Belgian Journal of Zoology
www.belgianjournalzoology.be

ISSN 2295-0451

Research article

https://doi.org/10.26496/bjz.2025.201

Food web structure in a rapidly changing coastal environment: the West Antarctic Peninsula

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Abstract. The West Antarctic Peninsula (WAP) is one of the most rapidly changing regions in the world. Steep environmental gradients in sea ice cover and glacier melting are observed, but much remains to be documented regarding the impact of these differences on biological communities and ecosystem processes. Here, we study how environmental variability impacts trophic interactions and ecological habitats of benthic communities along the WAP. During the Belgica 121 expedition, dominant benthic mega- and macrofauna, as well as primary producers, were sampled in multiple stations featuring different environmental conditions around the Gerlache Strait. Stable isotope ratios of carbon, nitrogen, and sulfur were measured and combined in an isotope niche analysis (SIBER). Our results suggest that changes in environmental features, notably ice-related conditions, could alter food source availability and organic matter fluxes towards benthic organisms. Isotopic compositions of abundant species were more variable in stations with stronger ice-related disturbance. Besides variability in isotopic baseline, this result could possibly also be linked to the use of a wider diversity of food sources (niche expansion) in stations affected by different ice-related conditions. Overall, our findings provide important insights towards understanding the interplay between environmental conditions and ecological habits of benthic consumers along the WAP.

Keywords. Stable isotopes, trophic ecology, benthic communities, West Antarctic Peninsula.

Voisin A., Lepoint G., Danis B., Guillaumot C., Kristiansen A., Pasotti F., Saucède T. & Michel L.N. (2025). Food web structure in a rapidly changing coastal environment: the West Antarctic Peninsula. *Belgian Journal of Zoology* 155: 93–119. https://doi.org/10.26496/bjz.2025.201

Introduction

Polar ecosystems are mainly constrained by seasonal light cycles which affect sea ice dynamics, wind forcing, and ocean circulation (Lumpkin & Speer 2007; Ducklow *et al*. 2012; Marshall & Speer 2012). Globally, Antarctic sea ice cover slowly increased from the late 1970s to 2010 (Parkinson & Cavalieri 2012; Holland 2014), but has decreased rapidly from 2014 to 2017 (Parkinson 2019). Regardless of global trends, local decreases in sea ice cover around the West Antarctic Peninsula (WAP) have been reported for decades (Parkinson & Cavalieri 2012; Holland 2014; Hendry *et al*. 2018). Consequently, this region is highly relevant in a climate change context, due to the steep environmental gradients that can be encountered (Hendry *et al*. 2018; Henley *et al*. 2019; Queirós *et al*. 2024; Griffiths *et al*. 2024).

In Antarctic communities, ice represents a major environmental driver (Smale & Barnes 2008; Convey *et al.* 2014; Griffiths *et al.* 2024). Glacier calving or iceberg scouring will result in direct physical damage to communities (Barnes 1999). Sea ice formation obstructs the water column, decreasing light availability for primary producers (Barnes 1999; Ingels *et al.* 2021; Amsler *et al.* 2023). Following sea ice breakup, significant algal blooms can be observed during southern summers (Moline *et al.* 2004; Ducklow *et al.* 2012). Sympagic (i.e., linked to sea ice) algae constitute an important part of primary production in polar environments (Lizotte 2001; Niemi *et al.* 2024). When sea ice melts, those algae fall, bringing a significant export of organic matter to the benthic ecosystem and maintaining sea ice-benthic coupling (Gillies *et al.* 2012; Henley *et al.* 2019; Rossi *et al.* 2019).

Organisms in Antarctica follow the seasonal cycle of sea ice. The benthic community is mainly composed of opportunistic or scavenging organisms, such as sea stars or sea urchins (Norkko *et al.* 2007; Henley *et al.* 2019; Griffiths *et al.* 2024). Suspension or deposit-feeding organisms may also be strongly represented because of high seasonal primary production export from the surface (Thomas *et al.* 2008; Henley *et al.* 2019; Griffiths *et al.* 2024). Other grazing or suspension-feeding gastropods or bivalves can be found in smaller abundance. Studies on benthic organisms' feeding have shown the importance of pelagic and sea ice primary producers in their diet (Gillies *et al.* 2012; Wing *et al.* 2012; Calizza *et al.* 2018; Henley *et al.* 2019; Rossi *et al.* 2019). However, benthic primary production also constitutes a significant part of consumers' diets (Dunton 2001). Benthic algae, mainly represented by large brown algae such as *Himantothallus grandifolius* and underlying red algae such as *Iridaea cordata*, form large amounts of organic matter (Ducklow *et al.* 2013; Amsler *et al.* 2023; Whippo *et al.* 2024). Even after their death, those macroalgae litter accumulations provide shelter and habitat for benthic fauna (Norkko *et al.* 2004; Whippo *et al.* 2024). Besides this macroalgae primary production, the development of an epilithic biofilm composed of microalgae (microphytobenthos), offers another primary source of energy (Corbisier *et al.* 2004; Calizza *et al.* 2018; Ha *et al.* 2019). Several studies observed trophic plasticity of benthic consumers in different Antarctic regions, in response to the environmental influence on the diversity and availability of basal food sources (Norkko *et al.* 2007; Michel *et al.* 2016; Rossi *et al.* 2019; Griffiths *et al.* 2024). For instance, a significant decrease in the trophic position of omnivorous organisms was observed in Adelie Land in the absence of a sea ice break-up, suggesting a shift towards a more herbivorous diet (Michel *et al.* 2019).

Food webs are typically described along two principal dimensions (Elton 1927): the diversity of producers supporting the food web and the different trophic levels of the consumers. Stable isotope analysis (SIA) is widely used to delineate the trophic structure of a community (Fry 2006; Norkko *et al.* 2007; Rossi *et al.* 2019). The isotopic composition of an organism is a proportional mix of the isotopic composition of its food sources, combined with a trophic enrichment factor (Fry 2006; Boecklen *et al.* 2011). The carbon isotope ratio (^{13}C:^{12}C) is commonly used to distinguish the basal food sources of the food web (Corbisier *et al.* 2004; Norkko *et al.* 2007; Gillies *et al.* 2012). Carbon sources might present distinct isotopic ratios, and ^{13}C:^{12}C can provide insights into the relative importance of these sources in the diet of consumers (Corbisier *et al.* 2004; Seyboth *et al.* 2018). The nitrogen isotope ratio (^{15}N:^{14}N)

can be used to define the trophic position of consumers, based on a food web baseline. A large and predictable stepwise variation is expected in $^{15}N:^{14}N$ values between each trophic level (Norkko *et al.* 2007; Casey & Post 2011; Gillies *et al.* 2012; Seyboth *et al.* 2018). Sulfur isotope ratio ($^{34}S:^{32}S$) may improve the understanding of source assimilation by consumers and can complement the analysis of carbon isotope ratios (Connolly *et al.* 2004; Connolly & Schlacher 2013). Pelagic production mostly relies on sulfates, leading to a ^{34}S-enriched ratio in food sources such as suspended particulate organic matter (SPOM) (Fry *et al.* 1988). Conversely, the use of sulfides by sediment-associated producers results in higher incorporation of the light isotope in food sources, and more ^{34}S-depleted tissues (Rees *et al.* 1978; Connolly *et al.* 2004). A wide range of $\delta^{34}S$ values has been found in estuarine and marine food web studies ($\delta^{34}S$ = -14.0 to +20.4‰ – reviewed by Connolly *et al.* 2004). Since there is natural variability in the isotopic compositions of organisms across environments, defining a trophic baseline is essential to compare food webs from different locations (Fry 2006). This baseline allows for meaningful interpretation of consumers isotopic differences being related to their diet instead of environmental variability (Post 2002; Fry 2006; Layman *et al.* 2012).

This work aims to describe and understand dietary habits of benthic organisms among a variety of environmental conditions. We studied the food web from the primary producers up to various trophic guilds found in consumers, in an attempt to answer the following question: are trophic diversity and the use of species food sources influenced by environmental variability? To address this question, we measured $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ ratios of representative species assemblages to build isotopic niches. We also studied isotopic variability of three benthic species (i.e., *Nacella concinna*, *Odontaster validus*, *Parborlasia corrugatus*) which are common in the Gerlache Strait. The main hypothesis of the current study is that environmental variability, at a spatial scale around 100 km, across the Gerlache Strait may influence benthic communities differently. High ice-related disturbance, such as iceberg scouring, may reduce trophic diversity through the loss of organisms or basal food sources. Benthic species might resort to trophic plasticity and shift towards other food sources. For instance, grazers may switch their feeding from macroalgae to biofilm growing on the surface of rocks, due to a loss of macroalgae that are stripped off by ice.

Material and methods

Sampling design

During the southern summer from February to March 2019, 7 stations, displaying different environmental features (Table 1 – more details in Danis *et al.* 2019), were sampled in shallow areas along the Gerlache Strait (Figure 1, Table 1), West Antarctic Peninsula (Danis *et al.* 2021; Danis *et al.* 2022). Sampling was conducted by scuba diving at depths ranging from 8 to 20 meters. Benthic organisms were stored in zip lock bags per taxa and grouped in larger bags per station. Primary producers as well as several other taxa and trophic guilds ranging from primary to higher consumers, were collected (Table 2). Organisms were identified on board, to the lowest taxonomic level possible with various documentation including, but not limited to, Rauschert & Arntz (2015) as well as De Broyer *et al.* (2014) and Danis *et al.* (2019). To assess primary pelagic producers' variability, 2 to 4 water samples were taken at each station. Samples were collected with a Niskin bottle and 3 L each were filtered through a 47 mm diameter Whatman GF/F glass microfiber filter. Each sample was frozen at -26°C and shipped to the Freshwater and Oceanic Science Unit of research at the University of Liege, Belgium.

Sample preparation

Different animal tissues have different biological turnover rates, which can influence the interpretation of isotopic data (Vander Zanden *et al.* 2015). Therefore, to characterize food web structure and study trophodynamics, it is necessary to select material with an adequate turnover rate (i.e., weeks to months),

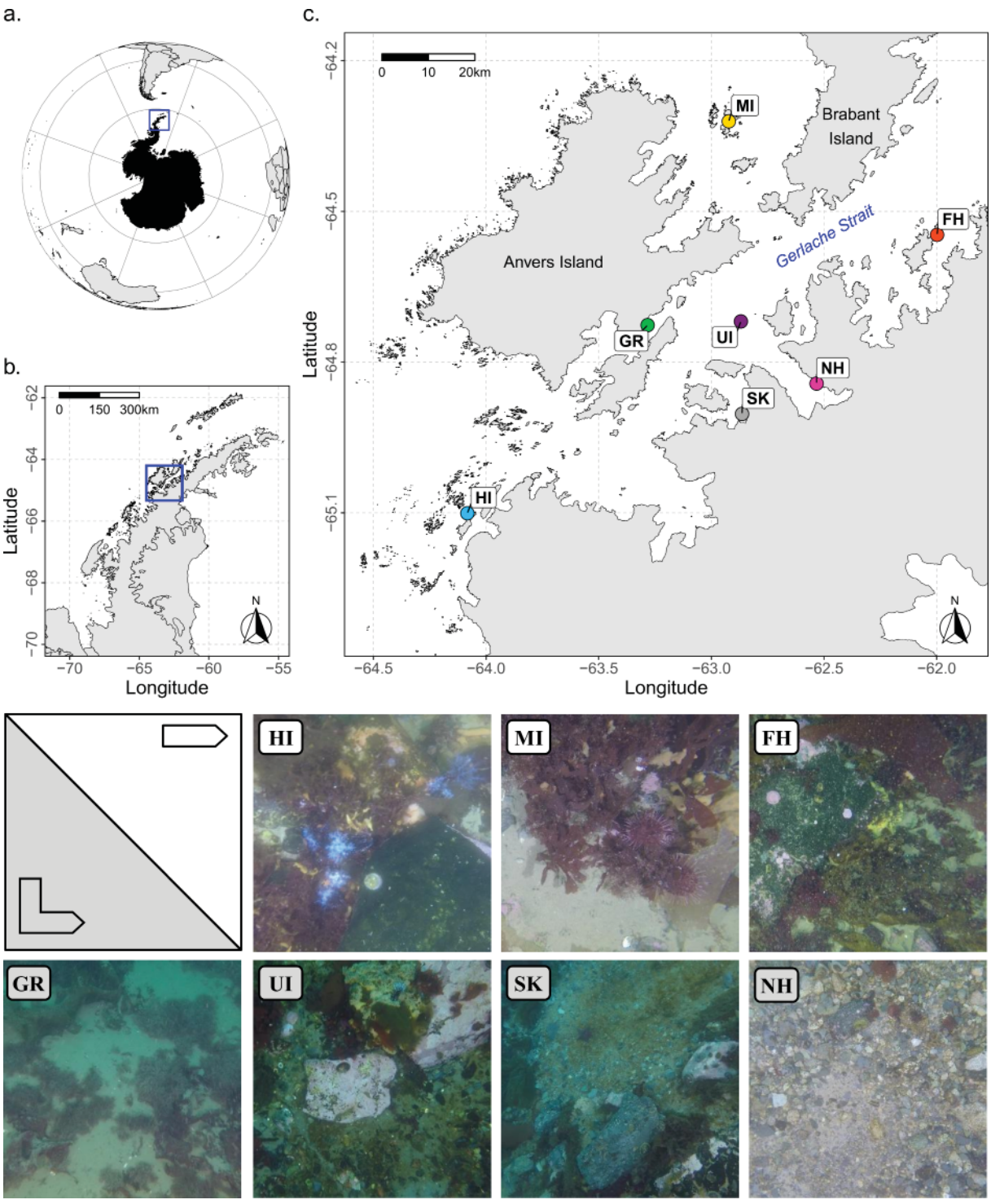

Figure 1 – General map of the sampling area: **a**. Southern Ocean. **b**. Western Antarctic Peninsula. **c**. Gerlache Strait (Stations details are provided in Table 1). Each pictured was taken underwater during scuba diving (more details in Danis *et al*. 2019). Gray highlights correspond to stations under ice-related disturbances (e.g., glacier calving, iceberg scouring), while white highlights indicate undisturbed stations.

TABLE 1

Location and description of the stations sampled during the Belgica 121 expedition. Gray highlights correspond to stations under different ice-related disturbances (e.g., glacier calving, iceberg scouring), while white highlights indicate undisturbed stations. Station characteristics describe local observations within the few points sampled. Due to high degrees of heterogeneity in Antarctic habitats, these do not represent an exhaustive description of the surrounding habitats.

Stations	Latitude (S)	Longitude (W)	Characteristics
Føyn Harbour (FH)	64°32.798	61°59.885	Protected cove with gradient in rock versus mud substrates.
Green Reef (GR)	64°43.590	63°16.974	Open to Neumayer Channel, muddy bottom with gravel
Hovgaard Islands (HI)	65°06.057	64°04.992	Highly protected and almost enclosed inner bay, soft sediments
Melchior Islands (MI)	64°19.246	62°55.375	Protected inner bay. Muddy bottom with gravels and dropstones
Neko Harbour (NH)	64°50.565	62°32.009	Continental fjord rocky and gravely bottom with fine sand patches
Skontorp Cove (SK)	64°54.190	62°51.845	Highly protected inner cove with muddy bottoms
Useful Island (UI)	64°43.146	62°52.159	Open sea, rocky shallows to muddy substrate with gravels at depth

providing relevant information on the integration of dietary intakes through an organism's life (Fry 2006; Mateo *et al.* 2008). Consequently, structural tissues and muscles were selected in contrast to soft, metabolically active tissues with faster and/or hard-to-predict turnover rates such as guts or gonads (Fry 2006). Due to differences in size and structure, dissection procedures and selected tissues differed among organisms (Table 2). For the water filters, deposited suspended particulate organic matter (SPOM) was scraped off with a scalpel blade. The whole filter, or a fraction of it, was analyzed depending on the overall amount of available matter. After dissection or scraping, samples were stored in 4 mL or 20 mL vials depending on the size of the selected tissue, and oven-dried at 50°C. Samples were then grounded to a homogeneous powder using mortar and pestle or, when required, a MM301 mixer mill (Retsch GmBH, Haan, Germany – cycles of 120 seconds at 25 Hz).

Organisms were carefully dissected to exclude skeletal parts with high inorganic matter concentrations (Jaschinski *et al.* 2008). Those tissues containing significant concentrations of carbonates were acidified to remove the inorganic carbon fraction (Table 2) before isotopic analysis (Mateo *et al.* 2008). Some acidification methods can alter nitrogen (N) and sulfur (S) isotopic ratios by causing the deterioration of organic N and S (Bunn *et al.* 1995; Jaschinski *et al.* 2008; Mateo *et al.* 2008; Connolly & Schlacher 2013). To avoid this issue, a vapor phase acidification method was used to prevent isotopic alteration and the loss of organic compounds (Jaschinski *et al.* 2008). Samples were put in a closed glass container with an opened vial of fuming HCl 37% to release acid vapors. Several "Champagne tests" were performed to check the acidification method's efficiency in removing all carbonates from samples (Hedges & Stern 1984; Jaschinski *et al.* 2008). Afterwards, the samples were dried again completely depending on the degree of acid moistening.

TABLE 2

List of organisms sampled and tissues selected for analyses. Trophic groups (TG) with associated references: DF = deposit feeder; F = basal food source; G/H = grazer/herbivore; O = omnivore; P = predator; S = scavenger; SF = suspension feeder. There is a tick in the "HCl" column when organisms were acidified before analysis.

Group	Taxa	HCl	Analyzed tissue	Trophic groups and references	
Suspended particulate organic matter (SPOM)			Filter fragments	F	
Ochrophyta	Macroalgae (not identified)		Blade fragments	F	
Rhodophyta	*Iridaea cordata*		Blade fragments	F	
	Trematocarpus antarcticus		Blade fragments	F	
	(not identified)		Blade fragments	F	
Porifera	*Dendrilla antarctica*		Body fragments	SF	McClintock *et al.* (2005)
	Homaxinella balfourensis		Body fragments	SF	McClintock *et al.* (2005); Thurber (2007)
	Mycale acerata		Body fragments	SF	McClintock *et al.* (2005)
	(not identified)		Body fragments		
Cnidaria	*Glyphoperidium bursa*		Ectoderm, lower body region	P	Danis *et al.* (2019)
Nemertea	*Parborlasia corrugatus*		Body wall, anterior region	P/S	Gibson (1983); Clarke (2008)
Annelida	Serpulidae (not identified)	√	Whole animal		
Arthropoda					
Amphipoda	*Eusirus* sp.	√	Whole animal	P	Nyssen *et al.* (2005)
	(not identified)	√	Whole animal	G/H DF	Iken *et al.* (1998); Huang *et al.* (2007); Amsler *et al.* (2009)
Isopoda	*Glyptonotus antarcticus*	√	Pereopods	P/S	Presler (1986); Corbisier *et al.* (2004)
	(not identified)	√	Whole animal		
Mollusca					
Bivalvia	*Aequiyoldia eightsii*		Adductor muscle	SF	Danis *et al.* (2019)
	Laternula elliptica		Adductor muscle	SF	Ahn (1993); Norkko *et al.* (2007)
Gastropoda	*Margarella refulgens*	√	Whole without shell	G/H	Michel *et al.* (2019)
	Nacella concinna		Foot muscle	G/H	Corbisier *et al.* (2004); Clarke (2008)
	Austrodoris sp.		Foot muscle	O	Wägele (1989)
	Trophon sp.	√	Whole without shell	P	Harper & Peck (2003); Curelovich *et al*. (2016)
	(not identified)	√	Whole animal		
Polyplacophora	(not identified)	√	Whole animal		

Group	Taxa	HCl	Analyzed tissue	Trophic groups and references	
Bryozoa	(not identified)	√	Whole animal	SF	Wood (2015)
Echinodermata					
Asteroidea	*Odontaster validus*	√	Tegument	O/S	McClintock (1994); Clarke (2008)
	Odontaster meridionalis	√	Tegument	P	Dayton *et al*. (1974)
	Odontaster roseus	√	Tegument	O	Dayton *et al*. (1974)
	Perknaster sp.	√	Tegument	O/S	McClintock (1994)
	Cuenotaster involutus	√	Tegument	P/S	McClintock (1994)
	Diplasterias brucei	√	Tegument	P/S	McClintock (1994)
	Granaster nutrix	√	Tegument	O	McClintock (1994)
	Psilaster charcoti	√	Tegument	P	Gillies *et al.* (2012)
	Neosmilaster georgianus	√	Tegument	P/S	McClintock (1994)
	Acodontaster sp.	√	Tegument	P	Dayton *et al*. (1974)
	Labidiaster sp.	√	Tegument	P/S	McClintock (1994)
	Lysasterias sp.	√	Tegument	P/S	McClintock (1994)
	Henricia sp.	√	Tegument	O	Jangoux (1982)
	(not identified)	√	Tegument		
Ophiuroidea	*Ophionotus victoriae*	√	Whole without gut	O	McClintock (1994)
Echinoidea	*Sterechinus neumayeri*		Aristotle's lantern muscle	O/DF	McClintock (1994); Norkko *et al*. (2007)
Holoturoidea	*Heterocucumis steineni*	√	Body wall	SF	Clarke (2008); Danis *et al.* (2019)
Chordata	Ascidiacea (not identified)		Body fragments	SF	Tatian *et al.* (2004)

Isotopic analysis

Stable isotope analysis of C, N, and S was conducted at the University of Liege. An isotope ratio mass spectrometer (IsoPrime100 isotope ratio mass spectrometer – Isoprime, Cheadle, United Kingdom) for continuous-flow, elemental analysis (vario MICRO cube C-N-S elemental analyzer – Elementar Analysensysteme GMBH, Hanau, Germany) was used to measure isotope ratios (precision: 0.3‰ for $\delta^{13}C$, 0.3‰ for $\delta^{15}N$, and 0.7‰ for $\delta^{34}S$), expressed in isotope ratios according to the delta notation (δ) in per mille (‰).

$$\delta X = \left(\frac{R_{sample} - R_{standard}}{R_{standard}} \right) \times 1000$$

The δ of X represents deviations of the analysed element isotope ratios from international standards as defined below. X is the heavy isotope of the sample (^{13}C, ^{15}N, or ^{34}S) and R refers to the ratio of the heavy isotope over the light isotope ($^{13}C/^{12}C$, $^{15}N/^{14}N$, or $^{34}S/^{32}S$). International reference standards used

were Vienna Pee Dee Belemnite for carbon, Atmospheric Air for nitrogen, and Vienna Canyon Diablo Troilite for sulfur. The analysis sequence was made of primary analytical standards, certified by the International Atomic Energy Agency (IAEA): sucrose (IAEA-C6; $\delta^{13}C$ = -10.80 ± 0.47‰), ammonium sulfate (IAEA-N1; $\delta^{15}N$ = 0.40 ± 0.20‰), and silver sulfide (IAEA-S1; $\delta^{34}S$ = -0.30‰ and IAEA-S2; $\delta^{34}S$ = 22.70 ± 0.20‰). As secondary analytical standard, sulphanilic acid was used (Sigma-Aldrich; $\delta^{13}C$ = -25.62 ± 0.36‰; $\delta^{15}N$ = -0.13 ± 0.55‰; $\delta^{34}S$ = 5.87 ± 0.50‰). Replicates allowed to correct the deviation of the spectrometer during analyses on multi-batch measurements. For animal batches, replicates of the sea star *Psilaster charcoti* tegument were used, whereas replicates of brown algae *Himantothallus grandifolius* blade fragments were used for plant batches.

Sample powder was put in 4 × 4 × 5 mm tin cups (Elementar Analysensysteme GmbH) and weighed on a 0.001 mg precision scale. Animal and plant samples were split into different batches. An amount of 2 to 2.5 mg for animal samples, and around 4mg for plant samples were analyzed, except for red algae where analysed sample size was limited to around 2 mg because of their high sulfur concentrations (Foltran *et al.* 1996). For small samples, a specific batch was made with tin cups containing between 0.5 and 1 mg of powder. SPOM scraped from filters was put into 8 × 8 × 15 mm cups. Tungsten oxide was added to all samples to enhance combustion and improve the performance of sulfur isotope analysis.

$\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values were presented as mean ± standard deviation (SD) according to species or taxonomic groups (Appendix 1). Isotopic ratios were plotted to compare organisms' isotopic compositions among sampled stations in the Gerlache strait.

Data analysis

Each species or taxa was assigned to a trophic group depicting their overall feeding behavior and diet. A total of 7 groups were defined: basal food source (F), predator (P), scavenger (S), omnivore (O), deposit feeder (DF), grazer/herbivore (G/H), and suspension feeder (SF). Omnivores were considered as organisms feeding on both plant and animal matter and scavengers as necrophagous organisms feeding on dead animal matter. These trophic categories were made according to the available literature and do not allow a precise categorization of organisms' feeding habits. For instance, the line between omnivorous and scavenging, or between suspension and deposit feeding behaviors can be very subtle, depending on the circumstances in which a species thrives (Getz 2011; Williams & Martinez 2004; De Santana *et al.* 2013). However, these categories allow a description of ecological processes through species groups with similar trophic functions (Table 2).

The following analyses were performed in the R statistical computing environment (R Core Team 2022), using the SIBER package (Jackson & Parnell 2023). Layman metrics were quantified using mean isotopic ratio values of all individual measurements for each species in each station (Layman *et al.* 2007), both in a $\delta^{13}C$-$\delta^{15}N$ and a $\delta^{13}C$-$\delta^{34}S$ space. Six metrics, illustrated in Appendix 2, were quantified to interpret the trophic structure among stations (Table 3). $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ ranges describe the distance between the most enriched and depleted species for each element. The total area (TA) of the convex hull including all species at each sampling station represents the space covered by the isotopic niche, a proxy for the overall trophic diversity of the sampled species assemblage. The mean distance to the centroid (CD) also provides an average measure of the degree of trophic diversity and is less sensitive to outliers than TA. It also highlights distinct ecological habits of organisms, illustrated by a greater distance. The CD is an average Euclidean distance of each species to the $\delta^{13}C$-$\delta^{15}N$ or $\delta^{13}C$-$\delta^{34}S$ centroid, described as the mean of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values for all species in the food web. Finally, two other metrics provide details on species' relative positions to each other in the niche area. The mean nearest neighbor distance (MNND) measures the species aggregation level, also named ecological redundancy. The standard deviation of the nearest neighbor distance (SDNND) estimates the evenness of species aggregation in space.

We focused on changes in trophic habits for three common species from the Gerlache Strait (Figure 2): *Nacella concinna* is a gastropod from the Nacellidae family described as a herbivore grazing various basal food sources that might be available in the benthic compartment (Corbisier *et al.* 2004; Clarke 2008). The sea star *Odontaster validus* is an Asteroidea that has been reported as an omnivore with predominantly predatory behavior (McClintock 1994; Clarke 2008; Le Bourg *et al.* 2021). *Parborlasia corrugatus* is a Nemertean exhibiting a wide range of diets, mainly characterized by predatory and scavenging behaviors but sometimes also described as omnivorous, feeding on more basal sources (Gibson 1983; Smale *et al.* 2007; Clarke 2008; Michel *et al.* 2019). To make direct comparisons possible while taking potential isotopic baseline effects into account (Fry 2006), the mean isotopic values of *Iridaea cordata* were used (Appendix 1). This macroalgae was chosen by the guidelines suggested by Post (2002) for estimating a suitable trophic baseline. This macroalgae was collected at the same time as the consumers and covered almost all the spatial variability of the study, only being absent from Hovgaard Islands. The method developed by Turner *et al*. (2010) was used to determine the need for correction. This test calculates the Euclidean distance between centroids of two distributions, based on bivariate means: δ^{13}C-δ^{15}N or δ^{13}C-δ^{34}S. Centroid positions are then considered different if this distance is significantly greater than zero (Turner *et al.* 2010). Results from the data on *I. cordata* (Appendix 3) showed significant differences among certain stations and confirmed natural isotopic variability. Then, to correct the isotopic ratios of benthic consumers, mean isotopic ratios of *I. cordata* were subtracted from the isotopic ratios of the studied species at each station: $\Delta X = \delta X_{consumer} - \delta X_{primary\ producer}$, where X is ^{13}C, ^{15}N, or ^{34}S (full results in Appendix 3). Once the corrected isotopic values were obtained, these distance computations and significance tests were also carried out for the three benthic species (Table 5). Corrected SIBER standard ellipse areas (SEAc) were used to provide a more robust analysis of consumers' isotopic niche for small samples, as suggested by Jackson *et al*. (2011). SEAc, illustrated in Appendix 2, is a proxy for the size of the "core" consumer isotopic niche (i.e., most typical individuals in the population). Like TA, it is a measure of the trophic diversity but is less sensitive to outliers and small sample sizes than the Layman metrics (Jackson *et al.* 2011). Bayesian Standard Ellipse Areas (SEAb) were also estimated to provide unbiased estimates of isotopic niche width with 95% credibility intervals (Table 4). SEAb were computed based on 2.10^4 iterations, and the burn-in was set at 10%. Finally, using the Turner *et al*. (2010) method described above, the distance between species' centroids was calculated at each station to assess any significant differences.

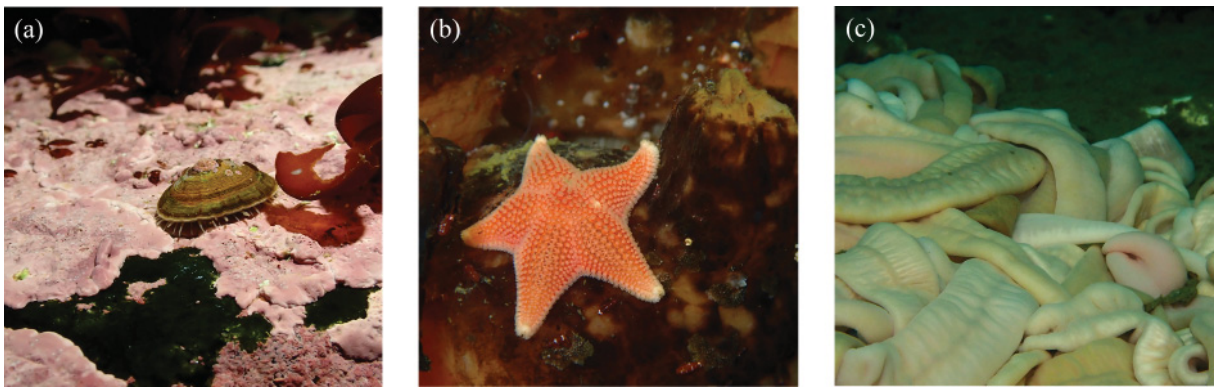

Figure 2 – Benthic species studied in SIBER analyses: (**a**) *Nacella concinna* (Strebel, 1908), (**b**) *Odontaster validus* (Koehler, 1906), (**c**) *Parborlasia corrugatus* (McIntosh, 1876). © Camille Moreau

TABLE 3

Layman metrics in (a) $\delta^{13}C$-$\delta^{15}N$ and (b) $\delta^{13}C$-$\delta^{34}S$ space for each sampled station of the Belgica 121 expedition. Abbreviations: TA = total convex hull area; CD = mean distance to the centroid; MNND = mean nearest neighbor distance; SDNND = standard deviation of the nearest neighbor distance. Gray highlights correspond to stations under ice-related disturbances (e.g., glacier calving, iceberg scouring), while white highlights indicate undisturbed stations.

Stations	Range			TA		CD		MNND		SDNND	
	$\delta^{15}N$	$\delta^{13}C$	$\delta^{34}S$	a	b	a	b	a	b	a	b
FH	7.8	15.4	11.5	62.5	91.9	4.6	4.9	1.5	1.9	0.7	1.6
GR	6.1	9.4	6.3	27.4	23.7	2.6	3	2	1.8	1.4	0.5
HI	10.4	16.2	7.2	79.8	68	4	3.8	2.3	2	2	1.5
MI	9.2	13.9	6.8	41.1	36.2	3.8	3.5	1.7	1.6	2.2	1.9
NH	7	6.7	9.9	18.8	35.1	2.4	2.9	1.4	2.1	1.2	1.4
SK	10.5	12.5	4.6	76.8	40	3.8	3.2	1.6	1.1	1	0.9
UI	7.4	14.5	6.5	59.6	60.7	3.7	4	1.7	1.5	1.1	1.2

TABLE 4

Standard ellipse area corrected for small sample size (SEAc) and estimated through Bayesian models (SEAb) in (a) $\Delta^{13}C$-$\Delta^{15}N$ and (b) $\Delta^{13}C$-$\Delta^{34}S$ space for each sampled station of the Belgica121 expedition. No data are provided if too few samples (less than 6) were collected to fit an ellipse and compute associated parameters. Gray highlights correspond to stations under ice-related disturbances (e.g., glacier calving, iceberg scouring), while white highlights indicate undisturbed stations.

SIBER	Stations	*Nacella concinna*		*Odontaster validus*		*Parborlasia corrugatus*	
		a	b	a	b	a	b
SEAc	FH	1.8	6.3	1.3	3.5	2.2	5.3
	GR	0.9	4.2	2.2	2.1	1.5	2
	MI	–	–	–	–	3	8.9
	NH	24.1	15.6	17	10.4	–	–
	SK	1.9	2.6	4.3	2.6	–	–
	UI	6.2	4.3	10.7	8	2.4	7.9
SEAb	FH	1.8±0.6	6.4±2.2	1.3±0.5	3.4±1.2	3.6±1.3	6.2±2.3
	GR	0.9±0.3	4.2±1.6	2.2±0.6	2.1±0.6	1.8±0.7	2.1±0.8
	MI	–	–	–	–	3.8±1.9	8.7±4.0
	NH	24.2±8.8	15.4±5.3	17.0±3.8	10.4±2.1	–	–
	SK	1.9±0.5	2.6±0.7	4.2±1.8	2.6±1.1	–	–
	UI	6.5±2.5	4.4±1.6	10.7±3.0	8.0±2.3	2.4±0.9	8.0±3.0

TABLE 5

Mean distance between centroids of three benthic species for each station, in both bidimensional isotopic space. Significant p-values from the Turner tests are indicated by: * < 0.05, ** < 0.01, and *** < 0.001. No data means the absence of data for at least one species. Gray highlights correspond to stations under ice-related disturbances (e.g., glacier calving, iceberg scouring), while white highlights indicate undisturbed stations.

Stations	**$\Delta^{13}C$-$\Delta^{15}N$**		
	Nacella concinna – Odontaster validus	*Nacella concinna – Parborlasia corrugatus*	*Odontaster validus – Parborlasia corrugatus*
FH	8.71 ***	7.88 ***	4.72 ***
GR	4.85 ***	4.50 ***	3.47 ***
NH	3.79 ***	–	–
SK	7.25 ***	–	–
UI	8.00 ***	7.79 ***	4.08 ***
	$\Delta^{13}C$-$\Delta^{34}S$		
FH	7.50 ***	8.96 ***	1.4 *
GR	1.39 ***	5.20 ***	6.18 ***
NH	2.41 ***	–	–
SK	1.40 ***	–	–
UI	6.01 ***	7.64 ***	3.74 ***

Results

Species assemblage

Layman metrics showed different patterns among stations (Table 3). Regarding the $\delta^{15}N$ range, higher values were found in HI, SK, and MI while lower values were observed in FH, NH, and UI. The lowest value occurred in GR, a station with ice-related disturbances (Table 3). The highest $\delta^{13}C$ range value was found in HI, followed by FH with both values being above 15‰ (Table 3). Slightly lower values were obtained in MI, SK, and UI, while two ice-related, disturbed stations (i.e., GR and NH) had the lowest values, below 10‰. Ranges of $\delta^{34}S$ showed higher inter-station differences: FH had the highest value, closely followed by NH, with values up to two times higher than SK. MI, GR, and UI displayed similar values ranging between 6 and 7‰ (Table 3). The lowest value was observed in SK, a station with ice-related disturbances (Table 3). For TA, stations with the highest $\delta^{34}S$ values also had high $\delta^{15}N$ values. However, in the $\delta^{13}C$-$\delta^{34}S$ space, FH had a higher TA (Table 3). Indeed, in FH, the value increased considerably in the $\delta^{13}C$-$\delta^{34}S$ space, while the value of SK almost dropped by half compared to the $\delta^{13}C$-$\delta^{15}N$ space (Figure 3).

Similar to FH, an increase in TA values between the two isotopic spaces was observed in NH and UI. The same pattern as at SK was also observed at HI and MI, two undisturbed stations (Table 3) while GR showed a lower decrease (Table 3). In both isotopic spaces, the lowest values of CD were found in GR and NH, whereas the highest values were reported in FH (Table 3). Low values and limited variation were observed for MNND values (Table 3). Overall, SDNND values were low (Table 3).

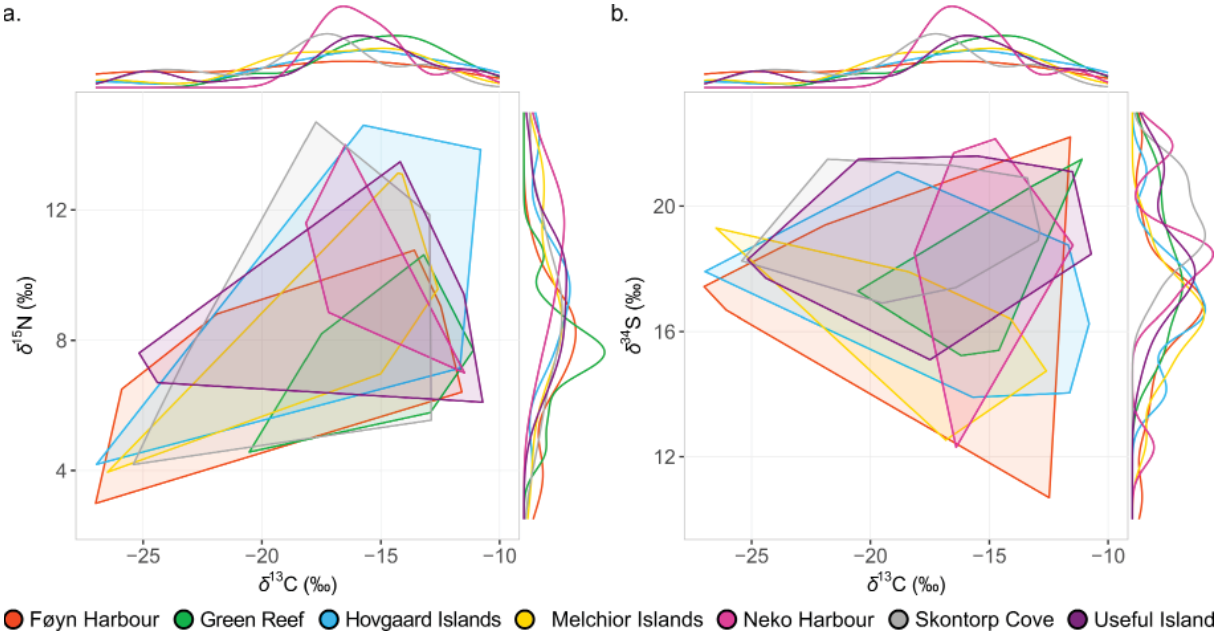

Figure 3 – Species assemblage-wide isotopic niches in a (**a**) δ^{13}C-δ^{15}N and (**b**) δ^{13}C-δ^{34}S space of stations sampled during the Belgica 121 expedition. Lines and shapes refer to convex hulls used to estimate Layman metrics. Density plots on the side, show the distribution of δ^{13}C, δ^{15}N, and δ^{34}S values for each assemblage of benthic consumers (mean values for each taxon).

Species

Nacella concinna showed lower Δ^{15}N values for each station than the other two consumers (Figure 4a). The Δ^{13}C of *N. concinna* was less negative than for the other two species, with high variability in NH. The ellipses for *N. concinna* were spread over the Δ^{34}S axis (Figure 4b), reducing the overlap among the stations for this species, as observed in the Δ^{13}C-Δ^{15}N space (Figure 4a). High variability in isotopic ratios was also illustrated by the computation of the SEA (Table 4). Indeed, SEAc and SEAb showed similar results, and the highest values and standard deviations were obtained for both at NH, SK, and UI stations, which are classified as stations with ice-related disturbances.

The Δ^{15}N values of *P. corrugatus* varied depending on the station, ranging from being just above the mean values of *N. concinna* to Δ^{15}N values of *O. validus* (Figure 4a). Δ^{13}C values of *P. corrugatus* were lower than *N. concinna*. The lowest values were found in FH and MI, while higher values were observed in GR and UI, two stations with ice-related disturbances (Figure 4a). Δ^{34}S values showed the opposite trend, with higher values in FH and MI, but lower values in GR and UI (Figure 4b).

Odontaster validus had the highest mean Δ^{15}N values. Higher values and more variability were found at stations with ice-related disturbances (i.e., NH and UI – Figure 4a, Appendix 4) as obvious by calculating SEAs (Table 4). *Odontaster validus* had a wide range of Δ^{13}C values (Figure 4a) depending on the station. A high variability of Δ^{34}S was also noted in NH and UI (Figure 4b, Table 4) while Δ^{34}S in individuals from FH and UI was lower than in NH, SK, and GR.

In the Δ^{13}C-Δ^{15}N space, the mean distance between the centroids of the three species was significantly different, regardless of the station (Table 5). This means that no overlap was found between the three species. However, in the Δ^{13}C-Δ^{34}S isotopic space, *N. concinna* and *O. validus* overlapped in GR (Figure 4b). Moreover, the centroid distance between these two species was the lowest computed and

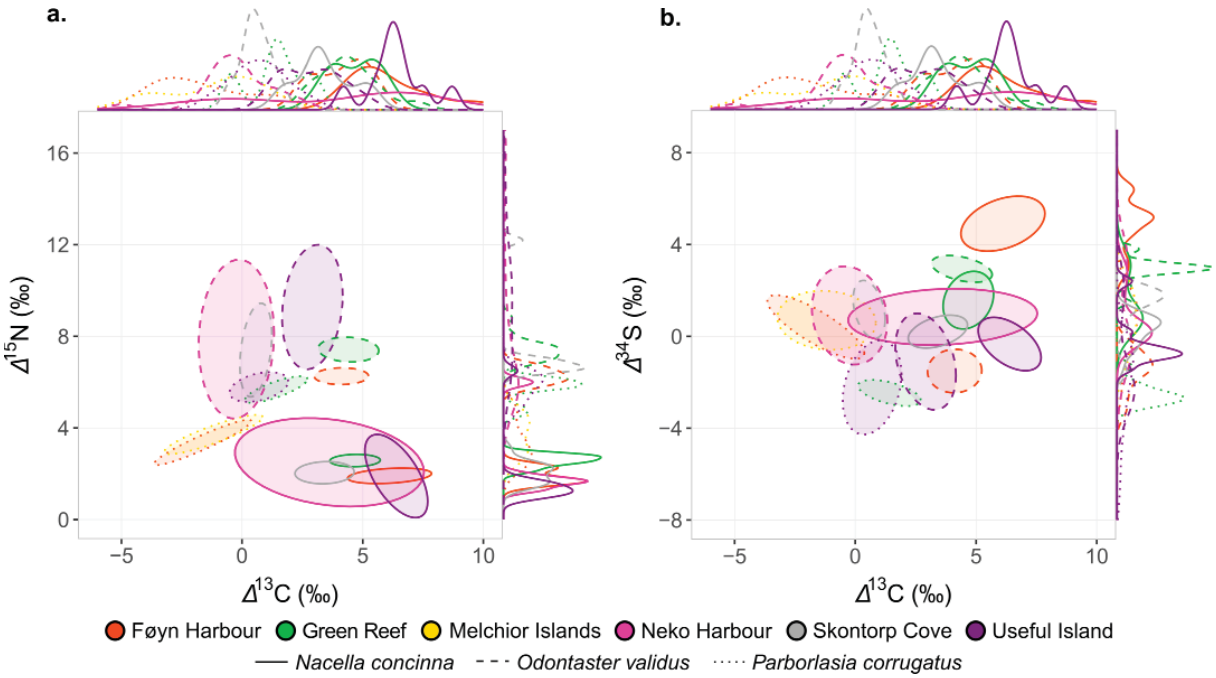

Figure 4 – Isotopic values in (**a**) Δ^{13}C-Δ^{15}N and (**b**) Δ^{13}C-Δ^{34}S space of three benthic species for each station. Ellipses represent standard ellipse areas, following the method of Jackson *et al*. (2011). Density plots on the side show distribution of individual Δ^{13}C, Δ^{15}N, and Δ^{34}S values for each station.

did not significantly differ from zero, a pattern that was also observed when comparing *O. validus* and *P. corrugatus* in UI (Table 5).

Discussion

Species assemblage

Analysis of basal food sources and consumers provides insights into the variability of trophic structures together with a better understanding of the environmental influence across locations (Fry 2006). At a species assemblage scale, Layman metrics revealed noticeable differences between stations being affected by different ice-related conditions and undisturbed stations. Overall, higher trophic diversity, measured by the convex hull's total area (TA), was found at two undisturbed stations: Føyn Harbour and Hovgaard Islands. These higher values of trophic diversity might be related to higher diversity in basal food source use as well as reliance on a wider range of trophic levels. Among grazers, *N. concinna* showed high δ^{34}S compared to other species, thereby increasing the TA of Føyn Harbour. Moreover, an unusually high δ^{15}N of *Margarella refulgens* might reflect different trophic levels in Hovgaard Island. These two stations were protected areas in coves or inner bays thereby reducing the impact of environmental variations and offering more sheltered habitats (Bartley *et al.* 2019; Jin *et al.* 2022). Less disturbances caused by iceberg scouring or glacier melting could then enable the growth of diverse basal food sources, such as macroalgae. Consequently, consumers might have more diverse diets and more divergent isotopic compositions (Layman *et al.* 2007). An assemblage of consumers that feed on completely different food sources might show a greater distance between each other and thus increase plot dispersion, convex hull's total area, distance from the centroid, and trophic diversity, like in Føyn Harbour (Layman *et al.* 2007).

However, Skontorp Cove, a station affected by ice-related disturbances, also had a high trophic diversity value in the δ^{13}C-δ^{15}N space, while in the δ^{13}C-δ^{34}S space, this station was more similar to other stations being affected by ice-related disturbances. Skontorp Cove also had the highest value of the δ^{15}N range, suggesting that its high trophic diversity is more due to the diversity of trophic levels increasing the convex hull. Even if the δ^{13}C range was high, the low δ^{34}S range value suggested less diversity in the basal food sources as compared to Føyn Harbour or Hovgaard Island. The benthic community in this area might be supported by diverse consumers with wide dietary spectra (Norkko *et al.* 2007; Michel *et al.* 2016; Rossi *et al.* 2019; Griffiths *et al.* 2024). In Skontorp Cove, samples were mainly represented by different species of sea stars, such as *Odontaster meridionalis*, known as a predator and having high standard deviations in δ^{13}C and δ^{15}N (Appendix 1).

Conversely, the lowest trophic diversity was found in two stations being affected by different ice-related conditions: Neko Harbour and Green Reef. This can be observed in both the vertical and horizontal structure of the food web (Layman *et al.* 2007). With ice-related disturbances, the loss of organisms or basal food source diversity can influence food web structure. Glacier calving, iceberg scouring, or anchored ice in winter could have reduced the availability of some basal food sources (e.g., macroalgae), which can be observed here by the low carbon range values (Barnes 1999; Brown *et al.* 2004; Barnes & Conlan 2007; Cordone *et al.* 2020; Ko *et al.* 2023). A decrease in δ^{15}N values, as observed here, could also reflect a loss of food source diversity, if the consumer turned to other, more basal food sources (Michel *et al.* 2019). For instance, a difference of 5.6‰ between the mean δ^{13}C values of *Laternula elliptica* in Føyn Harbour (δ^{13}C = -26.1 ± 1.0‰) and Green Reef (δ^{13}C = -20.5 ± 3.0‰) might suggest such a shift in food source use.

Species

Consumers' isotopic ratios are proportional mixtures of their food sources' isotopic compositions (Fry 2006). A benthic consumer feeding on a ^{13}C-depleted food source can therefore end up with less negative isotope values if it also feeds on other ^{13}C-enriched sources food sources (Fry 2006). The observed changes in δ^{13}C, δ^{15}N, and δ^{34}S values could therefore be the result of two processes: dietary shifts or changes in isotopic composition of baseline items. By explicitly removing the latter through mathematical correction, our results indicate potential differences in feeding behavior.

Nacella concinna is described in the literature as a grazer feeding on microphytobenthos and microbial films (Corbisier *et al.* 2004; Clarke 2008). The lowest Δ^{15}N values of this species were consistent with this diet, compared to *O. validus*, an omnivorous sea star (McClintock 1994; Clarke 2008), and *P. corrugatus*, a nemertean predator/scavenger (Gibson 1983; Clarke 2008). Not all basal food sources could be sampled or analyzed in this study (i.e., sediments, microphytobenthos, and sea ice algae), but the high carbon isotopic variability of *N. concinna* suggested that different individuals may rely on basal food sources with distinct δ^{13}C. Overall, macroalgae are known to have ^{13}C-depleted carbon values: -23.18 ± 0.46‰ (Paeophyceae, *Desmarestia menziesii*, East Antarctica – Gillies *et al.* 2012) or -34.6 ± 1.6‰ (Rhodophyta, *Phyllophora antarctica*, East Antarctica – Michel *et al.* 2019). Conversely, other basal food sources found at the benthic level had ^{13}C-enriched values. Studies in King George Island showed that microphytobenthos had δ^{13}C of -16.7 ± 2.1‰ (Corbisier *et al.* 2004) or -13.15 ± 0.35‰ (Pasotti *et al.* 2015). In other ecosystems around Antarctica, sea ice algae showed δ^{13}C values ranging from -16.0 ± 0.1‰ to -12.4 ± 1.9‰ in the Ross Sea (Calizza *et al.* 2018) to -12.5 ± 1.7‰ in Adelie Land (Michel *et al.* 2019). As shown above, the diversity of basal food sources can be related to the environment and different ice-related conditions in the current study. The sampling station Neko Harbour is located in a fjord with intense glacial activity. Glacier calving and run-off may change the overall geochemistry of an environment, increasing turbidity and sedimentation at a local scale (Smale & Barnes 2008; Ko *et al.* 2023). Moreover, induced iceberg scouring from glacier calving might directly

remove patches of benthic communities, thus considerably altering the availability of basal food sources (Barnes 1999; Ingels *et al.* 2021; Griffith *et al.* 2024). A decrease in macroalgal abundance might explain the reliance of grazers like *N. concinna* on other basal food sources like diatoms (e.g., microphytobenthos or sea ice algae), as observed by McMahon *et al*. (2006) in the Svalbard archipelago (Arctic). Δ^{34}S values observed in this study might also support this interpretation. In sediments, the recycling of organic matter by bacteria results in the use of sulfides and the incorporation of light isotopes. Consequently, organisms using food sources with links to sediments will have ^{34}S-depleted tissues (Rees *et al.* 1978; Fry *et al.* 1988; Connolly *et al.* 2004; Raoult *et al.* 2024), as observed in the other stations of the current study being affected by ice-related disturbances.

Several metrics point towards considerable trophic plasticity in the two other consumer species. Wide ranges of Δ^{13}C, Δ^{15}N, and Δ^{34}S were observed for *O. validus* and *P. corrugatus*, the latter even showing different Δ^{15}N values depending on the sampling station. This consumer showed a gradual enrichment in ^{15}N among individuals. This feature might be more associated with a trophic continuum (France *et al.* 1998), as already documented for the Antarctic Peninsula (Kaehler *et al.* 2000; Corbisier *et al.* 2004; Jacob *et al.* 2006) and is often observed when consumers display high trophic plasticity. In the literature, *P. corrugatus* is documented as a scavenger that feeds on dead organisms or may shift to more basal food sources, eventually being classified as an omnivore (Gibson 1983; Smale *et al.* 2007; Clarke 2008; Michel *et al.* 2019) feeding on higher consumers or dead organisms which both can lead to ^{15}N-enriched tissues (Fry 2006). In Useful Island and Green Reef, two stations affected by different ice-related conditions, *P. corrugatus* showed higher Δ^{15}N values and lower Δ^{34}S values compared to the other stations. This species might have a higher trophic position, feeding on benthic and dead organic matter in these two stations, while in Føyn Harbour and Melchior Islands higher presence of macroalgae could lead to more omnivorous behavior and lower Δ^{15}N values. *Odontaster validus* showed high variability in isotopic composition and SEA. The Δ^{13}C values suggested that its diet was based on different basal food sources. This is also reflected in the Δ^{34}S with lower values being observed in Føyn Harbour as compared to Green Reef, even if Δ^{13}C values of this species were similar at both stations. Under ice-related disturbance, *O. validus* had a larger ellipses area in the Δ^{13}C-Δ^{15}N space. Individual specimens showed scattered isotope ratios, (e.g., *O. validus* from Neko Harbour) potentially indicating ecological differences between each individual and resulting in large ellipse areas (Le Bourg *et al.* 2021). *Odontaster validus* is an omnivore able to feed on a great diversity of prey (McClintock 1994; Le Bourg *et al.* 2021). Its diet can range from primary producers and associated detritus to higher consumers such as suspension feeders, omnivores, or even predators (Zenteno-Devaud *et al.* 2022), and it has also been reported to feed on carrion (Clarke 2008). Therefore, this species can be considered as a generalist consumer (Bearhop *et al*. 2004; Norkko *et al.* 2007; Gillies *et al.* 2012; Michel *et al.* 2019). Previous studies, together with the results presented in the current study, suggest that trophic plasticity allows *O. validus* to adapt its diet to food item availability.

Conclusion

The results obtained in this study provided information on the potential effects of environmental variations on the trophic ecology of Antarctic benthic communities. Undisturbed stations such as Føyn Harbour and Hovgaard Island had higher trophic diversity. In contrast, high glacial activities and ice-related disturbances might result in low trophic diversity, as observed in Neko Harbour. This could be linked with lower specific diversity, resulting in decreased availability of certain food items. Skontorp Cove, despite being a station affected by ice-related disturbances, displayed high trophic diversity, driven rather by wide ranges of trophic levels than diversity in basal food sources. This finding emphasizes the complex interplay between environmental disturbances and dietary adaptations within benthic communities. A more detailed analysis of three consumer species belonging to different trophic

guilds showed how their trophic plasticity modulates their response to different conditions. Under ice-related disturbance, consumers appeared to turn to benthic recycled organic matter. The diverse diet of *O. validus* seemed to allow this species to remain flexible in its reliance on food sources, regardless of the environmental conditions. Further research is needed to understand how environmental conditions shape the trophic ecology of Antarctic communities. Studying these ecosystems over multiple time points (e.g., seasonal and longer-term periods) could improve our understanding of the dynamics that influence the ecology of these communities.

Acknowledgments

This research project was made possible by the execution of the Belgica 121 expedition (B121). Within the framework of the RECTO project (contract nr. BR/154/A1/RECTO) financed by the Belgian Science Policy, the expedition aimed to carry out a biodiversity census along the West Antarctic Peninsula using a nimble sampling platform, the R/V *Australis*, a steel-hulled, fully-rigged motor sailing vessel. G. Lepoint is a Senior Researcher at the National Fund for Scientific Research (FNRS).

Data availability

All data are available at https://doi.org/10.48361/ptbggs

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Manuscript received: 15 October 2024
Manuscript accepted: 17 September 2025
Published on: 1 October 2025
Branch editor: Steven Degraer

Appendix 1

$\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ mean ± standard deviation in per mille (‰) for each sample among stations. N = number of organisms or samples analyzed. *N corresponds to the number of organisms pooled to analyze small organisms.

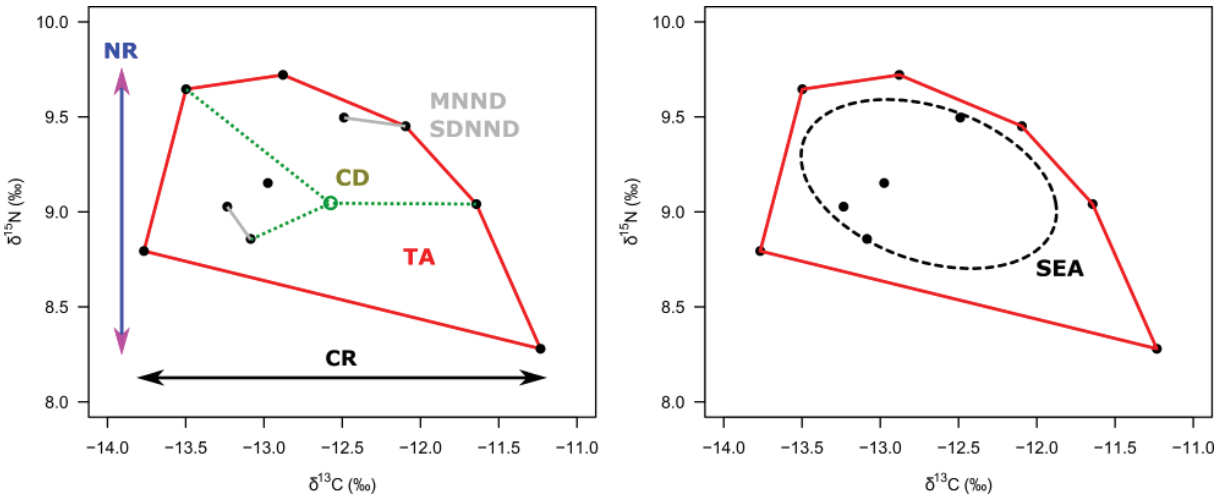
Samples		Stations	N	$\delta^{13}C$		$\delta^{15}N$		$\delta^{34}S$	
Suspended particulate organic matter (SPOM)		FH	2	-26.8	±0.9	5.3	±0.3	22	±0.1
		GR	4	-25.7	±0.4	7.4	±1.6	22	±0.2
		HI	2	-27.9	±0.8	6.1	±0.1	21.9	±0.1
		MI	1	-26.9		5.5		21.3	
		NH	1	-27.5		4.3		21.9	
		SK	2	-26.6	±1.4	9.3	±2.1	21.8	±0.8
		UI	1	-27.3		6.6		22.2	
Ochrophyta	(not identified)	FH	6	-28.6	±7.2	4.1	±0.5	15.2	±1.9
		MI	2	-22.7	±0.3	4.7	±0.1	17.9	±0.2
Rhodophyta	*Iridaea cordata*	FH	10	-17.7	±1.2	4.5	±0.6	17.3	±0.8
		GR	10	-17.6	±1.4	3.2	±0.7	17.7	±1.0
		MI	10	-17.2	±1.0	5.3	±0.6	17.2	±0.7
		NH	6	-15.1	±0.6	4.5	±0.3	17.9	±0.1
		SK	9	-16.3	±0.8	3.5	±0.5	19	±0.6
		UI	11	-17.1	±2.2	4.2	±1.6	18.8	±0.8
	Trematocarpus antarcticus	FH	10	-20.2	±1.3	5.3	±0.4	19.8	±0.1
		HI	10	-20.8	±4.4	5.5	±0.8	19.7	±0.1
	(not identified)	FH	1	-22.6		4.1		18.6	
		NH	3	-31.1	±0.4	3.2	±0.1	18.6	±0.4
Porifera	*Dendrilla antarctica*	FH	10	-27	±0.8	3	±0.2	17.4	±0.6
		MI	2	-26.5	±0.4	4	±0.2	19.3	±0.3
	Homaxinella balfourensis	HI	10	-27	±0.5	4.2	±0.1	17.9	±0.4
	Mycale acerata	GR	1	-14.3		6.9		17.1	
		SK	2	-23.2	±0.6	7.5	±0.7	18.7	±0.4
		UI	10	-25.2	±3.4	7.6	±1.5	18.3	±1.2
	(not identified)	UI	1	-24.4		6.7		17.7	
Cnidaria	*Glyphoperidium bursa*	FH	3	-17	±2.3	9.4	±0.5	16.9	±0.3
		HI	12	-14.9	±1.1	10.5	±0.9	17	±0.6
Nemertea	*Parborlasia corrugatus*	FH	9	-19.3	±1.9	7.9	±0.9	17.7	±1.3
		GR	9	-16.2	±1.2	8.9	±0.6	15.2	±0.5
		HI	6	-17	±1.0	9.8	±0.4	16.4	±0.5
		MI	7	-18.4	±1.9	9	±0.8	17.9	±1.2
		NH	2	-17.2	±0.6	8.9	±0.2	17.5	±0.5
		SK	1	-16.4		9.5		17.4	
		UI	9	-16.4	±1.2	10	±0.6	16.6	±2.0
Annelida	Serpulidae (not identified)	SK	4	-24.4	±1.2	5.8	±3.4	18.5	±0.6

Samples		Stations	N	δ^{13}C		δ^{15}N		δ^{34}S	
Arthropoda									
Amphipoda	*Eusirus* sp.	UI	1	-15.8		10.9		16.9	
	(not identified)	FH	19	-17.8	±2.5	7.2	±0.7	14.1	±1.4
		GR	1	-17.5		8.2		17.5	
		MI	3	-16.8	±0.5	6.9	±1.2	12.5	±1.3
		NH	3	-16.9	±1.1	9.1	±1.3	18	±2.4
		SK	2	-17.5	±0.4	8	±0.8	19	±1.8
Isopoda	*Glyptonotus antarcticus*	FH	4	-15.9	±2.1	8.6	±0.7	15.1	±2.0
		GR	12	-16.1	±2.0	7.6	±1.1	18.6	±0.7
		HI	5	-15.6	±1.8	8.8	±0.8	14.9	±1.8
	(not identified)	SK	2	-18.9	±0.9	6.9	±2.8	19.1	±2.7
		UI	2	-16.7	±5.0	8.1	±2.2	18.5	±3.7
Mollusca									
Bivalvia	*Aequiyoldia eightsii*	FH	2	-13.9	±1.5	8.8	±0.8	13.1	±2.5
		GR	1	-14.6		7.5		15.4	
	Laternula elliptica	FH	11	-26.1	±1.0	4.2	±0.9	16.7	±1.2
		GR	17	-20.5	±3.0	4.6	±0.5	17.3	±1.1
Gasteropoda	*Margarella refulgens*	FH	10	-16.6	±0.9	7.8	±0.8	16.4	±1.1
		HI	3	-15.7	±1.5	14.6	±4.0	16.4	±0.4
		MI	10	-15	±0.8	7	±0.6	15.8	±1.3
		UI	10	-14.2	±0.4	7.7	±1.1	18.1	±1.5
	Nacella concinna	FH	10	-11.6	±1.7	6.4	±0.3	22.2	±1.2
		GR	9	-12.9	±1.0	5.8	±0.3	19.3	±1.2
		HI	11	-11.7	±0.4	7.1	±0.3	18.8	±0.5
		NH	10	-11.5	±3.8	7	±1.9	18.8	±1.2
		SK	15	-12.9	±1.2	5.5	±0.5	19.2	±0.7
		UI	9	-10.7	±1.2	6.1	±1.7	18.5	±1.1
	Austrodoris sp.	FH	10	-18.1	±1.1	7.4	±0.5	16.7	±0.5
		MI	7	-19	±2.4	8.5	±0.4	16.6	±0.7
	Trophon sp.	HI	2	-14.1	±0.2	11.4	±0.6	16.6	±0.6
	(not identified)	MI	1	-14.7		12.3		14.6	
Polyplacophora	(not identified)	HI	1	-15.7		10.2		13.9	
Bryozoa	(not identified)	FH	2	-24.1		4.1		17.5	
		HI	2	-19.1	±6.1	7.5	±4.4	17.6	±2.4
		NH	2	-18.2	±4.7	11.6	±3.5	18.5	±1.7
		SK	6	-25.4	±2.4	4.2	±1.6	18.3	±1.0

Samples		Stations	N	$\delta^{13}C$		$\delta^{15}N$		$\delta^{34}S$	
Echinodermata									
Asteroidea	*Odontaster validus*	FH	10	-13.6	±1.1	10.8	±0.4	15.8	±0.9
		GR	15	-13.2	±1.2	10.6	±0.5	20.6	±0.6
		NH	19	-15.3	±1.5	12.4	±3.4	18.8	±2.1
		SK	8	-15.7	±0.6	10.9	±2.0	20.2	±1.2
		UI	15	-14.2	±1.2	13.5	±2.6	17.7	±2.0
	Odontaster meridionalis	SK	3	-17.7	±4.5	14.7	±5.3	19.9	±1.4
	Odontaster roseus	UI	1	-20.5		8.6		21.5	
	Perknaster sp.	FH	1	-21.9		8.8		19.4	
		HI	1	-20.6		9.1		17.8	
		NH	1	-16.5		14		21.7	
		SK	2	-16.7	±0.8	12.2	±0.1	21.3	±0.6
	Cuenotaster involutus	MI	1	-14.1		13.1		16.4	
	Diplasterias brucei	MI	3	-18.7	±3.7	9	±1.5	16.9	±1.1
	Granaster nutrix	MI	1	-20.2		8.4		17.4	
		SK	2	-13	±1.2	11.9	±0.6	18.9	±2.0
		UI	1	-15.5		11		21.6	
	Psilaster charcoti	HI	2	-10.8	±0.6	13.9	±0.8	16.3	±1.2
		MI	10	-14.3	±1.5	13.1	±1.9	16.3	±1.1
	Neosmilaster georgianus	NH	12	-14.5	±1.6	10.2	±1.0	16.7	±0.9
	Acodontaster conspicuus	SK	1	-17.4		10.2		20.7	
	Acodontaster sp.	SK	1	-13.4		9.8		20.9	
	Labidiaster annulatus	NH	2	-14.8	±4.3	11.3	±0.6	22.2	±1.2
	Labidiaster sp.	NH	1	-16.4		12.4		12.3	
	Lysasterias sp.	GR	1	-11.1		7.7		21.5	
		SK	1	-21.8		8.7		21.5	
		UI	1	-14		10.6		20.8	
	Henricia sp.	SK	1	-16.6		9.4		21.3	
	(not identified)	UI	1	-11.5		9.4		21.1	
Ophiuroidea	*Ophionotus victoriae*	SK	4	-18	±6.0	7.6	±1.8	19.8	±1.5
Echinoidea	*Sterechinus neumayeri*	FH	10	-12.5	±0.6	9	±0.3	10.7	±1.6
		HI	10	-11.6	±0.3	9.7	±0.2	14	±0.4
		MI	10	-12.6	±0.4	9.6	±0.3	14.7	±2.1
		UI	4	-16.7	±0.8	9	±0.2	17.8	±0.3
Holoturoidea	*Heterocucumis steineni*	HI	2	-18.9	±0.2	8.2	±0.4	21.1	±0.3
Chordata	Ascidiacea (not identified)	FH	8	-25.9	±2.1	6.5	±0.5	16.7	±0.9
		SK	1	-19.5		8.7		16.9	

Appendix 2

Layman and SIBER metrics illustration: CD = mean distance to centroid; CR = carbon range; MNND = mean nearest neighbour distance; NR = nitrogen range; SDNND = standard deviation of nearest neighbour distance; SEA = Standard Ellipse Area; TA = convex hull's total area.



Appendix 3

Mean distance between centroids of *Iridaea cordata* for each station, in both biplots representation. Significant p-values obtained from the Turner test are represented by: * < 0.05, ** < 0.01, and *** < 0.001.

$\delta^{13}C$-$\delta^{15}N$	FH	GR	MI	NH	SK
GR	1.23				
MI	0.99	2.10 **			
NH	2.54 *	2.72 *	2.18		
SK	1.65 *	1.3	1.95 **	1.49	
UI	0.64	1.12	1.06	1.94	1.04
$\delta^{13}C$-$\delta^{34}S$	**FH**	**GR**	**MI**	**NH**	**SK**
GR	0.4				
MI	0.53	0.62			
NH	2.60 **	2.43 *	2.12 *		
SK	2.13 ***	1.77 **	1.92 **	1.57	
UI	1.63 **	1.24 *	1.61 **	2.15 *	0.77

Appendix 4

$\Delta^{13}C$, $\Delta^{15}N$, and $\Delta^{34}S$ mean ± standard deviation in per mille (‰) for each sample among stations. A correction based on mean *Iridiaea cordata* isotopic ratios. N = number of organisms or samples analyzed.

Phyla	Species	**Stations**	**N**	**$\Delta^{13}C$**		**$\Delta^{15}N$**		**$\Delta^{34}S$**	
Mollusca									
Gasteropoda	*Nacella concinna*	FH	10	6.1	±1.7	1.9	±0.3	4.9	±1.2
		GR	9	4.7	±1.0	2.6	±0.3	1.6	±1.2
		NH	10	3.6	±3.8	2.5	±1.9	0.9	±1.2
		SK	15	3.4	±1.2	2	±0.5	0.2	±0.7
		UI	9	6.4	±1.2	1.9	±1.7	-0.3	±1.1
Echinodermata									
Asteroidea	*Odontaster validus*	FH	10	4.1	±1.1	6.3	±0.4	-1.5	±0.9
		GR	15	4.4	±1.2	7.4	±0.5	2.9	±0.6
		NH	19	-0.2	±1.5	7.9	±3.4	0.9	±2.1
		SK	8	0.6	±0.6	7.4	±2.0	1.2	±1.2
		UI	15	2.9	±1.2	9.3	±2.6	-1.1	±2.0
Nemertea									
	Parborlasia corrugatus	FH	9	-1.6	±1.9	3.4	±0.9	0.4	±1.3
		GR	9	1.4	±1.2	5.7	±0.6	-2.5	±0.5
		MI	7	-1.2	±1.9	3.7	±0.8	0.7	±1.2
		UI	9	0.7	±1.2	5.8	±0.6	-2.2	±2.0