (McCarthy, 2007). The SIAR model was applied to consumers that likely rely on mixed sources of food with different isotopic signatures.

3. Results

3.1. Isotopic signatures of potential food sources and consumers

The stable isotopic compositions of the benthic diatom bush and other food sources were very similar. In particular, the diatom bush and MPB were indistinguishable in terms of both δ^{13}C and δ^{15}N values (Table 1). Compared with the diatom bush and MPB, SOM showed slightly more depleted C values and slightly higher nitrogen (N) values. The organic matter contents, however, were several times higher in the diatom bush than in MPB or SOM, and the C/N ratios were significantly higher in SOM than in the diatom bush or MPB (Table 2). Macroalgae exhibited a rather wide range of δ^{13}C values. The two red algae investigated, *P. decipiens* and *G. skottsbergii*, had very similar δ^{13}C and δ^{15}N values to those of the benthic diatom bush, while *Curdiea racovitzae* had highly enriched δ^{13}C values and slightly enriched δ^{15}N values compared with the other two red algae.

The filter feeders analyzed (bivalves, sponges and ascidians) exhibited the most depleted C isotopic values (−23.5 to −25.2‰) of all consumers, similar to those of the benthic diatom bush, MPB and SOM. The δ^{13}C values of the browser *Austrodoris kerguelenensis* (−22.6 ± 0.4‰) were close to the values of the filter feeder groups. Deposit feeders or omnivores such as the tube-dwelling polychaete Terebellidae sp. (−20.6 ± 0.4‰), the polychaete *Flabelligera* sp. (−18.4 ± 0.8‰) and the sea urchin *Sterechinus* sp. (−18.2 ± 0.5‰) had more enriched δ^{13}C values than those of the filter-feeding group. Among the scavenger and predator groups, the starfish *Cryptasterias* sp., scale worm Polynoidae sp., nemertean *Parborlasia corrugatus*, gastropod *Neobuccinum eatoni*, and brittle star Ophiuroidea sp. had δ^{13}C values (−18.3 to −19.92‰) similar to or slightly lower than those of the deposit feeders and omnivores. On the other hand, Actiniidae sp. (−16.1 ± 0.2‰), the starfish *Odontaster validus* (−16.4 ± 1.4‰) and the isopod *Glyptonotus antarcticus* (−17.3‰) had slightly higher δ^{13}C values than those of deposit feeders, omnivores and other predators and scavengers. The δ^{15}N values of the consumers ranged from 3.31‰ for the bivalve *Limatula* sp. to 10.74‰ for the isopod *G. antarcticus* (Table 1).

The C and N isotopic signatures of the consumers and potential food sources were displayed in a dual isotope plot (Fig. 2). Most consumer groups were readily distinguished by their δ^{13}C and δ^{15}N values. Among consumers, the filter-feeding bivalves *Laternula elliptica* and *Limatula* sp. exhibited the lowest N values, which were similar to those of the benthic diatom bush and MPB.

3.2. Contributions of benthic diatom bush and other food sources to the diets of other trophic groups

While benthic diatoms are the primary food source of the filter feeders, other primary consumers likely rely on mixed food sources in their diets. The SIAR model, shown in Fig. 3, indicated that the benthic diatom bush constituted approximately 25% of the potential diet of the nudibranch *A. kerguelenensis*, although demosponges constituted the largest proportion (~50%) of its diet. Red algae (*P. decipiens* and *G. skottsbergii*) also comprised a significant proportion (~25%) of the nudibranch diet. For the terebellid polychaete species, the diatom bush (~20%), MPB (~20%) and SOM (~20%) together comprised approximately 60% of its diet. By contrast, macroalgae constituted the primary food source of the polychaete *Flabelligera* sp. and the sea urchin *Sterechinus* sp.

3.3. Trophic levels and categories

The trophic levels calculated from the δ^{15}N values ranged from 2 to 5.2, with changes of 2–3‰ δ^{15}N per trophic level, showing that benthic

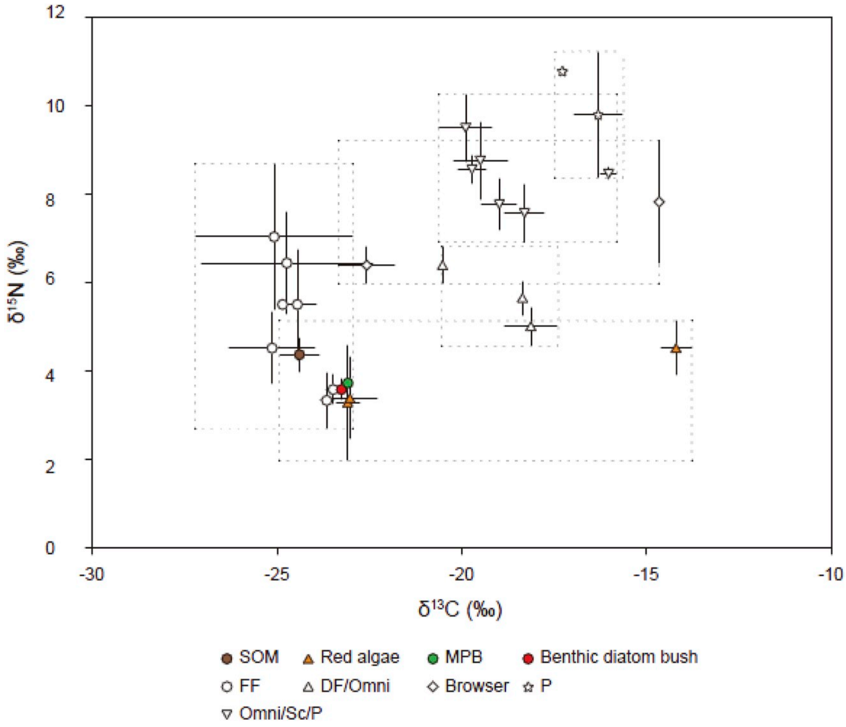

Fig. 2. A dual isotope plot of δ^{13}C and δ^{15}N values for megabenthic consumers and basal food sources in their diet, collected in Marian Cove (MC). Boxes with the dotted lines indicate the isotopic ranges of each feeding group.

consumers in this glacial cove comprise up to four levels, with the starfish *O. validus* and the isopod *G. antarcticus* at the apex (Fig. 4). These values were continuous rather than grouped into discrete levels. The consumer taxa were classified into five trophic groups based on information from the literature and isotopic data from this study: filter feeder, deposit feeder/omnivore, browser, predator/scavenger/omnivore, and predator (Fig. 4).

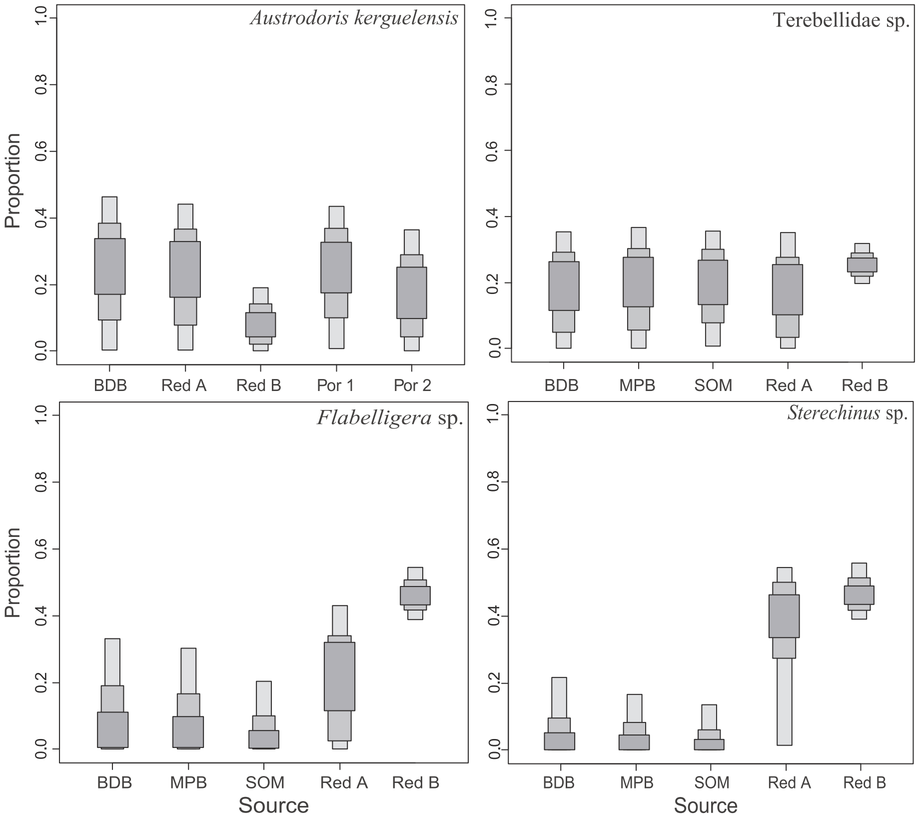

Fig. 3. SIAR model showing the relative contributions of various potential food items to the diets of primary consumers other than filter feeders. The potential food items for each consumer were determined based on feeding mode, the isotopic values obtained from this study and underwater observations of habitat. BDB, benthic diatom bush; MPB, microphytobenthos; SOM, sedimentary organic matter; Red A, *Palmaria decipiens* and *Gigartina skottsbergii*; Red B, *Curdiea racovitzae*; Por 1, Porifera sp. 15; Por 2, Porifera sp. 4. The gray bars of different widths (from darkest to lightest) show the 95, 75, 50 and 25% confidence intervals.

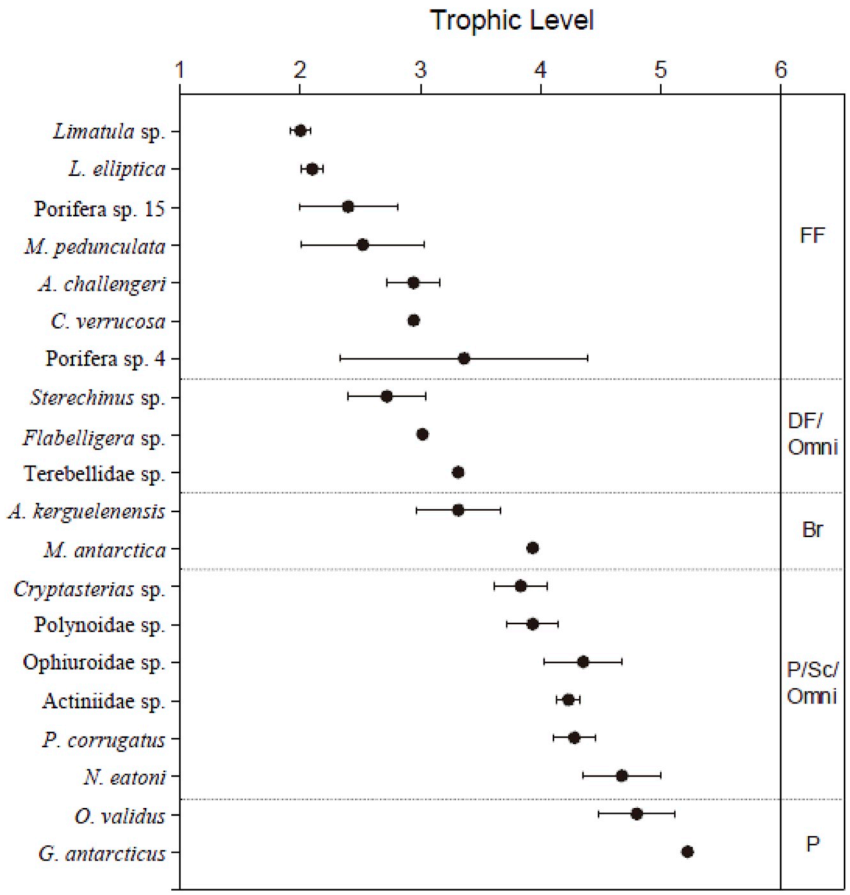

Fig. 4. Trophic levels and feeding modes of the consumers analyzed. The consumer taxa were classified into five trophic groups based on information from the literature and isotopic data from this study. FF, filter feeder; DF, deposit feeder; Omni, omnivore; Br, browser; Sc, scavenger; P, predator. Literature references regarding feeding modes: Pearse and Giese (1966a and 1966b), Presler (1986), Wägele (1989), Ahn (1993), McClintock (1994), Barnes and Bullough (1996), Gambi et al. (1997), Kowalke (1999), Corbisier et al. (2004), Norkko et al. (2007), Tatián et al. (2008a and 2008b), Jumars et al. (2015). Values are means ± standard deviation.

4. Discussion

4.1. *Benthic diatoms as the primary food source of common filter feeders in MC*

The filter feeders analyzed (bivalves, demosponges and ascidians) exhibited the most depleted $\delta^{13}C$ values (−23.5 to −25.2‰) of all consumers, similar to those of the benthic diatom bush, MPB and SOM, strongly suggesting that they rely predominantly on these benthic food sources. The similarity of C signatures among the benthic food sources, particularly between the diatom bush and MPB indicated the same origin of organic matter: benthic diatoms. However, the diatom bush could be regarded as the primary food source. First, the diatom bush had the highest apparent nutritional value, as evidenced by the highest organic content and lower C/N ratio. The C/N ratio of the diatom bush was most similar to that of freshly grown primary producers (Geider and La Roche, 2002). Second, the absolute quantity of the diatom bush was apparently much greater than that of the MPB, which formed a thin fluffy layer on the sediment surface. Recent photographs taken by a ROV and SCUBA divers clearly show that the formation of diatom bushes was intense and persistent, with no signs of depletion throughout the summer (Fig. 5). The benthic diatoms blooms were observed at most distances from the retreating glaciers, except for the innermost ice-proximal zone. In Choy et al. (2011), SPOM also had a similar $\delta^{13}C$ value (24.1‰), but in terms of quantity, the bush was much greater than SPOM and any of the other food sources. Moreover, the diatom bush, which remained physically close to the filter-feeding consumers, was apparently readily available as the principal dietary component of the consumers.

In a preliminary study, Ahn et al. (2016) reported that bush-like growth of benthic diatoms was likely due primarily to blooms of the chain-forming centric diatom *Paralia sulcata*. With additional sampling and microscopic analysis of bush samples collected from various sites during 2017–2018, we confirmed that the diatom bush overgrowing a variety of filter feeders was almost exclusively composed of this diatom species (Fig. 6A). There are only a few reports on *P. sulcata* in Antarctic or sub-Antarctic waters (Olguín et al., 2006; Jeon, 2014), whereas another species in the same genus, *P. sol*, was occasionally reported in Antarctic coastal waters at various localities (Thomas and Jiang, 1986; Ligowski, 2000; Majewska et al., 2016). Furthermore, the recent development of morphometric and molecular techniques revealed the cryptic diversity of the genus *Paralia* (MacGillivary and Kaczmarska, 2015; Yun et al., 2016). Therefore, in this study, due to uncertainty in identification, the species previously reported as *P. sulcata* in this study area (Ahn et al., 2016) was described as *Paralia* sp.

Paralia spp. are cosmopolitan species, commonly occurring in shallow neritic waters with varying salinity (McQuoid and Nordberg, 2003; Gebühr et al., 2009). They are observed more frequently in sediment than in the water column, likely because they have very thick, heavy silica walls, which prevents them from being easily suspended in the water column, while allowing them to be well preserved in sediment. Therefore, *Paralia* spp. have frequently been used as shallow-water indicators of the paleoclimate and paleoenvironment in various geographic localities, including the Antarctic (e.g., Sancetta, 1982; Bao et al., 1997; Crosta and Pichon, 1998; Cunningham et al., 1999; McQuoid and Nordberg, 2003; Ryu et al., 2005; Bart and Iwai, 2012).

Although *Paralia* sp. is heavily silicate and lacks buoyancy, it is likely readily available to the tightly associated consumers, as the *Paralia* bushes were physically very close to their consumers. Moreover, water movement easily disaggregated the diatom bushes, which were resuspended in the water, making them available for filter feeders (personal observations). In addition, the lack of buoyancy of *Paralia* sp. may be advantageous in terms of its availability to benthic herbivores in comparison with pelagic competitors such as herbivorous

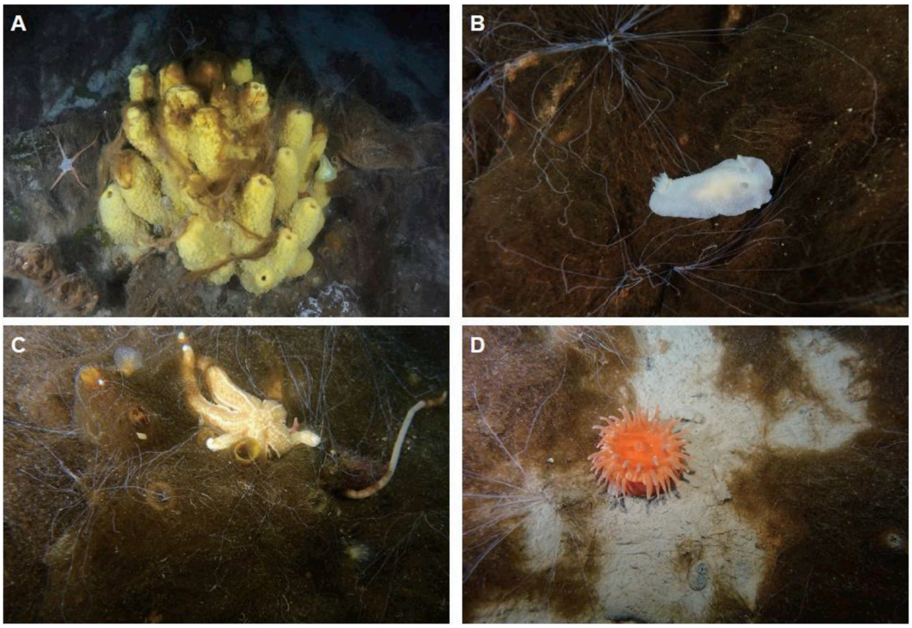

Fig. 5. A wide variety of taxa (ascidians, demosponges, terebellid polychaetes, starfishes, sea anemones, burrowing bivalves, nemertean worms, brittle stars, and nudibranchs) were found in association with the benthic diatom bush. These diatom bushes occurred persistently, at least during the austral summer; photos were taken at ~30 m depth in MC in (A) Jan 2013, (B) Dec 2013 (C) and (D) Dec 2017.

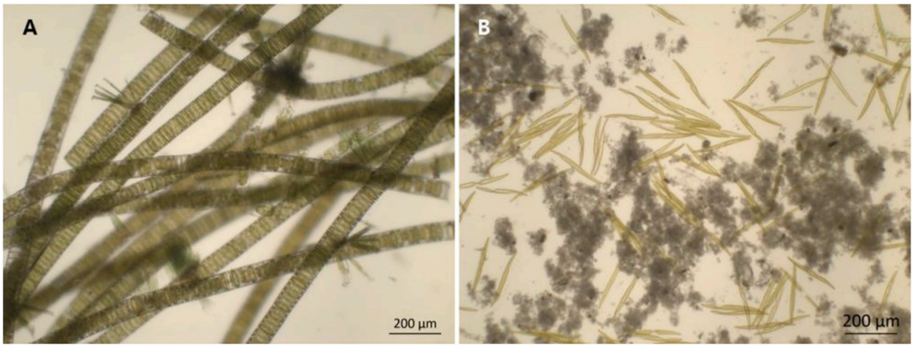

Fig. 6. (A) Strands of the chain-forming centric diatom *Paralia* sp. (previously reported as *P. sulcata* by Ahn et al., 2016) retrieved from the diatom bush overgrowing the surfaces of ascidians and demosponges and (B) *Pleurosigma* sp., the dominant diatom from a microphytobenthos (MPB) sample. These samples were collected from 20 to 30 m depths in MC in late January 2018 by SCUBA divers. LM (× 50, Axio imager A2; Zeiss, Germany).

zooplankton.

The dietary matter in MPB was also mainly benthic diatoms but was mixed with detrital matter, which likely explains the lower organic matter content. In addition, the species composition of MPB is likely distinct from that of the bush. One MPB sample was dominated by *Pleurosigma* sp. (Fig. 6B). In comparison, SOM had slightly more depleted C values and slightly higher N values, which may be attributed to mixed sources of organic matter including pelagic or sea ice algae (Pasotti et al., 2015; Jia et al., 2016).

Although the $\delta^{13}C$ and $\delta^{15}N$ isotopic values of two fresh macroalgae (*P. decipiens* and *G. skottsbergii*) were similar to those of the benthic diatoms, macroalgal fronds are unlikely consumed directly as a food source by filter feeders, which feed upon small suspended particles. However, detritus of macroalgal origin may contribute to their diet as a supplemental food source. These macroalgae are likely important food sources for some deposit feeders and omnivores, such as the sea urchin *Sterechinus* sp. and the polychaete *Flabelligera* sp.

4.2. *Contribution of benthic diatoms as an alternative food source to other trophic groups*

In addition to filter feeders, other trophic groups containing diverse taxa were observed on the diatom bush (Fig. 5), indicating that benthic diatoms may contribute to the diets of other trophic groups, in particular deposit feeders and omnivores. As shown in the SIAR model (Fig. 3), food sources derived from benthic diatoms constituted significant portions of the diets of the nudibranch *Austrodoris kerguelenensis* and terebellid polychaetes. *A. kerguelenensis* is a sponge browser (Wägele, 1989; Barnes and Bullough, 1996), but this species was frequently observed on the diatom bush at various sites in MC (Fig. 5B). Given that many sponges in MC are overgrown with the diatom bush, these diatoms appear to be consumed haphazardly by *A. kerguelenensis* while browsing the sponges. The tentacles of the tube-dwelling polychaete Terebellidae sp. were observed at all sites, particularly in association with demosponges and ascidians (Fig. 5). The $\delta^{13}C$ values of the terebellid polychaete and *A. kerguelenensis* (−20.6 ± 0.4‰ and −22.6 ± 0.4‰, respectively) are similar to those of filter feeders, further supporting the idea that benthic diatoms constitute part of their diet. The trophic levels of *A. kerguelenensis* and Terebellidae sp. were approximately 3.3, which were close to those (2.0–3.0) of filter feeders and other primary consumers.

4.3. *Trophic structure and prevalence of omnivory*

Trophic levels determined from the $\delta^{15}N$ values indicated that the benthic food web in this glacial cove was comprised of up to four trophic levels of consumers, with starfish and isopods at the apex. These values were continuous, rather than grouped into discrete levels, indicating that omnivory is prevalent in this area, similar to other Antarctic regions. Many Antarctic benthic invertebrates are omnivorous due to highly variable food availability in time and space (Dayton, 1990; Arntz et al., 1994; Gili et al., 2001; Corbisier et al., 2004; Norkko et al., 2007; Pasotti et al., 2015).

The $\delta^{13}C$ values (−14.7 and −22.6‰) of secondary and tertiary consumers, including many predatory species (nemerteans, polychaetes, isopods, gastropods and starfish) were similar to those reported for omnivores in other shallow habitats of the Antarctic Peninsula (Dunton, 2001). In particular, most predatory groups, such as the nemertean *Parborlasia corrugatus*, the gastropod *Neobuccinum eatoni*, the brittle star Ophiuroidea sp., the starfish *Cryptasterias* sp. and the polychaete Polynoidae sp., had δ^{13}C values similar to or slightly higher than those of omnivores and deposit feeders, without a clear coupling to sources of organic matter. This indicated that their diets consist of a wide variety of prey and food types. In rapidly warming shallow waters like MC, omnivory (feeding plasticity, with potential to feed on a variety of food sources) and deposit feeding appear to be effective strategies of consumers leading to an unexpectedly complicated food web structure (Pasotti et al., 2015).

4.4. Tight trophic association between benthic diatoms and their filter-feeding consumers in a rapidly warming Antarctic fjord and its implications

Filter feeders such as ascidians, demosponges and bryozoans comprise the largest trophic group (~60% of the total number of taxa) among the epibenthic megafauna in MC (Moon et al., 2015). Given the dense distribution of filter feeders, particularly ascidians (KOPRI, 2014), filter feeders presumably constitute a greater percentage of megafauna benthic biomass in this fjord. Thus, the tight association between the diatom blooms and filter feeders likely constitutes the basic structure of the nearshore marine megabenthic food web in this rapidly warming fjord.

Epibenthic megafaunal community assemblages dominated by dense populations of filter feeders have been reported frequently in shallow nearshore Antarctic waters (Dayton et al., 1986; Brey and Gerdes, 1997a,b; Sahade et al., 1998; Tatián et al., 2008c; Lagger et al., 2017). This finding raises questions about whether the prolonged period of winter starvation is much shorter than anticipated and whether alternative food sources are available in addition to phytoplankton production, which occurs during a relatively short period in the austral summer months (Gili et al., 2001). Lateral transport and resuspension of food materials on the seafloor have been considered as a process potentially responsible for the thriving communities of benthic filter feeders in the Antarctic (Ahn et al., 1997; Tatián et al., 2004; Isla et al., 2006; Elias-Piera et al., 2013).

The unique and efficient trophic association between the benthic diatom bush and its consumers may provide a new explanation for how opportunistic ascidians and other filter-feeding populations can flourish in Antarctic coastal areas, including glacial coves like MC. The bush-like thick growth of chain-forming benthic diatoms on the surfaces of a variety of epibenthic megafauna, particularly filter feeders, appears to be a highly efficient trophic association that is beneficial to both producers and consumers. The filter feeders may benefit from an association with the benthic diatom bush by readily obtaining diatoms as a principal dietary component, while the animals provide substrates to which the benthic diatoms attach, thereby remaining at depths shallow enough to receive light for photosynthesis.

The C isotopic signatures of the filter feeders (bivalves, sponges, and ascidians) in MC were similar to those reported for the same species and similar taxa in nearshore Antarctic waters (Dunton, 2001; Pasotti et al., 2015). This strongly suggests that the benthic fauna in other shallow Antarctic waters also rely on benthic primary producers. Dayton et al. (1986) reported that in shallow Antarctic coastal waters, benthic faunal biomass was often related to benthic primary production rather than to planktonic microalgal production. Several studies have observed significant numbers of benthic diatoms in the gut contents of various filter-feeding macrobenthic fauna, including bivalves (Ahn, 1994), hydroids (Gili et al., 1996), some peracarid crustaceans (Błażewicz-Paszkowycz and Ligowski, 2002), ascidians (Tatián et al., 2004) and sponges (Totti et al., 2005).

The main contributor to the blooms in MC, *Paralia* sp. occurs commonly in shallow neritic waters with varying salinity (McQuoid and Nordberg, 2003; Gebühr et al., 2009), and is frequently used as a shallow-water indicator in paleoclimate and related studies in various geographic localities (e.g., Sancetta, 1982; Bao et al., 1997; Crosta and Pichon, 1998; Cunningham et al., 1999; McQuoid and Nordberg, 2003; Ryu et al., 2005; Bart and Iwai, 2012). Therefore, the *Paralia* sp. bloom in MC also indicates its potential utility as an indicator of glacier-retreat processes. However, further studies are needed to ascertain if the benthic diatom bush is a common feature in rapidly warming Antarctic fjords. Furthermore, determining whether these benthic diatom blooms are attributed to meltwater processes would provide new insights into future scenarios in the rapidly warming Antarctic fjord ecosystem.

5. Conclusions

This study shows isotopic evidence of a tight trophic association between benthic diatoms and filter-feeding consumers in a rapidly warming Antarctic fjord. This trophic feature is unique, and seemingly highly efficient in that the benthic primary producers stay physically close to the filter-feeding consumers by overgrowing on the consumers and that the main contributor to this production is a benthic diatom species rarely reported in Antarctic waters. This unique, highly efficient trophic association may provide a new explanation of how filter feeders are flourishing in this glacial cove and other Antarctic coastal areas. Given that filter feeders comprise the largest trophic group (~60% of the total number of taxa) among the epibenthic megafauna in MC (Moon et al., 2015), benthic diatom bushes likely play a central role in supporting the benthic food web in this rapidly warming fjord. The findings of this study warrant further research into the mechanisms underlying the benthic diatom bloom as well as its relevance to glacial retreat and subsequent processes to envisage future conditions under ongoing climate change.

Declarations of interest

None.

Acknowledgments

The authors extend special thanks to the divers, Mr. Seung-Goo Ra and Mr. Kwan-Young Song, for their hard work during underwater surveys and sampling. We also thank the 27th Korea Antarctic overwintering team members for field assistance. We extend our appreciation to Dr. Sung Joon Song for the microscopic photographs of benthic diatoms. This work was conducted as part of CHAMP2050 (PE18070) and supported by the Korea Polar Research Institute, Incheon.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2018.12.020.

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