Unraveling the multiple bottom-up supplies of an Antarctic nearshore benthic community

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ABSTRACT

Disentangling the bottom-up controls of natural ecosystems is key to understanding the capacity of local communities to resist natural and anthropogenic disturbances. Here, we used carbon and nitrogen stable isotope ratios with a Bayesian multiple source mixing model to trace diverse food sources supporting the benthic trophic network in Fildes Bay (South Shetland Island, Western Antarctic Peninsula). Individuals of 16 species of consumers and five potential food sources (e.g. inter- and subtidal macroalgae, suspended and sinking particulate organic matter, and particulate organic matter from sediment) were collected during January and February 2017. The results showed that benthic organisms of Fildes Bay assimilate a broad range of available organic matter: most of the energy channeled to upper trophic consumers comes from organic matter in the surface sediment, whereas energy moving among lower trophic consumers comes largely from macroalgae and pelagic primary food sources. Overall, our evidence indicates that the present-day nearshore benthic community of Fildes Bay relies on different primary food sources, channeling bottom-up supplies through multiple pathways, which leads to highly stable systems in the face of current scenarios of global change.

1. Introduction

Pulses of phytoplankton have been long recognized as the main primary food source sustaining Antarctic nearshore benthic communities (e.g. Barnes and Clarke, 1995). Nonetheless, several recent studies claim that the role of pelagic primary food sources has been overestimated, concluding that multiple primary food sources sustain these communities (Corbisier et al., 2004; Norkko et al., 2007; Gillies et al., 2013). The existence of different primary food sources implies that energy may flow through multiple pathways across the food web, enhancing its stability in the face of disturbances (e.g. Lawton, 1994). Accordingly, unraveling the multiple bottom-up supplies may be key to understanding the mechanisms underpinning the stability of food webs off coastal Antarctica.

Few studies have documented the importance of primary food sources for consumers in coastal areas off the Antarctic Peninsula (but see Kaehler et al., 2000; Dunton, 2001; Corbisier et al., 2004; Jacob et al., 2006). Thus, the fate of primary food sources and their role in sustaining benthic Antarctic communities remain uncertain. Benthic micro- and macroalgae may be regarded as primary food sources in Antarctic ecosystems (Fischer and Wiencek, 1992; Amsler et al., 1995; Corbisier et al., 2004), providing an important proportion of carbon to Antarctic benthic consumers (e.g. Reichardt, 1987; Dunton, 2001; Corbisier et al., 2004). The availability of subsidies of organic matter for benthic consumers depends, however, on the proportion of sea surface that is covered by ice. For instance, Norkko et al. (2007) found that consumption of detritus is higher in areas covered by ice, whereas the consumption of fresh macroalgae is higher in areas free of ice. Consequently, fresh and detrital matter play a relevant trophic role, increasing the availability of primary production in coastal areas of the Antarctic Peninsula (Smith et al., 2006; Norkko et al., 2007) and influencing the connections between the water column and benthic processes (Smith et al., 2006).

Stable carbon and nitrogen isotope analysis is a well-established method for tracing the dietary sources and trophic levels of organisms (DeNiro and Epstein, 1981; Tieszen et al., 1983). Carbon isotopic values (δ¹³C), on the other hand, help trace trends in marine habitat use between two extremes of a spatial gradient, namely inshore/benthic and offshore/pelagic habitats (Fry and Sherr, 1984; Wada et al., 1991; Cherel and Hobson, 2007). This gradient in marine habitat use occurs...
because primary producers in nearshore benthic areas are relatively more $^{13}$C-enriched than those in offshore and pelagic regions. Thus, in areas where $\delta^{13}$C values differ strongly among primary producers, it is possible to detect the relative influence that different sources have on consumer diets (Fry and Sherr, 1984; Hobson et al., 1995; Post, 2002).

Nearshore benthic communities in Fildes Bay off King George Island (South Shetland Islands) constitute a model system for assessing the relative importance of different primary food sources for consumers. Overall, this ecosystem is widely heterogeneous, with trophically linked organisms (Ortiz et al., 2016), and the combination of oceanic and fresh water contributions along with shifting sea ice distributions enhance variability in sea surface temperature, salinity, and primary productivity (Khim and Yoon, 2003; Moreno-Pino et al., 2016). Moreover, short-term simulations in this ecosystem suggest that the dominance of subtidal macroalgae provides greater resistance to disturbances than found in analogous communities dominated by kelp forests and seagrass meadows (Ortiz et al., 2016). All these features hint at the existence of different bottom-up supplies flowing through multiple pathways and sustaining the heterogeneous nearshore benthic community of Fildes Bay.

The objective of this study is to explore the trophic links between primary food sources (suspended and sinking particulate organic matter, superficial sediment organic matter and macroalgae) and consumers, using stable isotope ratios ($\delta^{13}$C and $\delta^{15}$N) and Bayesian statistical approaches. We tested the general hypotheses that lower and different sources have on consumer diets (Fry and Sherr, 1984; Hobson et al., 1995; Post, 2002).

2. Material and methods

2.1. Study area

This study was conducted in Fildes Bay, off the southwestern end of King George Island, in the South Shetland Islands (Fig. 1). Local hydrography is influenced by an inflow of oceanic water from Bransfield Strait (Khim et al., 1997) and local-origin water from melting glaciers and river runoff (Hong et al., 1991; Khim et al., 1997; Khim and Yoon, 2003). Despite extreme environmental conditions and the effect of winter sea surface ice, the benthic community of Fildes Bay is characterized by highly abundant and diverse macroinvertebrates and macroalgal (Valdivia et al., 2014; Aghmich et al., 2016). Specifically, the subtidal zone is dominated by brown and red macroalgae, along with several species of fishes, scavengers, grazers, sponges, bryozoans, and ascidians; the intertidal zone is dominated by amphipods, littorinid snails, littorinid snails, crustose algae, and several small, opportunistic macroalgae (mostly filamentous green algae) (Valdivia et al., 2014; Segovia-Rivera and Valdivia, 2016).

2.2. Primary food sources

To evaluate the contribution of different energy sources, samples of representative benthic and pelagic food sources were collected in austral summer (January–February 2017) in Fildes Bay (Fig. 1 and Table 1). Benthic primary food sources included subtidal and intertidal macroalgae and surface sediment organic matter (OM). Pelagic primary food sources included suspended particulate organic matter (POM) and sinking POM.

Subtidal macroalgae were collected by SCUBA diving along ten transects; samples were taken using a portable underwater venture-suction device equipped with a 20-µm mesh size at station C (Fig. 1), a rocky shore on the northern margin of Fildes Bay (depth < 30 m). Intertidal macroalgae were hand-picked at Station B (Fig. 1). For surface sediment OM, five cores were collected from the upper 3 cm layer by SCUBA diving, separated by at least 4 m. These samples were collected at subtidal station 5 (Fig. 1), along the 20 m isobaths. Macroalgae and surface sediment OM were washed with distilled water and frozen in a cold-room below −20 °C.

A 10-L go-flo bottle was used to sample suspended POM at 5-m depth, whereas sediment traps were used to collect sinking POM at 50-m depth (Fig. 1). Both suspended and sinking POM were collected by filtering seawater through a pre-combusted (4 h, 550 °C), 47-mm, GF/F glass fiber filter (0.7-µm pore size), until the flow of water decreased to a slow drip. Then the filters were frozen at −20 °C until the next treatment.

2.3. Consumers

Invertebrates and fishes were collected from intertidal and subtidal sites (depth < 30 m) off the north coast of Fildes Bay (Fig. 1). Subtidal invertebrates were collected by SCUBA diving, following the underwater venture-suction explained above, whereas intertidal organisms (N. concinna) were hand-picked during the diurnal low tide at Station B (Fig. 1). Invertebrates were kept alive for 24 h in the laboratory to allow evacuation of gut contents, then sorted and frozen (−20 °C) until analysis. Subtidal fishes were collected using lines fishing with different baits (e.g. pork, chicken, clams), and then individually sealed in plastic bags and frozen (−20 °C). Invertebrates were sorted and identified to the lowest taxonomic classification possible. Fishes were identified to

![Map of Fildes Bay](image_url)
Table 1 δ13C and δ15N values (mean ± SE) of taxa collected from Fildes Bay.

<table>
<thead>
<tr>
<th>Taxonomic group or species</th>
<th>n</th>
<th>δ13C (%)</th>
<th>δ15N (%)</th>
<th>Feeding strategies/Trophic group</th>
<th>References</th>
</tr>
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<tbody>
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<td><strong>Sources</strong></td>
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<td>2.6 ± 0.8</td>
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<td>Suspended POM</td>
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<td>−19.8 ± 0.1</td>
<td>2.4 ± 0.0</td>
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<td>Surface sediment POM</td>
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<td>Macroalgae</td>
<td>25</td>
<td>−17.8 ± 2.1</td>
<td>3.8 ± 1.2</td>
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<td>Adencosys urticularis</td>
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<td>Iridea cordata</td>
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<td>Palmaria decipiens</td>
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<td>−18.5 ± 0.5</td>
<td>2.4 ± 0.3</td>
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<td>Messoroma hirtioci</td>
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<td>3.9 ± 0.4</td>
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<td>5.5 ± 1.0</td>
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<td>6.5 ± 0.5</td>
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<td>Gibson (1983)</td>
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<td><strong>Mollusca</strong></td>
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<tr>
<td>Bivalvia</td>
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<tr>
<td>Laterula elliptica</td>
<td>5</td>
<td>−20.3 ± 0.3</td>
<td>3.8 ± 0.2</td>
<td>Suspensivore</td>
<td>Brockington (2001)</td>
</tr>
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<td>4.0 ± 0.2</td>
<td>Suspensivore</td>
<td>Martens (1885)</td>
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<td><strong>Gastropoda</strong></td>
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<td>Nacella concinna</td>
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<td>6.9 ± 0.2</td>
<td>Grazer (Intertidal)</td>
<td>Clarke et al. (2004)</td>
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<td>Lueciasmacuaantarctica</td>
<td>4</td>
<td>−16.5 ± 0.2</td>
<td>5.5 ± 0.2</td>
<td>Grazer (Subtidal)</td>
<td>Iken (1999)</td>
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<td>5.9 ± 0.3</td>
<td>Grazer (Subtidal)</td>
<td>Gutt and Schickan (1998)</td>
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<td>Asteridea</td>
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<td>Odontaster validus</td>
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<td>7.6 ± 0.9</td>
<td>Deposit Feeder/Predatory invertebrate</td>
<td>Dearborn (1977)</td>
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<td>Amphipoda</td>
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<tr>
<td>Bovalia gigantea</td>
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<td>−21.8 ± 0.4</td>
<td>6.6 ± 0.4</td>
<td>Carnivore/Predatory invertebrate</td>
<td>Bone (1972)</td>
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<td>Cheirimedon femoratus</td>
<td>6</td>
<td>−14.7 ± 0.6</td>
<td>4.4 ± 0.6</td>
<td>Omnivore/Scavenger amphipod</td>
<td>Seefeldt et al. (2017)</td>
</tr>
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<td>Gongodogenia antarctica</td>
<td>3</td>
<td>−19.4 ± 0.2</td>
<td>5.9 ± 0.3</td>
<td>Omnivore/Scavenger amphipod</td>
<td>Aumack et al. (2017)</td>
</tr>
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<td>Dytchoa furcipes</td>
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<td>−16.9 ± 0.3</td>
<td>4.8 ± 0.2</td>
<td>Hervibore amphipod</td>
<td>Nysen et al. (2005)</td>
</tr>
<tr>
<td>Pseudobranchia gracilis</td>
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<td>−18.7 ± 0.7</td>
<td>4.0 ± 0.4</td>
<td>Hervibore amphipod</td>
<td>Zamzow et al. (2010)</td>
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<td>Paracarcinus miersii</td>
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<td>−21.5 ± 0.6</td>
<td>4.8 ± 0.2</td>
<td>Scavenger/Benthic consumer</td>
<td>Obermüller et al. (2013)</td>
</tr>
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<td><strong>Chordata</strong></td>
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<td>Fish</td>
<td></td>
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<tr>
<td>Nothotemia rosii</td>
<td>16</td>
<td>−21.6 ± 1.2</td>
<td>10.0 ± 0.5</td>
<td>Omnivore/Predatory Fish</td>
<td>Barrera-Oro and Winter (2008)</td>
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<td>Nothotemus corticeps</td>
<td>13</td>
<td>−20.0 ± 0.8</td>
<td>10.9 ± 0.8</td>
<td>Omnivore/Predatory Fish</td>
<td>Daniels (1982)</td>
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<tr>
<td>Hapagopyr antarcticus</td>
<td>8</td>
<td>−16.7 ± 0.7</td>
<td>11.1 ± 0.6</td>
<td>Omnivore/Predatory Fish</td>
<td>Blankley (1962)</td>
</tr>
</tbody>
</table>

2.4. Stable isotope analysis

In the laboratory, filters, pelagic primary food sources, surface sediment OM, and macroalgae samples were dried at 60 °C for 36–48 h in an oven and then acidified for the removal of carbonate by wetting the filters with 1 mL 0.5 M hydrochloric acid (HCl). Consumers were thawed with distilled water, dried in an oven at 60 °C for 36–48 h, and ground to a fine powder with a mortar and pestle. Soft tissues were collected from sea stars, fishes, nemerteans, and mollusks. For small invertebrates (e.g., amphipods and some mollusks with body length < 100 mm), the entire organisms were analyzed, and roughly ten whole organisms constituted a single replicate sample.

Lipids were extracted from fish and invertebrate samples with a chloroform/methanol (2:1) solution (Bligh and Dyer, 1959). This is because, compared with other molecules, lipids are depleted in 13C (DeNiro and Epstein, 1978) and their concentration in tissues may vary between and within species. On the other hand, high concentrations of inorganic carbon in some invertebrate exoskeletons may cause undesirable variability in δ13C (Lorrain et al., 2003). Thus, each sample was divided into two aliquots, and calcium carbonate was removed by soaking subsamples in 0.5 M hydrochloric acid (HCl) until the CO2 was completely depleted (Newsome et al., 2006). Since this HCl treatment adversely affects the δ15N values (Bunn et al., 1995), the remaining aliquot was left untreated for δ15N analyses.

Approximately 10–15 mg of POM with filter, 0.8–1.0 mg of algae, 0.3 mg of mollusk mantle and fish muscle, and 0.3–0.5 mg of entire crustaceans were weighed into sterilized tin capsules and analyzed for dual stable carbon and nitrogen isotopes. Each pre-treated sample was combusted in a Thermo elemental analyzer integrated with an isotope ratio mass spectrometer. All the consumers and benthic primary food sources were analyzed at the Pontificia Universidad Católica de Chile (Flash EA200 IRMS Delta Series, Thermo Scientific, Germany), and the pelagic primary food sources were analyzed at the University of California Davis, using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

Stable isotope ratios were reported in standard (8) notation using the following equation:

$$\Delta X = \left[(R_{\text{sample}}/R_{\text{standard}}) - 1\right] \times 1000$$  (1)

where $X$ is either 13C or 15N, $R$ is the ratio of heavy to light isotopes, and the standard is either PDB for 13C or atmospheric N2 for 15N. The reproducibility, as determined by the standard deviation of the internal standards, was ± 0.18% and 0.30% for δ15N and δ13C, respectively.
2.5. Trophic position

Nitrogen stable isotope ratios at the base of the food-web are needed to estimate the trophic position (TP) of the consumers. Because $\delta^{15}\text{N}$ values of primary producers are strongly influenced by spatial temporal parameters (Post, 2002; Iken et al., 2010; Miller and Page, 2012), our baseline TPs were calculated using $\delta^{15}\text{N}$ values of *Laternula elliptica*, a suspensivore bivalve and primary consumer (i.e. assumed to occupy TP = 2) of phytoplankton (Brockington, 2001), and *Laevilacunaria antarctica*, a herbivorous gastropod that consumes mainly macroalgae (Iken, 1999).

Since outputs from the 1- and 2-source TP models (see Post, 2002) were similar, the following 1-source TP model was applied for all individuals:

$$TP_{\text{consumer}} = \left(\frac{\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{base}}}{\Delta \delta^{15}\text{N}}\right) + TP_{\text{base}}$$

where the mean $\delta^{15}\text{N}$ of *L. elliptica* was used as the baseline and represented a $T_L^{\text{base}}$ of 2. A value of 2.3‰ was used for trophic enrichment, $\Delta \delta^{15}\text{N}$ (McCutchan et al., 2003).

2.6. Data analyses

After calculating the isotopic mean values and standard deviations (SD) of the consumers and primary food or carbon sources (Table 1 and Fig. 2), we tested normality and homoscedasticity of residuals with the Lilliefors and Levene tests, respectively. For multiple comparisons, the data sets did not meet the normality and homoscedasticity requirements; thus, the non-parametrical Kruskal-Wallis test was used. In addition, we used a paired-samples t-test to compare the means between trophic groups and primary food sources considering the assumptions of the t-test. These analyses were carried out with PASW Statistics (version 17.0 for Windows, SPSS). Significance was assumed at 0.05.

To estimate the relative contribution of primary food sources to each species studied (Parnell et al., 2010), we used the upgrade function *simmr* from the package *Stable Isotope Mixing Models* within R. This upgraded version of the SIAR package contains a slightly more sophisticated mixing model that allows realistic assessments and discerning source contributions to a mixture (Parnell, 2016). Models were built over four Markov chains with 10,000 steps per chain and a burn-in of 1000 iterations. Data within each group fitted a normal distribution, as required by SIAR (Parnell et al., 2010).

The fractionation factor ($\Delta$) is a critical aspect in reconstructing diets and trophic web structures (Post, 2002). This is especially true for species inhabiting Antarctic ecosystems because few controlled feeding studies exist for these organisms, often making it particularly challenging to discern metabolic issues of isotopic incorporation. On the other hand, trophic position is one of the main factors influencing $\Delta \delta^{15}\text{N}$ values (DeNiro and Epstein, 1981; Minagawa and Wada, 1984). Thus,
we compared our own empirical observations with Δ calculated by meta-analyses (McCutchan et al., 2003) to obtain appropriate measurements of quantitative interactions between consumers and sources. For this, we used linear mixing models with a fractionation factor multiplied by the number of trophic positions (obtained by equation (2)) between the consumer and the basal resources to simulate the proportions of each food source in the consumer diet (Phillips et al., 2014). We assessed the differences in δ15N values between phytoplankton (POM at a 5-m depth) and the primary consumer, L. elliptica, to obtain the trophic shifts for δ15N values of Fildes Bay baseline. Our empirically observed δ15N (mean ± SD = 1.3 ± 0.2‰) fell within the fractionation factor range prescribed for lower trophic consumers (mean ± SD = 1.4 ± 0.2‰) by McCutchan et al. (2003). Consequently, we used their suggested Δ15N and propagated the Δ according the trophic position obtained by equation (1) (mean ± SD; TP2 = 1.4 ± 0.2‰; TP3 = 2.8 ± 0.4‰; TP4 = 4.2 ± 0.6‰; TP5 = 5.6 ± 0.8‰).

The mean Δ13C obtained from the differences in δ13C values between potential primary food sources and consumers was smaller than Δ15N values among trophic levels. For that reason, we used the general Δ13C (mean ± SD = 0.5 ± 0.2‰) obtained by McCutchan et al. (2003) for different species.

Finally, to analyze the overall contribution of the main energy pathways sustaining the nearshore benthic Antarctic communities (Kaehler et al., 2000; Dunton, 2001; Norkko et al., 2007; Gillies et al., 2013), we grouped the primary food sources collected in: (1) pelagic primary food sources (suspended and sinking POM), (2) surface sediment organic matter, and (3) macroalgae (intertidal and subtidal macroalgae). Moreover, for this analysis, species were assigned trophic groups according to the literature (Table 1), their trophic position, and a hierarchical cluster analysis using the mean values of each species (Fig. 3).

3. Results

3.1. δ13C and δ15N of food sources and consumers

The composition of both carbon and nitrogen stable isotopes differed significantly among sources (Kruskal-Wallis test; δ13C: χ² = 28.327, df = 4, p < 0.01; δ15N: χ² = 10.338, df = 4, p < 0.05). For macroalgae, the mean δ13C values varied widely from −20.8‰ (Iridaea cordata) to −13.9‰ (Adenocystis utricularis) (Fig. 2 and Table 1), with significant differences between intertidal and subtidal macroalgae (paired t-test; p < 0.000). Macroalgae were significantly more enriched in 13C than pelagic and surface sediment OM primary food sources (paired t-test; p < 0.001 and p < 0.01, respectively). The δ13C values of sinking POM ranged from −23.3‰ to −20.5‰, with a mean of −21.8‰; this was significantly lower than the suspended POM values (paired t-test; p < 0.01). The δ13C values of surface sediment OM were quite uniform within the group (standard deviations < 1‰), and no difference was found among surface sediment OM and pelagic primary food sources (t = −0.630, p > 0.05) (Fig. 2 and Table 1).

The mean δ15N values of primary food sources ranged from 2.5‰ (pelagic primary food sources) to −3.8‰ (surface sediment OM) (Fig. 2 and Table 1). The pelagic primary food sources were distinctly more 15N-depleted (mean ± SD = 2.5 ± 0.7‰) than the macroalgae (paired t-test; p < 0.001) and surface sediment OM (paired t-test; p < 0.001). Macroalgae and surface sediment OM (including microorganisms and detritus) had more similar signatures (3.5 ± 0.9‰ and 3.8 ± 0.6‰, respectively); no significant differences were detected between groups.

Most δ15N-depleted values were observed in the pelagic primary food sources (mean ± SD = 2.5 ± 0.7‰) and were significantly lower than macroalgae and surface sediment OM values. In addition, we detected a slight depth-related variation for pelagic food sources, with more 15N-enriched in sinking POM than suspended POM, and also a sharp variation in δ15N values between intertidal (4.0 ± 1.6‰) and subtidal macroalgae (3.4 ± 1.0‰).

Overall, these significant differences between groups support the premise of multiple energy sources for macrobenthic consumers in Fildes Bay.

A total of 98 consumers were sampled in Fildes Bay, covering a wide range of taxonomic groups (Table 1 and Fig. 2). The consumers exhibited significant differences for both δ13C and δ15N values (Kruskal-Wallis test; δ13C: χ² = 85.044, df = 15, p < 0.01; δ15N: χ² = 92.186, df = 15, p < 0.01).

Diet was used to sort species into seven different feeding groups: predatory fishes, predatory invertebrates, scavenger amphipods, subtidal grazers, intertidal grazers, herbivore amphipods, and suspension feeders (Table 1 and Fig. 2). A cluster analysis confirmed this classification (Fig. 3). Scavenger amphipods, herbivore amphipods, and subtidal grazers displayed more isotopic variability than the other groups, which showed quite similar isotopic signatures within each feeding group (paired t-test; p > 0.01).

Fig. 3. Dendrogram based on the mean δ13C and δ15N values of trophic group from the benthic community of Fildes Bay (South Shetland Island, Antarctic Peninsula).
The δ¹³C values of all consumers were distributed over a wide range, from −21.9‰ (B. gigantea) to −13.9‰ (N. concinna). The scavenger amphipods showed the widest range of δ¹³C values (−18.1‰ ± 3.2), followed by predatory fishes (−20.0‰ ± 2.1), and predatory invertebrates (−21.4‰ ± 1.0). In terms of δ¹⁵N signatures, the consumers ranged from 3.7‰ (L. elliptica) to 11.1‰ (H. antarcticus) (Table 1 and Fig. 2). The predatory fishes showed the widest range of δ¹⁵N (10.4‰ ± 0.9), followed by the predatory invertebrates (7.0‰ ± 0.8).

Finally, we found that predatory fishes and the predatory sea star occupied the upper trophic level (TP5-TP4), whereas scavenger amphipods, predatory invertebrates, grazers, and suspensivores occupied the range of TP3-TP2 (Fig. 4).

3.2. Relative contribution of food sources to consumers

Assimilation of δ¹³C and δ¹⁵N derived from pelagic and benthic trophic pathways differed among consumers in Fildes Bay (Fig. 5). Overall, The SIAR output showed that, for most consumers analyzed, contributions of surface sediment OM and macroalgae tended to prevail over pelagic primary food sources (Fig. 4). The predatory fishes, N. coriceps and N. rossii, derived a high proportion of their diets (> 50%) from surface sediment OM (Fig. 5a and b). Conversely, H. antarcticus derived over 80% of its diet from the intertidal macroalgae, A. utricularis (Fig. 5c). The predatory invertebrate, O. validus, showed a similar proportion of food sources, although surface sediment OM was slightly larger (Fig. 5d). Similarly, surface sediment OM played a major role in the diets of P. corrugatus (Fig. 5e) and B. gigantea (Fig. 5g).

Scavenger amphipods showed a marked variation in the proportion of primary food sources making up their diets. Whereas G. antarctica (Fig. 5i) and P. miersii (Fig. 5h) mainly assimilated pelagic sources, Ch. femoratus mainly assimilated intertidal macroalgae (Fig. 5f).

At lower trophic levels, grazers and herbivore amphipods received >60% of their diet from macroalgal material. On the contrary, as expected, the suspensivores (L. elliptica and K. bicolor) derived a high proportion of their diets from pelagic food sources.

4. Discussion

The overall evidence reported here indicates that, currently, the nearshore benthic community of Fildes Bay assimilates different primary food sources, revealing a system sustained by multiple pathways of organic matter, but with variable degrees of benthopelagic coupling depending on the consumers’ trophic positions. These results are consistent with previous studies of shallow benthic Antarctic communities (e.g. Kaehler et al., 2000; Dunton, 2001; Norkko et al., 2007; Gillies et al., 2013). Although some primary food sources were not assessed in this study, our results certainly reflect the main energy pathways believed to sustain the macrobenthic marine communities off Antarctica, namely pelagic primary food sources, surface sediment OM, and macroalgae primary food sources (Kaehler et al., 2000; Dunton, 2001; Norkko et al., 2007; Gillies et al., 2013).

4.1. Surface sediment organic matter (OM) as a food source for upper trophic levels

The dominant energy channel in the upper trophic level was the surface sediment OM and, to a lesser degree, macroalgae and pelagic primary food sources. Similar patterns have been observed in other regions off Antarctica (Norkko et al., 2007), suggesting that sediment OM is an important source of detritus to higher trophic levels, contributing strongly to bottom-up controls and dampening seasonality. The mineralization and utilization of C by microbial communities depletes the δ¹³C values of surface sediment OM (Hollander and Smith, 2001). Similarly, it is also highly likely that bacterial degradation increases δ¹⁵N values (Macko and Estep, 1984). Surface sediments from the Antarctic Peninsula are characterized by high nutrient contents and a large presence of diatoms (e.g. Chaetoceros), Bacteroidetes, and Cercozoan (Learman et al., 2016), which can, in turn, benefit upper consumers via trophic mediation. For instance, Norderhaug et al. (2003) experimentally showed low C:N ratios in decomposed
Macroalgae due to decreased phytotoxin concentrations. Similarly, Norkko et al. (2004) reported that fragmentation and bacterial degradation facilitates the entrance of accumulated *Phyllophora antarctica* drifts into the food web in McMurdo Sound, but with a slow degradation rate due to the cold temperatures (Brouwer, 1996). These results are demonstrating that high nutrient concentrations and microbial activity in sediments constitute a relevant component of benthic food webs in these low-temperature ecosystems.

Stable isotope ratios of some predatory invertebrates (*P. corrugatus*, *B. gigantea*) and predatory fishes (*N. coriiceps*, *N. rossii*) were clearly coupled with the surface sediment OM. The overlaps observed among surface sediment OM, pelagic primary food sources, and macroalgae suggest a mixing of detrital and fresh organic matter derived from phytoplankton and macroalgae material. Thus, it is likely that these predatory invertebrates and fishes are consuming prey that feed on a mix of fresh and detrital material accumulating in the surface sediment. Fishes are usually more mobile than their prey, which allows them to integrate different energy pathways originating in different food sources. Accordingly, the high contribution of surface sediment OM (> 50%) in the *N. rossii* diet may be related to the wider home range observed for this species (Burchett, 1983; Barrera-Oro and Winter, 2008). On the other hand, for *N. coriiceps*, a cryptic species (Casaux et al., 1999), the integration of different sources of OM could be associated with an efficient detritivore pathway. The macroalga, *A. utricularis*, contributes heavily to the *H. antarcticus* diet, suggesting a lower integration of different energy sources likely related to the species’ specialist feeding behavior and narrow home range: under rocks on the seafloor of the Antarctic Peninsula (Casaux, 1998).

### 4.2. The polyphagous nature of scavenging amphipods

Stable isotope ratios varied widely for scavenger amphipods, confirming the high diversity of feeding modes in this taxon (Dauby et al., 2001; Amsler et al., 2014). Specifically, the broad range of δ¹³C values recorded here reflects the selection of different primary food sources based on scavenger amphipod foraging locations (Amsler et al., 2014; Aumack et al., 2017). *Paracerodocus miersii* and *G. antarctica* displayed depleted δ¹³C values, indicating the importance of pelagic prey items, but macroalgae also comprised a significant portion of the *G. antarctica* diet. Actually, digestive tract analyses revealed that diatoms contributed 50% of the *G. antarctica* diet (Aumack et al., 2017). Consistent with our results, previous isotopic measurements also revealed less enriched δ¹³C values for this species, associated with the consumption of the subtidal macroalgae, *P. decipiens* (Dunton, 2001; Aumack et al., 2017). Interestingly, our results showed a strong link between *C. femoratus*, a scavenger amphipod, and *A. utricularis*, an abundant macroalga in the Fildes Bay intertidal zone (Aghmich et al., 2016), underscoring the opportunistic feeding behavior of this Antarctic amphipod (Bregazzi, 1972). Furthermore, this result agrees with controlled-diet experiments, in which *A. utricularis* was more palatable to *C. femoratus* than *G. skottsbergii* and *P. decipiens* (Nuñez-Pons et al., 2012).

### 4.3. The role of macroalgal and pelagic primary food sources in lower trophic levels

At the lower trophic levels, the dominant energy pathways were macroalgae and pelagic food sources. Benthic suspensivore organisms were clearly separated from the other consumers on the δ¹³C axis, showing a stable isotope ratio similar to those of pelagic food sources and, to a lesser extent, surface sediment OM. This is consistent with previous records (e.g. Barnes and Clarke, 1995; Ahn, 1997; Gili et al., 2001). Regional variability in food available for benthic suspensivores is
closely tied to oceanographic processes (Barnes and Clarke, 1995). For instance, Ahn (1997) found that benthic diatoms are the dominant food supply for *L. elliptica* in summer, whilst smaller-sized plankton fractions and resuspended sediment dominate in winter. The high δ13C and δ15N values of pelagic primary food sources found here were among the highest recorded for the Antarctic Peninsula (e.g. Wada et al., 1987), most likely a consequence of the massive diatom blooms (chlorophyll > 30 mg m⁻²) and high primary production rates (e.g. 6.28 g Cd m⁻²) recorded within Filides Bay during January 2017 (Höffer et al., in this volume). Furthermore, we found significant differences between the δ13C values of suspended and sinking POM, which could be explained by different successional stages of the phytoplankton bloom (Ostrom et al., 1997), with benthic suspendeds heavily assimilating the 13C-depleted sinking POM. On the other hand, contributions of surface sediment OM in suspensivore diets suggest persistent resuspension of organic material by winds or iceberg scouring in Filides Bay (Brandini and Rebello, 1994).

As in other studies in Antarctic waters (Corbisier et al., 2004; Norkko et al., 2007; Gillies et al., 2013; Aumack et al., 2017), δ13C enrichment was higher in macroalgae than in the other analyzed sources, although some overlapping occurred with suspended POM. This overlap could be explained by the incorporation of the 13C-depleted from eiphyte/endophyte species (e.g. green algae filament, phaeophytes, and diatoms) growing in macroalgal tissues (e.g. Aumack et al., 2017).

Stable isotopes ratios of gastropod grazers and herbivore amphipods were closely aligned with the enriched δ13C values of macroalgal primary food sources, confirming that most of the carbon utilized by these organisms is derived from benthic production. Aumack et al. (2017) reported patterns of quantitative interactions in macroalgae and Antarctic amphipods at different sites near Anvers Island (Antarctic Peninsula) using isotopic measurements and gut contents. This study showed that macroalgal material (both filamentous and multilayerate) comprise a significant portion of the amphipod assemblage’s diet, but also that benthic diatoms are a significant dietary element for most amphipods. Nevertheless, the accidental ingestion of frustules probably inflates these percentages (Dauby et al., 2001). In any case, the overall evidence indicates a prevalence of macroalgae over surface sediment and pelagic sources as primary food sources for gastropod grazers and herbivore amphipods. Nonetheless, on a seasonal scale, the melting/freezing regime may considerably influence biomass production and species composition in macroalgal assemblages (Clark et al., 2013), leading to qualitative and quantitative differences in individual inter-actions of benthic food webs. Hence, further studies are necessary to elucidate shifts in the trophic connections of these heterogeneous assemblages of the Antarctic Peninsula.

4.4. A cautionary note and future directions

Our assessment of the assimilation of primary food sources by consumers is based on the assumption that the analysis of a relatively small number of food sources can be extrapolated to build generalizations of trophic pathways. Thus, a number of confounding factors should be considered. Firstly, this approach can lead to biased conclusions because of a low sampling effort of other potential primary food sources (e.g. the microphytobenthos, benthic diatoms, allochtho-nous material, and filamentous algae). Secondly, spatial variability in advection processes, or increased deposition, can affect the assimilation of food sources by consumers, especially in hydrographically complex areas (Tu et al., 2015). Finally, turnover times and the fractionation factor may affect variations of isotopic composition among consumers (Tieszen et al., 1983; Hobson et al., 1995; Post, 2002). Consequently, additional work combining isotopic composition, grazing experiments, and fatty acid analyses is needed to tease out the complex trophic links mobilizing primary food sources to consumers (Layman et al., 2012).

4.5. Conclusion

In summary, our work shows that the primary food sources analyzed can flow through multiple pathways across the benthic food web of Filides Bay, with upper trophic consumers receiving most energy from surface sediment OM, and lower trophic consumers supported mainly by macroalgae and pelagic primary food sources. In addition, this is the first attempt to apply quantitative Bayesian methods to the study of the nearshore benthic community in Filides Bay, and it certainly advances knowledge of the mechanisms that determine the resistance of local communities to environmental disturbances.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2018.10.016.

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