# Latitudinal changes in the trophic structure of benthic coastal food webs along the Antarctic Peninsula

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A R T I C L E   I N F O

A B S T R A C T

Stable isotopes of C and N have been used to assess the effect of the duration of the sea ice season on the structure of benthic, Antarctic coastal food webs. Samples of suspended particulate organic matter, macroalgae and macroinvertebrates were collected at five subtidal rocky sites across a latitudinal gradient along the western Antarctic Peninsula and among the South Shetland Islands. We tested the hypotheses that trophic positions of omnivores decrease, and food web structure becomes more redundant at higher latitudes. A latitudinal shift in the isotope baseline was detected for both $\delta^{13}$C and $\delta^{15}$N, but the trophic positions of macroinvertebrates and their relative positions along the $\delta^{13}$C axis and were basically constant across sites, even after rescaling stable isotope ratios to account for shifts in the baseline. Although the northernmost and southernmost study sites differed significantly in most of the metrics of the food web structure, changes with latitude and the duration of the sea ice season were non-monotonic. Highly productive phytoplankton blooms during the ice-free season at Esperanza Bay and Rothera Point may explain the observed pattern, as they result in a massive supply of planktonic organic matter to the detritus bank in the seabed and, hence, shorten the C range and increase trophic redundancy. If this hypothesis is correct, the intensity of the summer phytoplankton bloom can be as relevant for the structure of the benthic marine food web as the duration of the sea ice season.

## 1. Introduction

Antarctic marine ecosystems are unique because of the characteristics of their environment, with extremely low temperatures, strong oceanic currents, and extensive seasonal sea ice cover (Knox, 2006; Thomas et al., 2008). The presence of sea ice and the accumulation of snow above them heavily determines the underwater light regime and hence, the growth of phytoplankton, sea ice microalgae (i.e. sympagic), benthic macroalgae, and ultimately the overall food web structure (Dayton et al., 1986; Clarke 1988; Nedwell et al., 1993; Barnes and Clarke 1995; Smith et al., 2006; Norkko et al., 2007; Mincks et al., 2008; Thomas et al., 2008; Clark et al., 2013; Michel et al., 2019; Rossi et al., 2019). This seasonality in primary production is critical for both pelagic and benthic Antarctic ecosystems, which differ notwithstanding in the central role of grazing by krill in the pelagic food web (Knox 2006; Trathan and Hill 2016) and the accumulation of a detritus bank that serves as a major food source in benthic ecosystems (Smith et al., 2006; Norkko et al., 2007; Thomas et al., 2008; Michel et al., 2019).

The sharp seasonality in the growth and proliferation of primary producers results in the accumulation of large amounts of decaying organic matter in the sediment during the austral summer, serving as the staple food for most benthic, coastal invertebrates year-round (Corbisier et al., 2004; Norkko et al., 2007; Mincks et al., 2008; Thomas et al., 2008; Gillies et al. 2012, 2013; Michel et al., 2019; Zenteno et al., 2019). Antarctic benthic mobile invertebrates are often described as opportunistic omnivores with a high degree of trophic plasticity (McClintock 1994; Smith et al., 2006; Gillies et al. 2012, 2013; Michel et al. 2016, 2019), interspersed along with sessile communities of suspension feeders (Gili et al., 2006; Thomas et al., 2008). As a result, benthic, Antarctic coastal food webs are characterized by high numbers of species with similar ecological functions and hence, high trophic redundancy *sensu* Layman et al. (2007).

Antarctic benthic food webs can have up to five trophic levels (Gillies et al., 2013; Michel et al., 2019; Zenteno et al., 2019), but food web

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theory predicts that severe resource limitation reduces food web length (Post 2002a; Takimoto and Post 2013). In this context, a longer ice cover is expected to result in reduced annual primary production, increased reliance on the benthic bank of detritus, and thus, higher levels of trophic redundancy, and shorter food webs (Norkko et al., 2007; Mincks et al., 2008; Michel et al., 2019). Unfortunately, two limitations hinder our understanding of the relationship between the duration of the sea ice season and the trophic structure of benthic, coastal food webs.

First, comparing the structure of known benthic food webs from different sites around Antarctica is difficult because of variation in species or community composition between studies (Nedwell et al., 1993; Corbisier et al., 2004; Mincks et al., 2008; Smith et al., 2006; Norkko et al., 2007; Gillies et al. 2012, 2013; Michel et al., 2019; Zenteno et al., 2019). Second, comparing the structure of food webs from geographically distant places is critical to detect the influence of large-scale oceanographic processes on the structure of polar food webs (Kedra et al., 2012; Iken et al., 2010; Gillies et al., 2013; Divine et al., 2015; Stasko et al., 2018), but only a few comparative studies exist on the trophic ecology of Antarctic benthic invertebrates (Norkko et al., 2007; Gillies et al., 2013; Michel et al. 2016, 2019; Rossi et al., 2019).

The South Shetland Islands and the western Antarctic Peninsula offer an ideal setting for comparative studies over a broad, but relatively homogenous region. Sea ice covers the coastal waters of the South Shetland Islands and the western Antarctic Peninsula for only two months annually at latitude 62°S to as much as 9 months at latitude 68°S (National Snow & Ice Data Center, https://nsidc.org/data/sea ice_index). This suggests that major differences could exist in the trophic structure of benthic, coastal ecosystems along that latitudinal gradient, a hypothesis not addressed in previous studies on the Antarctic Peninsula (Corbisier et al., 2004; Dunton, 2001; Zenteno et al., 2019). It should be noted that latitude has no relationship with food web length on a global scale (Vander Zanden and Fetzer 2007) but can be a strong determinant of sea ice duration along the Antarctic Peninsula.

Here, we use the stable isotopes of C and N, together with recently developed metrics to characterize food-web structure using isotopic data (Layman et al., 2007; Jackson et al., 2011; Perkins et al., 2014), to assess the effect of the duration of the sea ice season on the structure of benthic, Antarctic coastal food webs. More precisely, we focus on a few abundant and widespread species representing different trophic positions to test the following hypotheses:

1) The trophic position of coastal Antarctic benthic macroinvertebrates varies across localities.

2) The level of trophic redundancy of benthic, Antarctic coastal food webs increases southwards, as sea ice lasts for longer there.

## 2. Materials

Samples were collected from February 12th to February 22nd, 2016 at five sites along the western Antarctic Peninsula: Fildes Bay, Esperanza Bay, Cierva Cove, Paradise Harbor, and Rothera Point (Fig. 1). Sampling sites ranged in latitude from 62°12′7″S to 67°34′30″S. From March 2015 to February 2016, sea ice had been present for 2 months at Fildes Bay, 4 months at Esperanza Bay and Cierva Cove, 6 months at Paradise Harbor, and 8 months at Rothera Point (National Snow & Ice Data Center).

The following 11 species were collected by SCUBA diving on rocky bottoms at depths from 10 to 15 m at each site: unidentified encrusting coralline algae, the fleshy red alga *Palmaria decipiens* (Reinsch) R.W. Ricker, 1987, the canopy-forming brown macroalgae *Himantothallus grandifolius* (A.Gepp & E.S.Gepp) Zinova, 1959 and *Desmarestia anceps* Montagne, 1842 (except at Fildes Bay, where *Desmarestia menziesii* J. Agardh, 1848 was collected instead), the sponge *Dendrilla antarctica* Topsent, 1905 (except at Esperanza, where *Kirkpatrickia variolosa* (Kirkpatrick, 1907) was collected), the sea cucumber *Heterocucumis steineni* (Ludwig, 1898), the limpet *Nacella concinna* (Strebel, 1908), the snail *Margarella antarctica* (Lamy, 1906), and the sea stars *Odontaster validus* Koehler, 1906 and *Diplasterias brucei* (Koehler, 1907). Sampling details are provided in Table 1 and selected species are shown in Fig. 2. Additionally, particulate organic matter was collected with a plankton net (50 μm mesh size) at each site. Microscopic observation confirmed that suspended particulate organic matter (SPOM hereafter) was dominated largely by diatoms (*Thalassiosira* sp., *Pseudonitzschia* sp., and *Corethron* sp.) and dinoflagellates (*Protoperidinium* sp.).

After collection, samples were rinsed with seawater, stored frozen at −20 °C, and transported to the University of Barcelona. Once in the laboratory, specimens were defrosted. A sample of 2 mL of net-collected SPOM was included in each replicate. A 2 × 2 cm section of epibiont-free blade was selected for each replicate of the four species of macroalgae. All animals were dissected to remove the gut and its content. After dissection, the whole body of limpets (excluding radula and shell), a 2 cm wide section of the body wall of holothurians, and a section of the arms of the sea stars (one to three arms, depending on body size), were dried at 60 °C for 24 h. Once dry, samples were manually grounded to a fine powder with a ceramic mortar and pestle. Echinoderm and encrusting coralline algae samples were later split into two aliquots. This is because $CaCO_3$ and lipids have to be removed to obtain unbiased $\delta^{13}C$
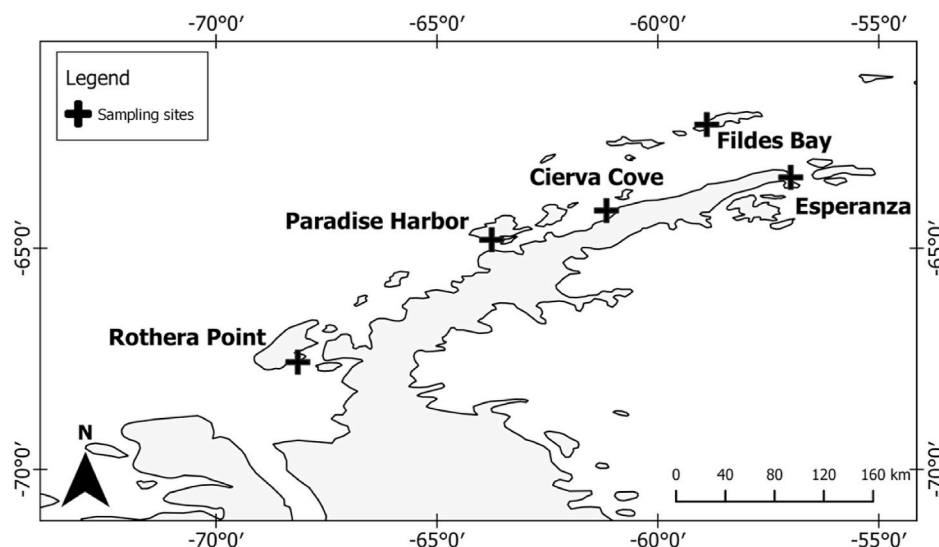


**Fig. 1.** Sampling sites along the Antarctic Peninsula and among the South Shetland Islands.

**Table 1**

Sample size (number of individuals) of each species per location. The number for SPOM indicate the replicates collected by plankton net. The numbers for the remaining species, collected by SCUBA, indicate the number of specimens.

| | Fildes Bay | Esperanza Bay | Cierva Cove | Paradise Harbor | Rothera Point |
|---|---|---|---|---|---|
| | 62°12′7″S | 63°23′54″S | 64°9′00″S | 64°49′00″S | 67°34′30″S |
| | 58°53′34.5″W | 56°59′26″W | 61°9′39.9″W | 63°45′21.6″W | 68°9′10.8″W |
| **SPOM** | 5 | 5 | 5 | 5 | 5 |
| **Encrusting coralline algae** | 5 | 4 | 5 | 5 | 5 |
| **Macroalgae** | | | | | |
| *Desmarestia anceps* | 0 | 5 | 5 | 5 | 5 |
| *Desmarestia menziesii* | 5 | 0 | 0 | 0 | 0 |
| *Himantothallus grandifolius* | 5 | 5 | 5 | 5 | 5 |
| *Palmaria decipiens* | 5 | 5 | 5 | 5 | 5 |
| **Macroinvertebrates** | | | | | |
| *Dendrilla antarctica* | 5 | 0 | 5 | 5 | 5 |
| *Diplasterias brucei* | 5 | 5 | 5 | 5 | 5 |
| *Kirkpatrickia variolosa* | 0 | 5 | 0 | 0 | 0 |
| *Heterocucumis steineni* | 5 | 5 | 5 | 5 | 5 |
| *Margarella antarctica* | 5 | 5 | 5 | 5 | 5 |
| *Nacella concina* | 5 | 5 | 5 | 5 | 5 |
| *Odontaster validus* | 5 | 5 | 5 | 5 | 5 |

values (Bas and Cardona 2018; Guiry et al., 2016) but demineralization consistently increases $\delta^{15}$N values (Bas and Cardon, 2018). Accordingly, one of the aliquots from encrusting coralline algae and echinoderms was used to assess the $\delta^{15}$N values without further processing (hereafter bulk samples) and the other was treated with a chloroform-methanol solution (2:1) to remove lipids and with 0.5 N hydrochloric acid (HCl) to remove carbonates before the assessment of the $\delta^{13}$C values. The samples of limpets, sponges, macroalgae, and SPOM were also treated with a chloroform-methanol solution to remove lipids. All samples were dried at 60 °C (for 24–72 h) after processing and stored dry until weighted in tin capsules. An amount of 0.7 mg was weighted for the bulk samples of echinoderms, encrusting coralline algae, and macroalgae. Only 0.3 mg was necessary for the remaining samples.

All tin cups were combusted at 900 °C and analyzed in a continuous-flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA, Thermo Finnigan; www.thermofisher.com) at Centres Científics i Tecnològics de la Universitat de Barcelona (www.ccit.ub.edu). The abundance of stable isotopes is expressed using the $\delta$ notation, where the relative variations of stable isotope ratios are expressed as per mil (‰) deviations from predefined reference scales: Vienna Pee Dee Belemnite (VPDB) $CaCO_3$ for $\delta^{13}$C and atmospheric nitrogen (AIR) for $\delta^{15}$N. However, due to limited supplies of VPDB, isotopic reference materials, which included known isotopic compositions relative to international measurement standards were analyzed instead. For carbon, isotopic reference materials of known $^{13}$C/$^{12}$C ratios, as given by the International Atomic Energy Agency (IAEA; www.iaea.org) in Vienna (Austria), were used for calibration at a precision of 0.05‰. These included polyethylene (IAEA $CH_7$, $\delta^{13}$C = −32.1‰), L-glutamic acid (IAEA $USGS_{40}$, $\delta^{13}$C = −26.4‰), and sucrose (IAEA $CH_6$, $\delta^{13}$C = −10.4‰). For nitrogen, isotopic reference materials of known $^{15}$N/$^{14}$N ratios were used to a precision of 0.2‰, and these were namely: $(NH_4)_2SO_4$ (IAEA $N_1$, $\delta^{15}$N = +0.4‰ and IAEA $N_2$, $\delta^{15}$N = +20.3‰), L-glutamic acid (IAEA $USGS_{40}$, $\delta^{15}$N = −4.6‰), and $KNO_3$ (IAEA $NO_3$, $\delta^{15}$N = +4.7‰). All these isotopic reference materials were employed to recalibrate the system once every 12 samples and were analyzed to compensate for any measurement drifts over time. The raw data were recalculated taking into account a linear regression previously calculated for isotopic reference materials (Skrzypek, 2013).

We used the R package tRophicPosition (Quesada-Romegialli et al., 2017) to calculate the trophic position of the macroinvertebrate species using a Bayesian framework. The trophic position of benthic algae and SPOM was assumed to be "1" and their individual $\delta^{13}$C and $\delta^{15}$N values were used to set the benthic and the pelagic baselines respectively at each sampling site. By default, tRophicPosition uses the trophic discrimination factors (TDF) reported by Post (2002b). We used those default TDF values for sponges, as laboratory-derived TDF values are not available for this taxonomic group (van Duyl et al., 2011). However, we used $\Delta^{13}$C = 0.6‰ and $\Delta^{15}$N = 1.7‰ for the three echinoderm species, according to (Prado et al., 2012); and $\Delta^{13}$C = 0.8‰ and $\Delta^{15}$N = 2.2‰ for the two gastropods, according to Choy et al. (2011).

General linear models, run in IBM SPSS for Windows v. 24, were used to explore differences in the $\delta^{13}$C and $\delta^{15}$N values across species and sampling sites, and hence, detect local shifts in the isotope baseline. Differences in the trophic position of each macroinvertebrate species between sites were tested with the function pairwise comparisons as implemented in tRophicPosition (Quesada-Romegialli et al., 2017).

As GLMs revealed shifts in the isotopic baseline (see results), we followed Fry and Davis (2015) and rescaled each $\delta^{13}$C and $\delta^{15}$N value into a Z-score, which is a measure of how many standard deviations below or above the population mean a raw score is. This approach allows comparing the isotopic spaces of the five study sites without the influence of the isotopic baseline. Furthermore, the Fry-Davis' method gives rescaled individual distances to the community mean in ‰ units and not in standard deviation units.

Rescaled individual distances ($\Delta^{13}$C and $\Delta^{15}$N hereafter) were used to compare the structure of the food web using SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al., 2011), a Bayesian version of Layman's metrics (Layman et al., 2007). The N range (NR) provides information on the trophic length of the community, the C range (CR) is the width of the food web and gives us an idea of the diversity of C sources fueling the food web, the total area of the convex hull (TA) and the mean distance to the centroid (CD) provide measures of the average degree of trophic diversity within a food web, the mean distance to the nearest (MNND) provides a measure of the overall density of species packing and the standard deviation of the nearest distance (SDNND) gives a measure of evenness of spatial redundancy. All codes for SIBER analyses are contained in the package SIBER (Jackson et al., 2011).

## 3. Results

The $\delta^{13}$C and $\delta^{15}$N values of the primary producers varied across species and sampling sites, with a significant interaction term revealing that species differed in their patterns of geographic variation (Table 2). A post hoc Tukey test revealed the existence of three groups of localities differing in the average $\delta^{13}$C values of the primary producers; the lowest average values were observed in Fildes Bay and Cierva Cove, intermediate values were observed in Esperanza Bay and Rothera Point and the highest average value in Paradise Harbor. A post hoc Tukey test revealed a similar pattern for the $\delta^{15}$N values of the primary producers, with three groups of localities differing significantly: the lowest $\delta^{15}$N average
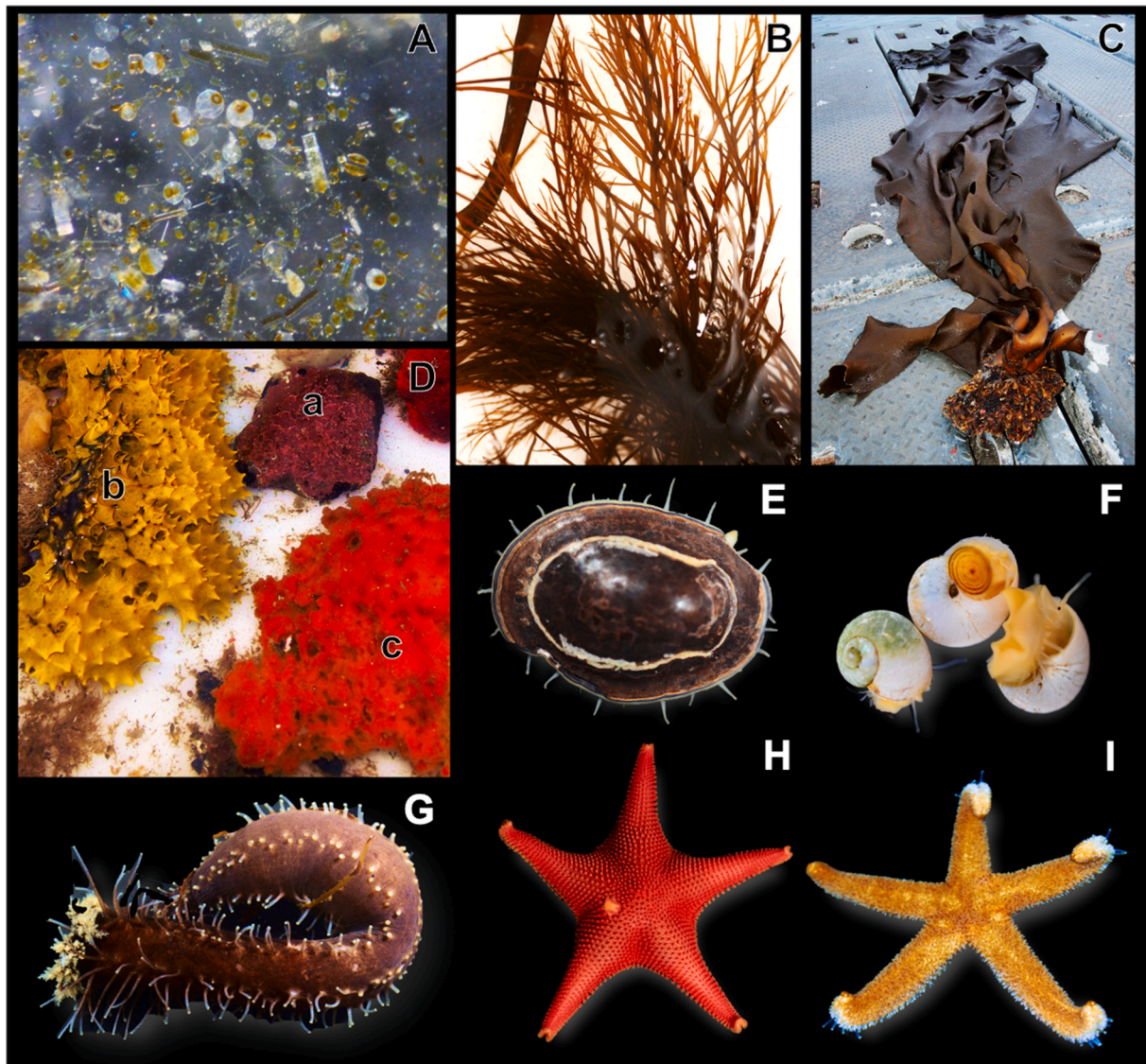
**Fig. 2.** Live pictures of the main taxa studied here. (A) Suspended particulate organic matter (SPOM) sample under the stereomicroscope. (B) The canopy-forming macroalga *Desmarestia anceps*. (C) The canopy-forming macroalga *Himantothallus grandifolius*. (D) Encrusting coralline algae on a rock (a), the sponge *Dendrilla antarctica* (b), the sponge *Kirkpatrickia variolosa* (c). (E) The limpet *Nacella concinna*. (F) Three specimens of the snail *Margarella antarctica*. (G) The sea cucumber *Heterocucumis steineni*. (H) The sea star *Odontaster validus*. (I) The sea star *Diplasterias brucei*. Photo credits: DISTANTCOM and BLUEBIO research teams (A, B, C, D) and Juan Junoy (E, F, G, H, I).

**Table 2**
Summary statistics of the general linear models (GLMs) run to assess differences in the stable isotope ratios of C and N of primary producers across sampling sites.

| | Df | $\delta^{13}C$ | | $\delta^{15}N$ | |
|---|---|---|---|---|---|
| | | F | P-value | F | P-value |
| Model | 24 | 60.3 | <0.001 | 27.7 | <0.001 |
| Species | 4 | 195.9 | <0.001 | 53.7 | <0.001 |
| Site | 4 | 52.2 | <0.001 | 43.1 | <0.001 |
| Species x site | 16 | 24.4 | <0.001 | 17.3 | <0.001 |
| Total | 124 | | | | |

values were observed in Fildes Bay and Cierva Cove, intermediate values at Esperanza Bay and Paradise Harbor and the highest values at Rothera Point. This pattern emerged primarily because the encrusting coralline algae and the canopy-forming macroalgae (*H. grandifolius* and *D. anceps* or *D. menziesii*) shared a similar pattern of increasing $\delta^{13}C$ and $\delta^{15}N$ values as latitude increased, thus revealing a latitudinal shift in the

isotope baseline. Nevertheless, *D. anceps* from Esperanza was more enriched in $^{13}C$ and $^{15}N$ than expected according to latitude. SPOM had a similar pattern for $\delta^{15}N$, but the highest $\delta^{13}C$ values were observed at Paradise Harbor and Cierva Cove and the lowest at Rothera Point. *Palmaria decipiens* separated from that latitudinal pattern and was highly enriched in $^{15}N$ at Esperanza Bay and Fildes Bay (Fig. 3).

Despite the above reported latitudinal shift in stable isotope ratios, the topology of the benthic primary producers within the isotopic space was basically constant, both when raw (Fig. 3) and rescaled data (Fig. 4) were used. At all sites, the encrusting coralline algae and *P. decipiens* were more enriched in $^{13}C$ than the canopy-forming species of *Desmarestia*, with *H. grandifolius* laying in between. Likewise, the encrusting coralline algae or *P. decipiens* were the most $^{15}N$ enriched benthic primary producers at all sites and *H. grandifolius* was the most $^{15}N$ depleted, with canopy-forming species of *Desmarestia* laying in between (Figs. 3 and 4). The most usual position of SPOM was in between that of encrusting coralline algae and *H. grandifolius*, except at Rothera Point, where SPOM was the most $^{13}C$ depleted primary producer.

Macroinvertebrates differed in their $\delta^{13}C$ and $\delta^{15}N$ values both

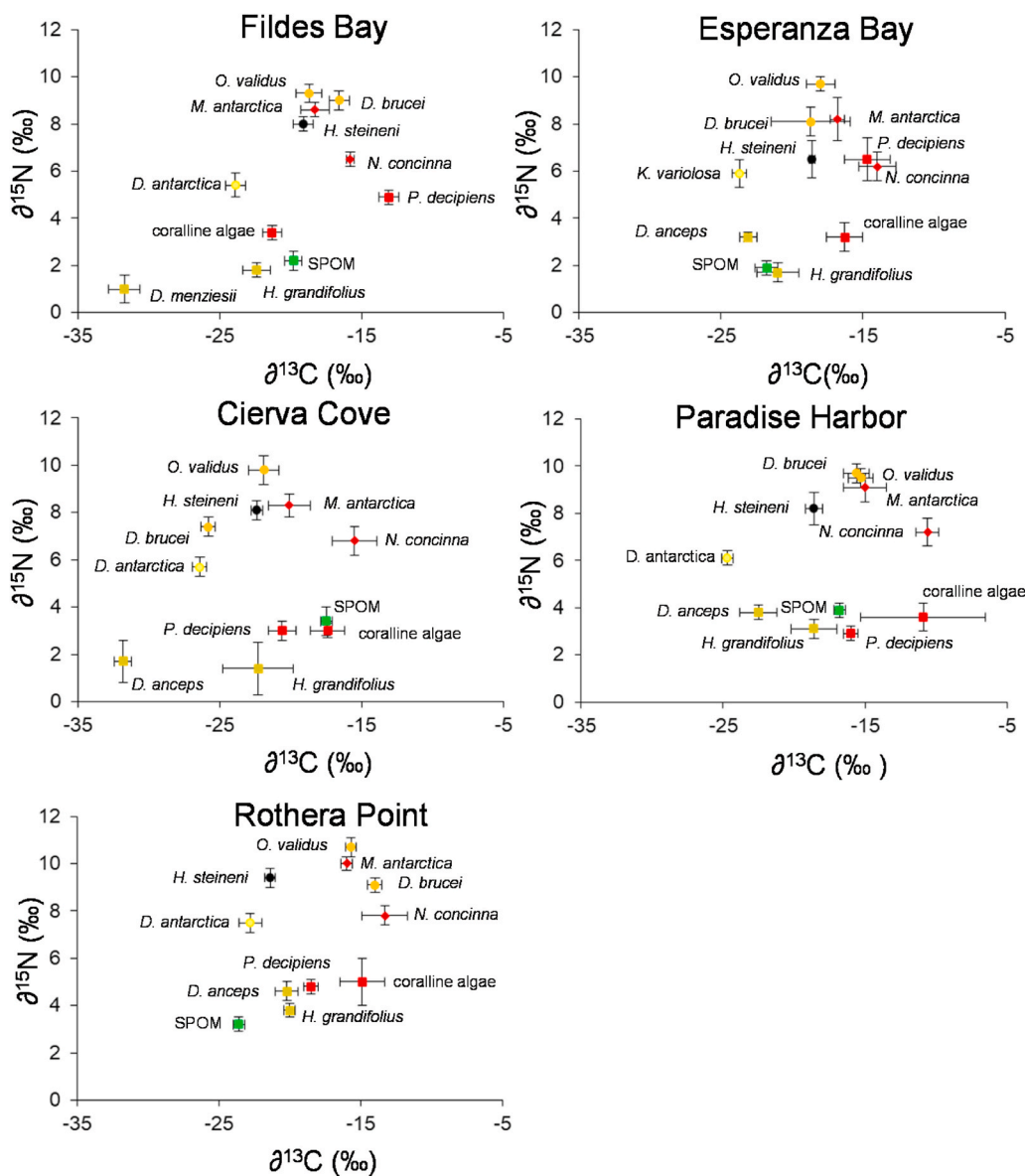**Fig. 3.** Topology in the $\delta^{13}$C-$\delta^{15}$N space of the shallow rocky bottom benthic community from five sites along a latitudinal gradient along the Antarctic Peninsula ordered from north (Fildes Bay) to south (Rothera Point). Each species is represented by the average of its raw stable isotope ratios and error bars show standard deviation. Sea stars: orange circles; sea cucumbers: black circles; snails and limpets: brown diamonds; sponges: yellow diamonds; red algae: red squares; brown macroalgae: olive squares; SPOM: green squares. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

between species and across localities (Table 3; Fig. 3). The species × site interaction terms were statistically significant, revealing species-specific patterns of geographic change (Table 3). The most remarkable anomalies were those of the sea cucumber *H. steineni* and the sponges for $\delta^{13}$C and the sea star *O. validus* for $\delta^{15}$N (Fig. 3). Nevertheless, a post hoc Tukey test revealed that the latitudinal changes in the $\delta^{13}$C and $\delta^{15}$N values of the primary producers were conserved across the food web. The analysis identified three groups of localities differing significantly in the average $\delta^{13}$C values of consumers, with the lowest values observed in Cierva Cove, intermediate values at Fildes Bay and Esperanza Bay, and the highest average values in Paradise Harbor and Rothera Point. A post hoc Tukey tests revealed a similar latitudinal increase in the $\delta^{15}$N values of consumers, also with three statistically different groups: the lowest average values in Cierva Cove, Fildes Bay and Esperanza Bay, intermediate values at Paradise Harbor, and the highest values at Rothera Point.

Macroinvertebrates had rather consistent trophic positions across sampling sites, although statistically significant differences existed for three species (Fig. 5). Sponges (*D. antarctica* or *K. variolosa*) had at all sites a trophic position close to 2 (herbivores), that of the limpet *N. concinna* was close to 2.5, and that of the sea cucumber *H. steineni* was close to 3, except at Esperanza Bay. The sea star *D. brucei* and the snail

*M. antarctica* also had a trophic position close to 3 at most sites, but the former foraged at a higher tropic position at Fildes Bay. Finally, the trophic position of the sea star *O. validus* was usually close to 3.5. It should be noted, that the credible interval of the trophic position of the animal species more dependent on the benthic baseline (the limpet *N. concinna* and the snail *M. antarctica*) were lower at Esperanza Bay because the high $\delta^{15}$N value of the red macroalgae *P. decipiens* at that site increased the uncertainty of trophic position estimation (see Fig. 3).

The position of consumers along the $\delta^{13}$C and $\Delta^{13}$C axes was also rather consistent (Figs. 3 and 4). At all sites, sponges were the most $^{13}$C depleted species and the limpet *N. concinna* the most enriched in $^{13}$C, with the sea cucumber *H. steineni*, the sea star *O. validus*, and the snail *M. antarctica* laying in between, ordered from the most $^{13}$C depleted to the most $^{13}$C enriched. The sea star *D. brucei* was the only species with a remarkable variability within the $\delta^{13}$C-$\delta^{15}$N space: very close to the sea star *O. validus* at Paradise Harbor, in between the sea star *O. validus* and the limpet *N. concinna* at Rothera and Fildes, and in between the sea star *O. validus* and the sponges at Cierva Cove.

Variability was detected across sampling sites for most of the Layman's metrics, except for the mean distance to the nearest neighbor, which ranged 2–2.5‰ at all sites (Fig. 6). The southernmost site
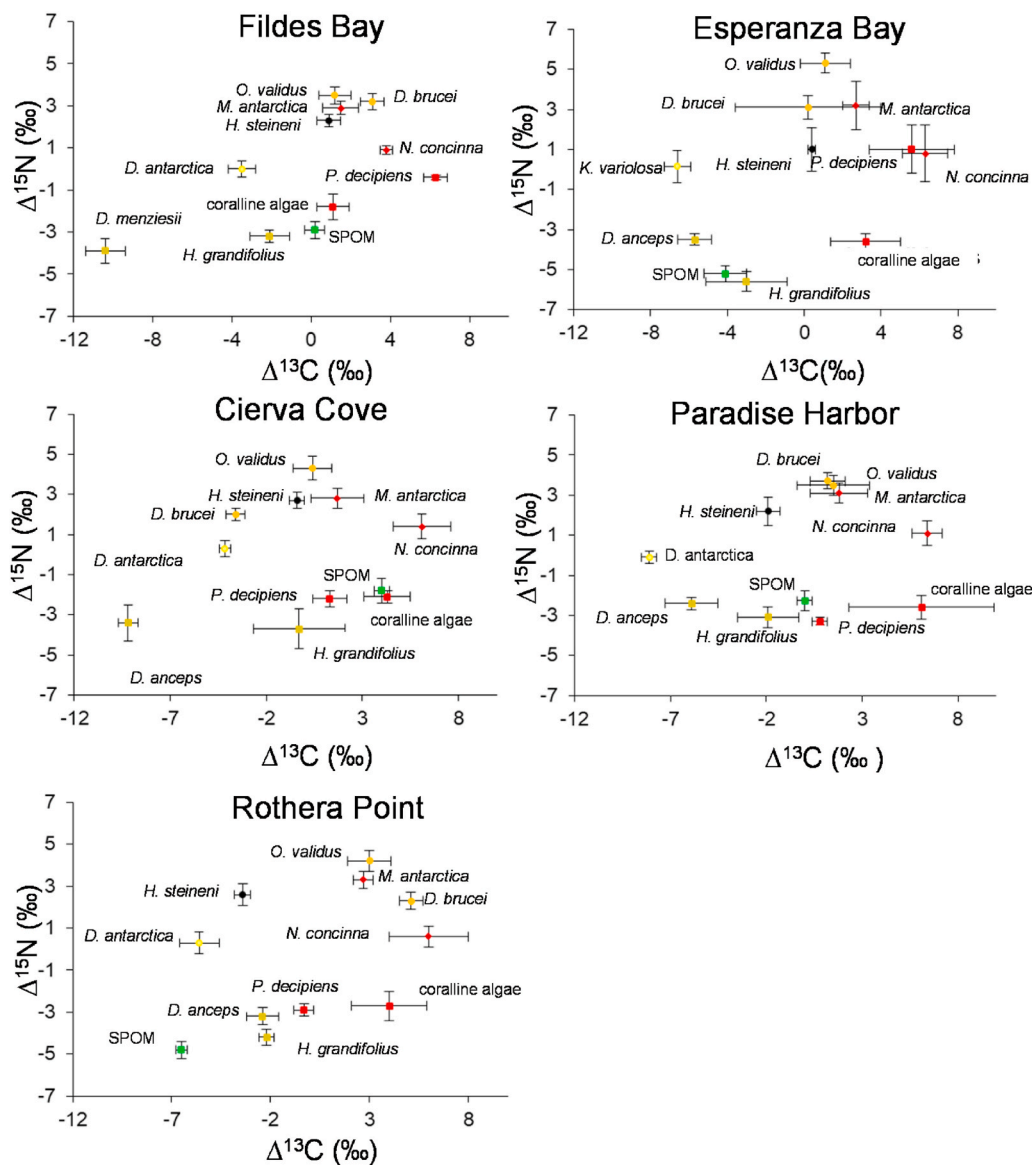
**Fig. 4.** Topology in the $\Delta^{13}$C-$\Delta^{15}$N space of the shallow rocky bottom benthic community from five sites along a latitudinal gradient along of the Antarctic Peninsula, from north to south. Each species is represented by the average of its rescaled stable isotope ratios and error bars show standard deviation. Sea stars: orange circles; sea cucumbers: black circles; snails and limpets: brown diamonds; sponges: yellow diamonds; red algae: red squares; brown macroalgae: olive squares; SPOM: green squares. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

**Table 3**

Summary statistics of general linear models (GLMs) run to assess differences in the stable isotope ratios of C and N of macroinvertebrates across sampling sites.

| | Df | $\delta^{13}$C | | $\delta^{15}$N | |
|---|---|---|---|---|---|
| | | F | P-value | F | P-value |
| Model | 29 | 75.5 | <0.001 | 39.1 | <0.001 |
| Species | 5 | 280.8 | <0.001 | 171.7 | <0.001 |
| Site | 4 | 124.1 | <0.001 | 46.2 | <0.001 |
| Species x site | 20 | 14.5 | <0.001 | 4.5 | <0.001 |
| Total | 149 | | | | |

(Rothera Point) and northernmost site (Fildes Bay) differed significantly in the length of both the N range and the C range, the total area of the convex hull, the distance to the centroid, and the standard deviation of the mean distance to the nearest neighbor, thus, revealing significant differences in the structure of their food webs. The values of the Layman's metrics at Cierva Cove and Paradise Harbor were in between those of Rothera Point and Fildes (Fig. 5), thus matching with the existence of a latitudinal gradient. However, the values of the Layman's metrics at Esperanza Bay differed significantly from those of the nearby Fildes Bay and Cierva Cove and were not different from those of Rothera

Point.

## 4. Discussion

Studies on the diet of benthic Antarctic invertebrates, particularly echinoderms, often describe them as omnivores with a high degree of trophic plasticity and diets including from detritus and algae to decaying carcasses of vertebrates (McClintok 1994; Norkko et al., 2007; Michel et al. 2016, 2019). However, the results reported here revealed a highly consistent trophic position and a rather constant topology along the $\delta^{13}$C axis for the six common and abundant species of macroinvertebrates studied in the South Shetland Islands and the Antarctic Peninsula. This concurs with other studies suggesting that Antarctic benthic rocky communities share homogeneous trophic features among distant geographical areas (Gillies et al., 2013), despite the differences resulting from dissimilarities in sea ice duration (Norkko et al., 2007). Nevertheless, it should be noted that our limited taxon sampling might have artificially restricted our capacity to detect variation since food web length is sensitive to both species richness (Sokolowski et al., 2012) and the presence of certain taxonomic groups (Vander Zanden and Fetzer, 2007). The absence of fish in our sampling is particularly relevant because fish species often have highly flexible diets and, hence, their
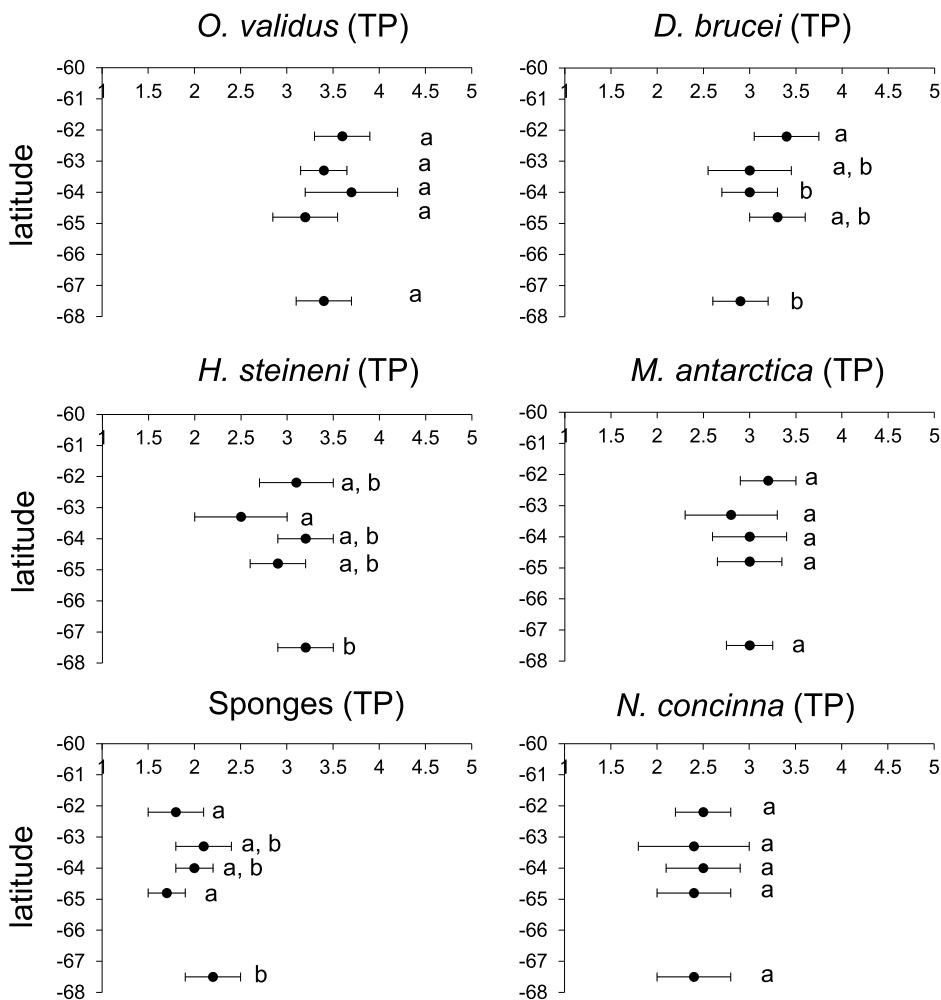
**Fig. 5.** Trophic position (TP; median and 95% credible interval) of macroinvertebrates along a latitudinal gradient along the Antarctic Peninsula and the South Shetland Islands, with each species depicted in separate panels. North to south sampling sites are arranged from top to bottom within each panel (i.e., Fildes Bay, Esperanza Bay, Cierva Cove, Paradise Harbor, and Rothera Point). The black circles correspond to the median values and error bars denote the 95% credible interval. Populations from the same species sharing letters (a, b) do not differ significantly in trophic position. Sponges: *Dendrilla antarctica* was collected everywhere, except at Esperanza, where it was replaced by *Kirkpatrickia variolosa*.

trophic levels may respond more vigorously to changes in the duration of the sea-ice and food availability than those of macroinvertebrates (McMullin et al., 2017; but see Michel et al., 2019).

The sponges studied here were often the most $^{13}$C depleted organisms analyzed. Recent research has demonstrated that some species of Antarctic sponges can recycle Si from diatoms (Riesgo et al., 2020), but the very low $\delta^{13}$C values compared to SPOM suggest that both *D. antarctica* and *K. variolosa* rely mostly on a different carbon source, likely bacterioplankton. Conversely, the herbivorous limpet *N. concinna* was at all sites highly enriched in $^{13}$C and hence, more likely to rely on coralline encrusting algae than on canopy-forming macroalgae such as *H. grandifolius* or *Desmarestia* spp. Similar results have been reported elsewhere indicating a diet based on microphytobenthos or intertidal macroalgae (Corbisier et al., 2004; Choy et al., 2011; Daglio et al., 2018; Zenteno et al., 2019; Valdivia et al., 2019), although some related species from Patagonia are best described as omnivores (Andrade and Brey 2014). The snail *M. antarctica* was a carnivore highly positioned in the food web at the five sites studied, although it has been reported previously to be a herbivore (Gutt and Schickan 1998; Amsler et al., 2019; Michel et al., 2019) and was here sometimes found crawling on macroalgae, likely suggesting this species grazes on animal epiphytes. Likewise, the sea star *O. validus* was a strict carnivore atop the five benthic food webs studied, in accordance with previous findings along the Antarctic Peninsula (Dunton, 2001). However, other studies have suggested a more variable trophic position, ranging from herbivory to carnivory (McClintock 1994; Norkko et al., 2007; Gillies et al., 2012; Michel et al., 2019). This variability is not associated with the study method (gut contents analysis vs. stable isotope analysis) but probably

related to a shorter and more variable ice-free season in Eastern Antarctica compared to the South Shetland Islands and the Antarctic Peninsula.

Only the sea star *D. brucei* and the sea cucumber *H. steineni* exhibited major changes in their trophic positions across the five sites studied; the sea star *D. brucei* also exhibited major changes in $\delta^{13}$C values. As a result, most of the variability in the topology of the consumer community in the isotopic space of the five sites studied across the South Shetland Islands and the Antarctic Peninsula was associated with these two species. Previous research has revealed the sea star *D. brucei* as being a carnivore or coprophage, while *H. steineni* is an active suspension feeder or planktivore (McClintock 1994 and references therein; Michel et al., 2019). The variability reported here fits those descriptions, although *H. steineni* usually has a trophic position more consistent with selective zooplankton feeding than with passive suspension feeding at the South Shetland Islands and the Antarctic Peninsula, except at Esperanza Bay. Nevertheless, high reliance on detritus has already been reported in other sites along the Antarctic Peninsula (Mincks et al., 2008).

It should be noted that the $\delta^{13}$C and $\delta^{15}$N baselines changed with latitude, fitting previously reported isoscapes for plankton off the South Shetland Islands and the western Antarctic Peninsula (Brault et al., 2018). Furthermore, a longer sea ice season southward is expected to increase the $\delta^{13}$C values of the detritus bank and hence that of consumers, independently of any change in the baseline, simply because sympagic microalgae are often enriched in $^{13}$C (Michel et al., 2016; Cozzi and Cantoni, 2011). However, the results reported here do not support a smooth latitudinal gradient along the Antarctic Peninsula, but a more complex pattern with high levels of local variability. This is
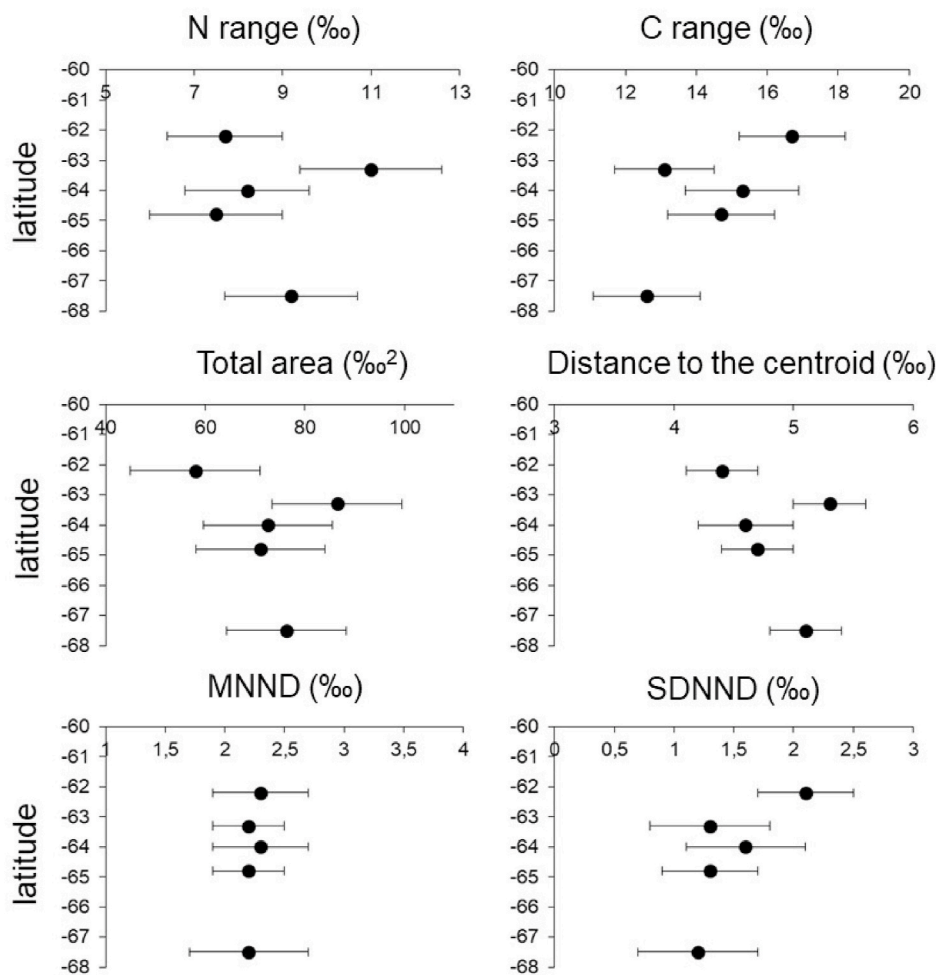
**Fig. 6.** Layman's metrics of the shallow rocky bottom benthic community from five sites along a latitudinal gradient of the Antarctic Peninsula and the South Shetland Islands, with each metric in a separate panel. North to south sampling sites arranged from top to bottom within each panel as follows: Fildes Bay, Esperanza Bay, Cierva Cove, Paradise Harbor, Rothera Point. The black circle corresponds to the median values and error bars denote the 95% credible interval. *MNND*: mean nearest neighbor distance; *SDNND*: standard deviation of the distance to the nearest neighbor.

because the two most distant sampling sites (Fildes Bay and Rothera Point) certainly differed in the $\delta^{13}C$ and $\delta^{15}N$ values of both primary producers and consumers and a third site (Paradise Harbor) consistently laid in between or clustered with Rothera Point. However, the $\delta^{13}C$ and $\delta^{15}N$ of the primary producers and consumers from Esperanza Bay and Cierva Cove exhibited more idiosyncratic patterns.

Raw stable isotope ratios were rescaled to cope with regional variability in stable isotope ratios when computing Layman's metrics (Fry and Davis 2015). The results offer only partial support to the hypothesis that the duration of the sea ice season is a major determinant of food web structure in benthic, coastal ecosystems of Antarctica. Observations matched predictions when the two most distant sampling sites were considered, because the C range and SDNN were significantly shorter at Rothera Point (sea ice season: 8 months) than at Fildes Bay (sea ice season: 2 months), thus revealing a lower variability of C sources and higher trophic redundancy in the southernmost sampling site. Rothera Point and Fildes Bay also differed in the total area of the convex hull and the distance to the centroid. The characteristics of the food web at Cierva Cove (sea ice season: 4 months) and Paradise Harbor (sea ice season: 6 months), midway from Fildes Bay to Rothera Point, also matched predictions, as the values of the C range, the standard deviation of the distance to the nearest neighbor, the total area of the convex hull and the distance to the centroid were intermediate between those of Fildes Bay and Rothera Point. However, Esperanza Bay (sea ice season: 4 months) departed largely from expectations, because its food web resembled that of distant Rothera Point and differed from than to nearby Fildes Bay and Cierva Cove, because of a very narrow C range, a larger total area of the convex hull, a longer distance to the centroid and a smaller standard

deviation of the distance to the nearest neighbor.

The differences in latitude and the highly dissimilar duration of the sea ice seasons in Esperanza Bay and Rothera Point (4 and 8 months respectively) strongly suggests that sea ice duration is not the only driver of the structure of the benthic food web. Interestingly, both areas experience a much higher phytoplanktonic productivity in spring and summer than any other area off the South Shetland Islands or the Antarctic Peninsula (Marrari et al., 2008). Previous studies have revealed a diversity of food sources for Antarctic benthic invertebrates, including sympagic algae, microphytobenthos, macroalgae, and phytoplankton (Dunton et al., 2001; Corbisier et a. 2004; Norkko et al., 2007; Michel et al., 2019; Zenteno et al., 2019). These sources differ in their $\delta^{13}C$ values, which often results in a diversity of isotopic niches among benthic invertebrates during the ice-free season (Corbisier et al., 2004; Dunton, 2001; Norkko et al., 2007; Michel et al., 2019; Zenteno et al., 2019; Rossi et al., 2019). However, such diversity decreases when a single source prevails, as in areas where there is no seasonal break of the sea ice or during the sea ice season, when sympagic microalgae are the only relevant source of organic C for the benthic food web (Norkko et al., 2007; McMullin et al., 2017; Michel et al., 2019; Rossi et al., 2019).

A diversity of primary produces thrived both at Rothera Point and Esperanza Bay in February 2016, with dense phytoplankton blooms in the water column and dense forests of large brown macroalgae on the shallow rocky bottoms, as elsewhere around Antarctica (Wiencke and Amsler 2012; Wiencke et al., 2014). It should be noted, however, that large brown Antarctic macroalgae are chemically defended from herbivores through phlorotannins (Fairhead et al., 2005; Amsler et al. 2008, 2014; Aumack et al., 2010; Núñez-Pons et al., 2012) and thus, they enter

the food web mainly as detritus after microbial processing (Dunton et al., 2001; (Corbisier et al., 2004); Zenteno et al., 2019). This is not true for marine snow, immediately available for benthic invertebrates. As a result, highly productive phytoplankton blooms during the ice-free season may result in a massive supply of planktonic organic matter to the detritus bank in the seabed, thus reducing the diversity of isotopic niches and leading to a short C range and high trophic redundancy observed in Esperanza Bay and Rothera Point.

In conclusion, the overall evidence suggests that sea ice duration can be a determinant of food web structure in Antarctic, shallow benthic ecosystems, but the intensity of the spring-summer phytoplankton bloom likely plays a relevant role and can be a major determinant of the food web structure where the sea ice season is short. Further studies should also address the role of community dynamics and local environmental conditions in the food webs.

## CRediT authorship contribution statement

**Luis Cardona:** Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Funding acquisition, Writing - original draft. **Elena Lloret-Lloret:** Investigation, Formal analysis, Writing - review & editing. **Juan Moles:** Conceptualization, Investigation, Writing - review & editing. **Conxita Avila:** Conceptualization, Methodology, Investigation, Funding acquisition, Writing - review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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