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What is the menu today in a subantarctic kelp food web from the Kerguelen Islands? Phytodetritus, phytoplankton and phytobenthos; not living kelp

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Abstract
Kelp forests dominated by *Macrocystis pyrifera* are widely distributed in coastal waters from boreal, temperate and subantarctic regions. This widespread distribution may result in regional differences in food web structure and functioning. In temperate northern regions, where most studies on kelp forest benthic food webs have been conducted, kelp grazing is a well-documented phenomenon and can lead to the overgrazing of *M. pyrifera* by sea urchins when their predators (e.g., sea otters) are absent. In contrast, little is known about their counterparts in subantarctic areas. The present study aimed to reconstruct the benthic food web of a kelp forest dominated by *M. pyrifera* in a subantarctic environment using stable isotope analysis. Stable carbon (δ^{13}C), nitrogen (δ^{15}N) and sulfur (δ^{34}S) isotope ratios were measured from food sources (macrophytobenthos, suspended particulate organic matter SPOM, and sediment) and consumers (sponges, bivalves, gastropods, sedentary and mobile polychaetes, arthropods and echinoderms) which were sampled in a kelp forest of the Kerguelen archipelago. Mixing models highlighted two interconnected trophic pathways which were either supported by SPOM and resuspended macrophytobenthos detritus (bentho-pelagic), or by live micro/macrophytobenthos (phytobenthos-based). No major prey were highlighted for several consumers, indicating the existence of potential supplementary trophic pathways. No consumer relying primarily on living *M. pyrifera* was highlighted by the mixing models. The investigated kelp forest is hence a complex ecosystem supporting multiple trophic pathways, and direct consumption of *M. pyrifera* is limited. Nonetheless, *M. pyrifera* and other macrophytobenthos species may constitute a pool of detritus supporting several trophic pathways.

Keywords Benthic communities · Food web · Kelp forests · Mixing models · Stable isotopes

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Introduction

Kelp forests host rich coastal benthic communities, and provide a wide range of ecosystem services (Smale et al. 2013; Bertocci et al. 2015). They are characterized by the dominance of large seaweeds from the class Phaeophyceae, order Laminariales, referred to as 'kelp'. Kelp provides physical protection against ocean swell, and shelters many resident organisms (Miller et al. 2015; 2018; Teagle et al. 2017). Furthermore, kelp is an important food source in benthic food webs through direct (grazing upon living tissues, i.e., the green food web) (Page et al. 2008; Koenigs et al. 2015) or indirect consumption (via detrital pathways, i.e., the brown food web) (Kaehler et al. 2000; 2006; Schaal et al. 2009; 2010). It also acts as a dispersal vector to the organisms living on it, when detached from the sea bottom and transported over long distances (Helmuth et al. 1994; Hobday 2000; Fraser et al. 2011). The dominant kelp species is often

associated with other species of the macrophytobenthos, including Rhodophyceae, Ulvophyceae and Phaeophyceae (Duchêne 1984; Wernberg et al. 2003), which represent key food sources for coastal benthic communities.

The kelp *Macrocystis pyrifera* (Linnaeus) Agardh (1820) has a large biogeographic range, and it is present in the boreal and temperate Eastern Pacific (North and South America), in South Africa, and in the subantarctic Southern Ocean (Patagonia, the Subantarctic islands, southern Australia and New Zealand) (Macaya and Zuccarello 2010; Teagle et al. 2017). It is commonly found in the Kerguelen Islands, a subantarctic archipelago located at the limit of the Indian and Southern oceans (Duchêne 1984; Belsher and Mouchot 1992).

Given the widespread distribution of *M. pyrifera* and the biogeographic variation in the structure of associated communities, geographic differences in functional ecology can be expected. Along the North American coasts, *M. pyrifera* is an important food source for the sea urchins of the genera *Strongylocentrotus*, *Mesocentrotus* and *Lytechinus* (Dean et al. 1984; Brown et al. 2014). In turn, sea urchins are the main prey of the sea otter *Enhydra lutris* and the sea star *Pycnopodia helianthoides* (Schultz et al. 2016; Burt et al. 2018). The absence of one of these predators is sufficient to release sea urchins from top-down control, resulting in overgrazing and a reduction of kelp density despite the presence of other predators (Burt et al. 2018).

Top-down control of *M. pyrifera* by sea urchins appears to be more limited in the kelp forests of the southern hemisphere. In Patagonia, the sea urchin *Loxechinus albus* mostly targets drifting kelp, and potential local overgrazing of live kelp is limited by the sea star *Meyenaster gelatinosus* (Castilla 1985; Dayton 1985). Other organisms than sea urchins may also feed directly on kelps, such as limpets (Andrade et al. 2016). In addition, a study in the subantarctic Prince Edward Islands suggests that kelp in subantarctic food webs is consumed by amphipods and isopods instead of sea urchins, but is also assimilated as detritus by suspension feeders (Kaehler et al. 2000). Kelp may also potentially support offshore subantarctic food webs, as kelp detritus were shown to be exported far from the coast (Kaehler et al. 2006). Furthermore, overall, kelp may be consumed in combination with other food sources (Kaehler et al. 2000; Andrade et al. 2016).

Coastal benthic ecosystems from Kerguelen Islands have been understudied so far and few data on the biomass of their components are available (Améziane et al. 2011). Furthermore, the functioning of Kerguelen Island's kelp forest is still poorly known, as most ecological studies of kelp forests dominated by *M. pyrifera* have focused on the northern hemisphere. In this regard, we here aimed to study the food web structure in a nearshore kelp forest in the subantarctic Kerguelen Islands. Specifically, our goals were to: (1)

identify dominant energetic pathways supporting benthic invertebrates living in the kelp forest; (2) quantify their reliance on living kelp tissue vs. other organic matter sources; and (3) highlight the presence of potential trophic cascades susceptible to modulating kelp abundance in nearshore subtidal ecosystems of the Kerguelen Islands.

To achieve these goals, we used stable isotope ratios as food web tracers. The ratios between stable isotopes of carbon (δ^{13}C), nitrogen (δ^{15}N), and sulfur (δ^{34}S) in organisms' tissues provide long-term information on their diet. δ^{13}C and δ^{34}S are generally used to determine the basal sources in food webs and their pelagic or benthic origin thanks to the differences of stable isotope composition between the different types of primary producers, to the differences of δ^{34}S between seawater sulfates and sediment sulfides, and to the low ^{13}C and ^{34}S enrichments in organisms relative to their diet (Michener and Kaufman 2007). δ^{15}N is generally used to estimate the trophic position of consumers, as organisms are generally more enriched in ^{15}N relative to their diet (Michener and Kaufman 2007). In addition, these tracers can be used to infer the diet of organisms using mixing models developed to assess the relative contribution of potential food sources to the diets of organism groups (Parnell et al. 2010; 2013).

Materials and methods

Sampling and sample treatment

Samples were collected in the Kerguelen Islands during the fifth summer campaign of the French Polar Institute programme Proteker (#1044; Motreuil and Saucède 2017), from November 17th to December 4th, 2016, near the Port-aux-Français scientific station (*ca* 49° 21' S and 70° 13' E, surface: *ca* 0.10 km^2, Fig. 1). Samples of benthic primary producers (i.e., kelp and other species of macroepiphytes), large kelp macrophytodetritus, surface sediment, and suspended particulate organic matter (SPOM) were collected by scuba divers between 5 and 13 m depth. Samples of SPOM were obtained from subsurface seawater samples (1.8 to 2.1 dm^3) filtered through pre-combusted (400 °C, 4 h) GF/F filters (Table 1). Limited information is available on the abundance and biomass of organisms from kelp forests of the Kerguelen Islands. Yet, Arnaud (1974) described the main benthic components of the flora and fauna and reported four main trophic groups represented by suspension feeders (sponges, bivalves), grazers (gastropods), carnivores (polychaetes, gastropods, sea stars) and omnivores (arthropods, polychaetes). In the present study, the most common (in terms of biomass) organisms of the flora and fauna reported by Arnaud (1974) were sampled. This ensured an acceptable representativeness and ecological relevance of our sampling despite logistics
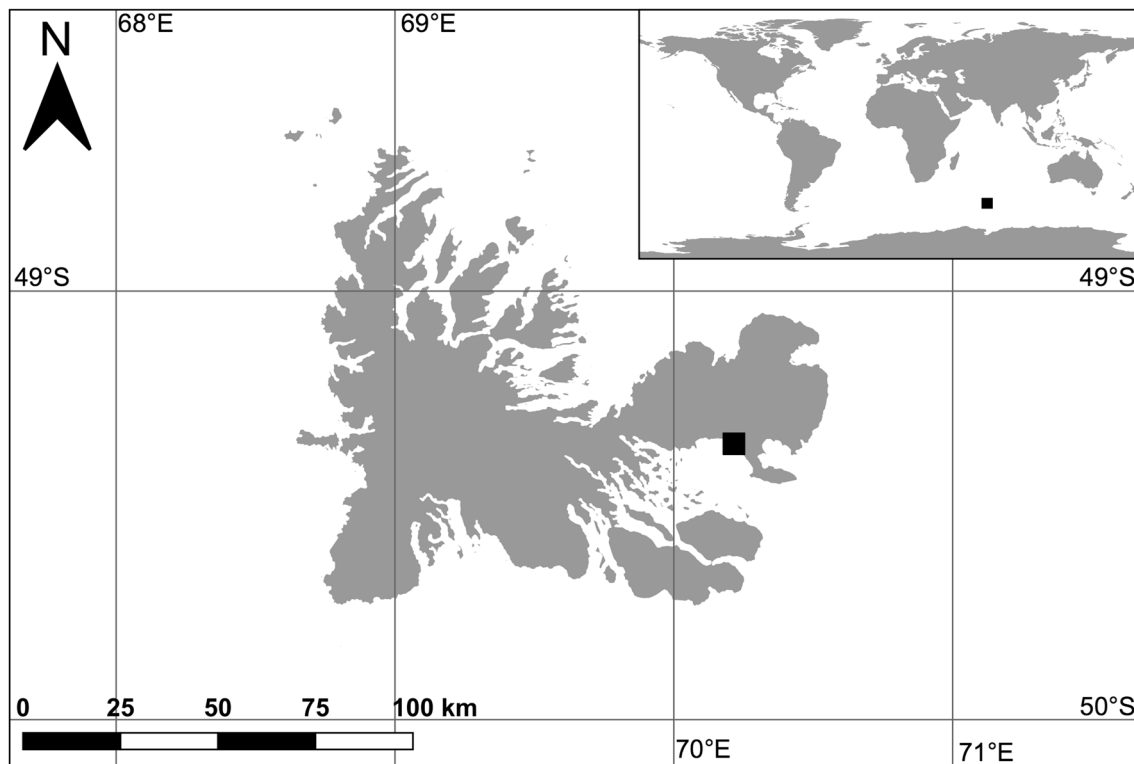
Fig. 1 Location of Port-aux-Français research base in the Kerguelen Islands

limitations preventing an exhaustive sampling. Samples included organisms from various taxa and feeding guilds, such as unidentified sponges, bivalves (*Aulacomya atra*, *Mytilus platensis*), gastropods (*Nacella edgari*, *Nacella kerguelenensis*, *Doris* cf. *kerguelenensis*, *Neobuccinum eatoni*), sedentary and mobile polychaetes (*Neanthes* cf. *kerguelensis*), arthropods (*Halicarcinus planatus* and Serolidae isopods) and echinoderms (the echinoid *Abatus cordatus*, the asteroids *Anasterias perrieri*, *Anasterias* sp., *Diplasterias meridionalis*, Echinasteridae, *Leptychaster kerguelenensis* and Pterasteridae and the Holothuroidea *Staurocucumis* sp.).

The samples were left 3–7 h in seawater aquariums to allow gut content evacuation, and were dissected to collect the target tissues for stable isotope analysis (SIA), which were then dried at 60 °C for 72 h, except *N. edgari* and sea stars which were preliminary stored at − 20 °C before dissection and drying at the laboratory of the University of Liège. The tissues selected for each item are reported in Table 1. Samples were then homogenized into powder prior to SIA using a mortar and a pestle or a mixer mill (MM301, Retsch, Haan, Germany) depending on toughness.

Stable isotope analysis

$\delta^{13}C$ ratios in carbonates in organism tissues are usually more positive than $\delta^{13}C$ ratios in their organic components,

and they cannot be related to the organism's diet (DeNiro and Epstein 1978). Consequently, it is necessary to remove carbonates in samples where they are present. 'Champagne tests' (Jaschinski et al. 2008), i.e., dropping a small amount of the sample in 37% hydrochloric acid, were thus conducted for each type of sample to assess the presence of carbonates. When effervescence was observed during the 'champagne tests', carbonates were removed from the samples. To do so, subsamples were exposed to 37% hydrochloric acid vapors for 48 h and then kept at 60 °C until proceeding with the sample preparation (Hedges and Stern 1984). The presence of remaining carbonates was assessed using a portion of the acidified subsamples for a supplementary 'champagne tests'. Table 1 indicates which primary producers, organic matter sources, and benthic invertebrates were acidified.

Sulfur biogeochemistry of coastal sediments is highly complex, with a mix of organic and mineral, particulate, dissolved or solid species co-occurring. The technique used here (flash combustion) cannot discriminate them, and instead extracts most of them with variable efficiency. $\delta^{34}S$ of bulk sediments can, therefore, not be unequivocally linked with ecosystem processes. It holds little relevant ecological information, and we chose not to present it here nor to include it in our models.

Subsamples were then weighed (*ca* 10 mg for SPOM, 25 mg for sediment, 1.5–5 mg for macrophytobenthos and

Table 1 Organism groups and their mean ± standard deviation of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and sulfur ($\delta^{34}S$) stable isotope ratios in the Kerguelen subtidal community

Organism group	Tissue analyzed	Acidification	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{34}S$ (‰)
PRIMARY PRODUCERS AND/OR ORGANIC MATTER SOURCES			**101**	**−17.5 ± 6.3**	**6.9 ± 1.6**	**16.9 ± 2.0**
Acrosiphonia **sp.**	Thallus fragment	No	**9**	**−23.4 ± 1.5**	**7.1 ± 0.5**	**17.4 ± 0.7**
Adenocystis **sp.**	Thallus	No	**11**	**−6.2 ± 1.7**	**8.0 ± 0.4**	**17.7 ± 0.8**
Rhodophyceae	Thallus fragment	No	**10**	**−31.0 ± 0.9**	**6.4 ± 0.3**	**17.5 ± 0.8**
Macrocystis pyrifera* and *Gigartina skottsbergii			**34**	**−16.7 ± 1.2**	**7.2 ± 1.0**	**17.4 ± 1.6**
Gigartina skottsbergii	Frond fragment	No	13	−16.8 ± 2.3	6.5 ± 0.7	17.3 ± 2.6
Macrocystis pyrifera	Frond fragment	No	14	−16.7 ± 1.2	7.9 ± 1.1	17.5 ± 0.5
Macrocystis pyrifera detritus	Frond fragment	No	7	−16.2 ± 2.8	7.3 ± 0.7	17.2 ± 0.7
SPOM and sediment			**20**	**−18.6 ± 1.1**	**4.4 ± 1.2**	**12.4 ± 1.3**
SPOM		No	10	−19.5 ± 0.7	5.2 ± 0.8	12.4 ± 1.3
Sediment		No	10	−17.7 ± 0.4	3.5 ± 1.0	NA
Ulva **sp.**			**17**	**−14.2 ± 0.9**	**8.5 ± 0.5**	**17.2 ± 0.8**
Ulva sp.	Thallus fragment	No	10	−13.8 ± 0.9	8.6 ± 0.4	16.9 ± 0.8
Ulva sp. detritus	Frond fragment	No	7	−14.8 ± 0.4	8.4 ± 0.6	17.8 ± 0.4
LOW-$\delta^{15}N$ CONSUMERS			**53**	**−15.2 ± 1.8**	**9.3 ± 0.5**	**17.7 ± 1.8**
Suspension feeders			**31**	**−16.5 ± 0.6**	**9.0 ± 0.4**	**16.8 ± 1.3**
Aulacomya atra	Adductor muscle	No	11	−16.1 ± 0.6	9.0 ± 0.3	16.9 ± 0.7
Mytilus platensis	Adductor muscle	No	9	−16.3 ± 0.3	8.9 ± 0.4	18.1 ± 1.2
Sponges	Body fragment	No	11	−17.1 ± 0.5	9.2 ± 0.5	15.6 ± 0.8
Grazers			**22**	**−13.3 ± 1.2**	**9.7 ± 0.4**	**19.0 ± 1.7**
Nacella edgari	Foot	No	11	−12.6 ± 1.3	9.6 ± 0.4	18.0 ± 1.4
Nacella kerguelenensis	Foot	No	11	−14.0 ± 0.6	9.8 ± 0.4	20.0 ± 1.3
INTERMEDIATE-$\delta^{15}N$ CONSUMERS			**76**	**−15.0 ± 2.0**	**11.3 ± 1.0**	**16.2 ± 1.8**
Abatus cordatus	Test	Yes	**10**	**−16.2 ± 0.8**	**11.0 ± 1.2**	**13.4 ± 0.8**
Doris* cf. *kerguelenensis	Foot	No	**11**	**−12.0 ± 0.9**	**12.1 ± 0.2**	**18.3 ± 0.9**
Neanthes* cf. *kerguelensis	Whole organism	No	**10**	**−17.8 ± 1.6**	**10.9 ± 1.0**	**17.6 ± 1.2**
Arthropods and polychaetes			**30**	**−15.5 ± 0.7**	**11.4 ± 0.9**	**15.7 ± 1.2**
Halicarcinus planatus	Appendage	Yes	10	−15.0 ± 0.8	10.8 ± 1.0	15.7 ± 0.9
Sedentary polychaetes	Whole organism	No	11	−15.8 ± 0.7	11.5 ± 0.4	15.7 ± 1.6
Serolidae	Tegument and muscle	Yes	9	−15.6 ± 0.4	12.0 ± 0.7	15.5 ± 0.8
Echinoderms			**25**	**−13.5 ± 1.2**	**11.2 ± 1.2**	**16.5 ± 1.0**
Echinasteridae	Tegument	Yes	5	−12.8 ± 1.4	11.5 ± 1.4	16.4 ± 1.6
Staurocucumis sp.	Tegument	Yes	10	−13.8 ± 1.0	11.0 ± 1.1	16.6 ± 0.7
HIGH-$\delta^{15}N$ CONSUMERS			**102**	**−11.8 ± 1.2**	**13.9 ± 1.3**	**16.7 ± 1.3**
Anasterias perrieri	Tegument	Yes	18	−10.8 ± 0.7	14.5 ± 0.3	16.5 ± 1.1
Anasterias sp.	Tegument	Yes	6	−9.7 ± 0.9	12.8 ± 0.2	15.2 ± 1.4
Diplasterias meridionalis	Tegument	Yes	34	−12.2 ± 0.9	13.4 ± 1.8	16.5 ± 1.3
Leptychaster kerguelenensis	Tegument	Yes	27	−11.5 ± 0.7	14.6 ± 0.4	17.1 ± 0.4
Neobuccinum eatoni	Foot	No	11	−13.0 ± 0.8	13.7 ± 0.7	18.2 ± 1.3
Pterasteridae	Tegument	Yes	6	−13.3 ± 0.6	12.9 ± 0.4	15.8 ± 1.8
TOTAL			**332**	**−14.8 ± 4.4**	**10.4 ± 3.1**	**16.8 ± 1.8**

In bold capitals are trophic groups highlighted by a Kruskal–Wallis test and a post hoc Dunn test with Benjamini–Hochberg adjustments on $\delta^{15}N$ values. In bold within trophic groups are organism groups highlighted by hierarchical clusterings (Fig. S1). Selected tissues for stable isotope analysis and carbonate removal with acidification are also reported

2.5–3 mg for invertebrates) in 5 × 8 mm tin cups. A similar mass of tungsten trioxide accelerator was added to each cup except those containing sediment, as $\delta^{34}S$ was not measured on sediment samples. The samples were analyzed with an elemental analyzer (vario MICRO Cube, Elementar, Hanau, Germany) coupled with a continuous-flow isotope-ratio

mass spectrometer (IsoPrime100, Elementar UK, Cheadle, United Kingdom). $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values were expressed in ‰ relative to international measurement standards (Vienna Pee Dee Belemnite for $\delta^{13}C$, N_2 in atmospheric air for $\delta^{15}N$, and Canyon Diablo troilites for $\delta^{34}S$) according to the following equation:

$$\delta X_{Sample} = \left[\frac{(X/x)_{sample}}{(X/x)_{standard}} - 1 \right] \times 1000 \qquad (1)$$

where X is the heavy isotope (^{13}C, ^{15}N, or ^{34}S), x is the lighter isotope (^{12}C, ^{14}N or ^{32}S), and $(X/x)_{sample}$ and $(X/x)_{standard}$ are the ratios of both stable isotopes in the sample and the standard, respectively.

The stable isotope ratios were normalized using a single-point normalization approach relative to certified isotopic reference materials from the International Atomic Energy Agency (IAEA, Vienna, Austria): IAEA N-1 (ammonium sulfate; $\delta^{15}N = 0.4 \pm 0.2$‰), IAEA C-6 (sucrose; $\delta^{13}C = -10.8 \pm 0.5$‰), and IAEA S-1 (silver sulfide; $\delta^{34}S = -0.3$‰). Secondary standards included sulfanilic acid (Sigma-Aldrich, Overijse, Belgium; $\delta^{13}C = -25.6 \pm 0.4$‰; $\delta^{15}N = -0.1 \pm 0.4$‰; $\delta^{34}S = 5.9 \pm 0.5$‰; means $\pm$ SD), used as quality control, and two sea stars sampled for other research work ($\delta^{13}C = -21.2 \pm 0.2$‰, $\delta^{15}N = 15.1 \pm 0.3$‰, $\delta^{34}S = 18.2 \pm 0.5$‰ for the first sample; $\delta^{13}C = -15.1 \pm 0.3$‰, $\delta^{15}N = 12.2 \pm 0.2$‰, $\delta^{34}S = 15.5 \pm 0.4$‰ for the second sample).

Data analysis

Trophic relationships between organism groups were assessed using mixing models (Parnell et al. 2010; 2013). To do so, preliminary analyses were undertaken to determine the food sources to include in the mixing model. This step was critical to avoid the confounding effects that certain food web components with similar isotopic composition to the actual food sources may have when assessing the relative contribution to an organism's diet (e.g., Robinson et al. 2018). All data analyses were performed using R 3.6.0 (R Core Team 2017).

Preliminary analyses

Preliminary knowledge of organisms' diets is necessary before computing mixing models to determine which food sources should be included in the mixing model for each organism (Phillips et al. 2014). Including food sources that would normally not be consumed by organisms could result in highlighting the consumption of these food sources if their isotopic compositions are similar to those of the food sources that are usually consumed. However, the diet of

most organisms included in this study was not investigated in detail in previous studies and can mostly be inferred from the diet of their congeners. Organisms were hence clustered into four trophic groups depending on their supposed feeding habits. The first trophic group, i.e., primary producers and/or organic matter sources, contained SPOM, sediment and all photosynthetic organisms, and it represented the lowest trophic level group. Because $\delta^{15}N$ values increase according to the animal's trophic position (Michener and Kaufman 2007), differences of $\delta^{15}N$ values between consumers were used to determine the consumer trophic groups. This was assessed with a Kruskal–Wallis test and a post hoc Dunn test with Benjamini–Hochberg adjustments. This approach allowed to define three $\delta^{15}N$-value based groups: low, intermediate, and high $\delta^{15}N$-groups (Table 1).

Confounding effects of food sources with similar isotopic compositions may occur in mixing models and it is hence recommended to include only food sources with isotopically distinct compositions (Phillips et al. 2014). Consequently, organisms with similar mean stable isotope ratios were grouped together using a Ward hierarchical cluster analysis based on the Euclidean distance between the mean stable isotope ratios of each organism group. Organism groups with a Euclidean distance between mean stable isotope values lower than 2.5 were grouped together. We chose this threshold because it allowed the grouping of seaweed species with their corresponding detritus, and the grouping of low-$\delta^{15}N$ consumers into two distinct functional groups, i.e., the suspension feeders, hypothesized to feed on pelagic suspended organic matter, and the grazers, hypothesized to graze on benthic components. This procedure was not applied to high-$\delta^{15}N$ consumers, as they were never used as food sources in mixing models.

Identification of food sources for each trophic group

Bayesian mixing models with 10^5 iterations were computed to quantify resource use by consumers using the R package simmr (Stable Isotope Mixing Models in R, Parnell et al. 2010; 2013). The models were run for each trophic group with the two lower trophic levels being used as organic matter sources, with the exception of the model run for primary consumers, which only used primary producers and/or organic matter sources. The Rhodophyceae group was also excluded from the baseline food sources in models due to their extremely low $\delta^{13}C$ ratios (-31.0 ± 0.9‰) which were far outside the range of values obtained for all other organisms (i.e., mixing polygon). Trophic enrichment factors (TEF) were not available in the literature for several sampled taxa, such as sponges and echinoderms. Consequently, the mean $\pm$ s.d. TEF reported for all marine organisms (1.0 ± 1.6‰, $n = 87$ for $\delta^{13}C$, 2.4 ± 1.7‰, $n = 90$ for $\delta^{15}N$, Caut et al. 2009) were

used for $\delta^{13}C$ and $\delta^{15}N$ values. Similarly, the mean ± s.d. TEF reported for all organisms was used for $\delta^{34}S$ values (0.5 ± 1.9‰, $n = 12$, McCutchan et al. 2003). Contributions of each food item to the diets of organisms computed by mixing models were presented as modes and 95% credibility intervals (CI_{95}) of probability density function distributions, i.e., the range of values in which the contribution of food sources has a 95% probability of being included. Food sources with a modal contribution to the diet higher than 20% were considered major food sources, while food sources with modal contribution to the diet between 10 and 20% were considered secondary. Food sources with a modal contribution to the diet lower than 10% were considered not to be a significant food source for the organism under assessment.

Results

Preliminary analysis

The result of the Kruskal–Wallis test (H18 = 187.927, $P < 0.001$) and the subsequent post hoc analysis led to the inclusion of the two bivalves *A. atra* and *M. platensis*, the two limpets *N. edgari* and *N. kerguelenensis*, and sponges in the low-$\delta^{15}N$ consumers. The high-$\delta^{15}N$ consumers included the sea stars *A. perrieri*, *Anasterias* sp., *D. meridionalis*, *L. kerguelenensis* and the Pterasteridae, as well as the gastropod *N. eatoni*. The intermediate-$\delta^{15}N$ consumers thus included the remaining consumers (Table 1).

In each trophic group, organisms with similar isotopic ratios (Euclidean distance < 2.5) were combined into unique food sources using the hierarchical clustering analysis of average $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values. The primary producers *Gigartina skottsbergii*, live *M. pyrifera* and *M. pyrifera* macrophytodetritus were combined into a single food source (Table 1, Fig. S1a). Live *Ulva* sp. and *Ulva* sp. detritus were also grouped together. *Adenocystis* sp. and the Rhodophyceae were kept as distinct food sources. Although $\delta^{34}S$ was not measured in sediment samples, SPOM and sediment were clustered together and hence grouped into a single food source. In low-$\delta^{15}N$ consumers, the two bivalves *A. atra* and *M. platensis*, as well as sponges, were grouped together into the suspension feeder trophic group while the two limpets *N. edgari* and *N. kerguelenensis* were grouped together into a grazer trophic group (Table 1, Fig. S1b). In intermediate-$\delta^{15}N$ consumers, sedentary polychaetes, the crab *H. planatus* and Serolidae isopods were grouped into an arthropod-polychaete group (Table 1, Fig. S1c). The Echinasteridae sea stars and the Holothuroidea *Staurocucumis* sp. were also combined into a common echinoderm group. The sea

urchin *A. cordatus* and the polychaete *N.* cf. *kerguelenensis* were left alone.

Identification of food sources for each trophic group

Low-$\delta^{15}N$ consumers

The results of the mixing model for low-$\delta^{15}N$ consumers (Fig. 2) show that the seaweed *Acrosiphonia* sp. is an important food source for the three suspension feeding taxa (mode = 26.9%, CI_{95} = 14.7–38.8% for *A. atra*, mode = 31.9%, CI_{95} = 16.3–48.7% for *M. platensis* and mode = 26.8%, CI_{95} = 15.9–38.6% for sponges). The SPOM and sediment are also important food sources for *A. atra* (mode = 23.7%, CI_{95} = 14.2–33.4%) and sponges (mode = 33.9%, CI_{95} = 22.7–45.1%). In contrast, limpets appeared to graze upon different species of macrophytobenthos, with *N. edgari* feeding mostly on *Adenocystis* sp. (mode = 35.8%, CI_{95} = 21.4–48.3%) while *N. kerguelenensis* had a more diversified diet composed of the three seaweeds *Adenocystis* sp. (mode = 24.6%, CI_{95} = 12.3–37.7%), *Ulva* sp. (mode = 24.2%, CI_{95} = 5.9–48.3%) and *Acrosiphonia* sp. (mode = 20.4%, CI_{95} = 6.6–35.3%) in similar proportions. The modal contribution of *M. pyrifera* and *G. skottsbergii* to the diet of limpets never exceeded 20%, but it was the second most important food source for *M. platensis* (mode = 18.4%, CI_{95} = 3.8–44.2%).

Intermediate-$\delta^{15}N$ consumers

The results of the mixing model for the intermediate-$\delta^{15}N$ consumers (Fig. 3) highlighted four groups of consumers. The first group contained the crab *H. planatus* and the Serolidae isopods, which fed on suspension feeders (mode = 30.5%, CI_{95} = 3.4–58.3% for *H. planatus*, mode = 47.1%, CI_{95} = 9.4–69.9% for the Serolidae). Nevertheless, secondary prey items differed between both taxa with *H. planatus* feeding on SPOM and sediment (mode = 22.0%, CI_{95} = 4.4–40.4%) and Serolidae feeding on *Acrosiphonia* sp. (mode = 13.9%, CI_{95} = 2.5–28.3%). The second group was represented by sedentary polychaetes that appeared to feed on SPOM and sediment (mode = 34.3%, CI_{95} = 2.1–46.3%), as well as suspension feeders (mode = 15.7%, CI_{95} = 3.1–69.5%). The third group included *N.* cf. *kerguelensis*, which was shown to predominantly feed on *Acrosiphonia* sp. (mode = 42.7%, CI_{95} = 17.3–57.1%). The fourth group was only represented by *D.* cf. *kerguelenensis*, which appeared to feed on limpets (mode = 39.9%, CI_{95} = 11.6–61.0%) and *Adenocystis* sp. (mode = 20.0%, CI_{95} = 8.1–33.3%).

The mixing model did not highlight major food sources contributing to the diet of the Echinasteridae sea stars or the Holothuroidea *Staurocucumis* sp., as none of the food
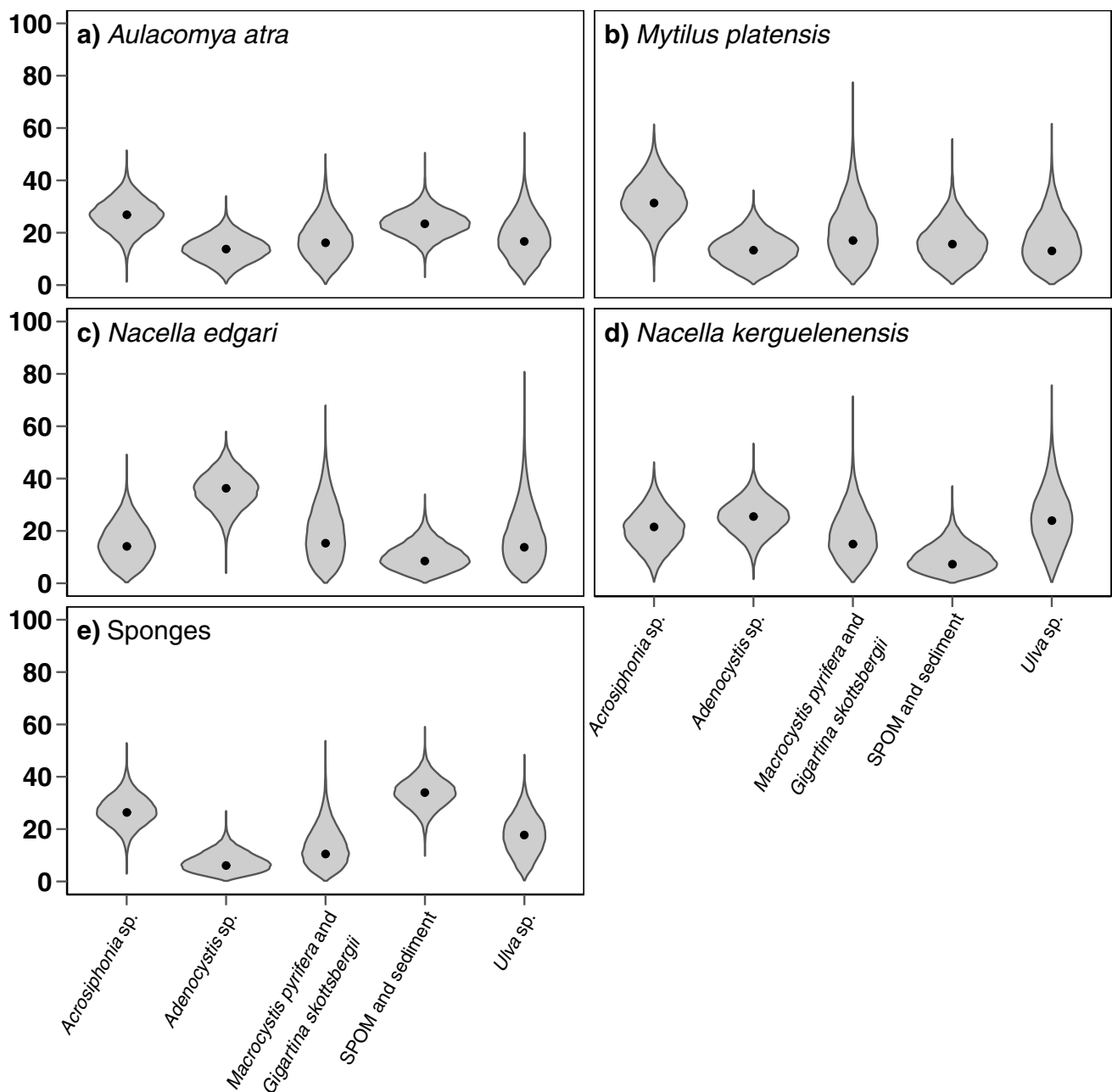
Fig. 2 Percentages of the relative contributions of primary producers and/or organic matter sources to the diet of each low-δ^{15}N consumer group determined by a Bayesian mixing model. Violin plots are the full distribution of the estimated contributions to the diet. The black dots are the modes

sources had a modal contribution to their diet higher than 20%. Modal contributions higher than 10% were highlighted for the seaweed *Adenocystis* sp. in both the Echinasteridae (mode = 17.4%, CI$_{95}$ = 2.1–39.3%) and *Staurocucumis* sp. (mode = 13.7%, CI$_{95}$ = 3.0–26.7%). Modal contributions higher than 10% were also observed for the SPOM and the sediment (mode = 12.0%, CI$_{95}$ = 2.4–28.4%) and suspension feeders (mode = 11.1%, CI$_{95}$ = 2.5–52.2%) in *Staurocucumis* sp. only. Similarly, no major food sources to the diet

of the sea urchin *A. cordatus* were highlighted by the model (no modal contribution higher than 20%), but the seaweed *Acrosiphonia* sp. had a modal contribution higher than 10% (mode = 17.2%, CI$_{95}$ = 1.8–35.4%). Furthermore, it should be noted that 95% confidence intervals were high for many food sources in several consumers, indicating high uncertainties in their contributions to the diet of these consumers and/or highly variable diets.
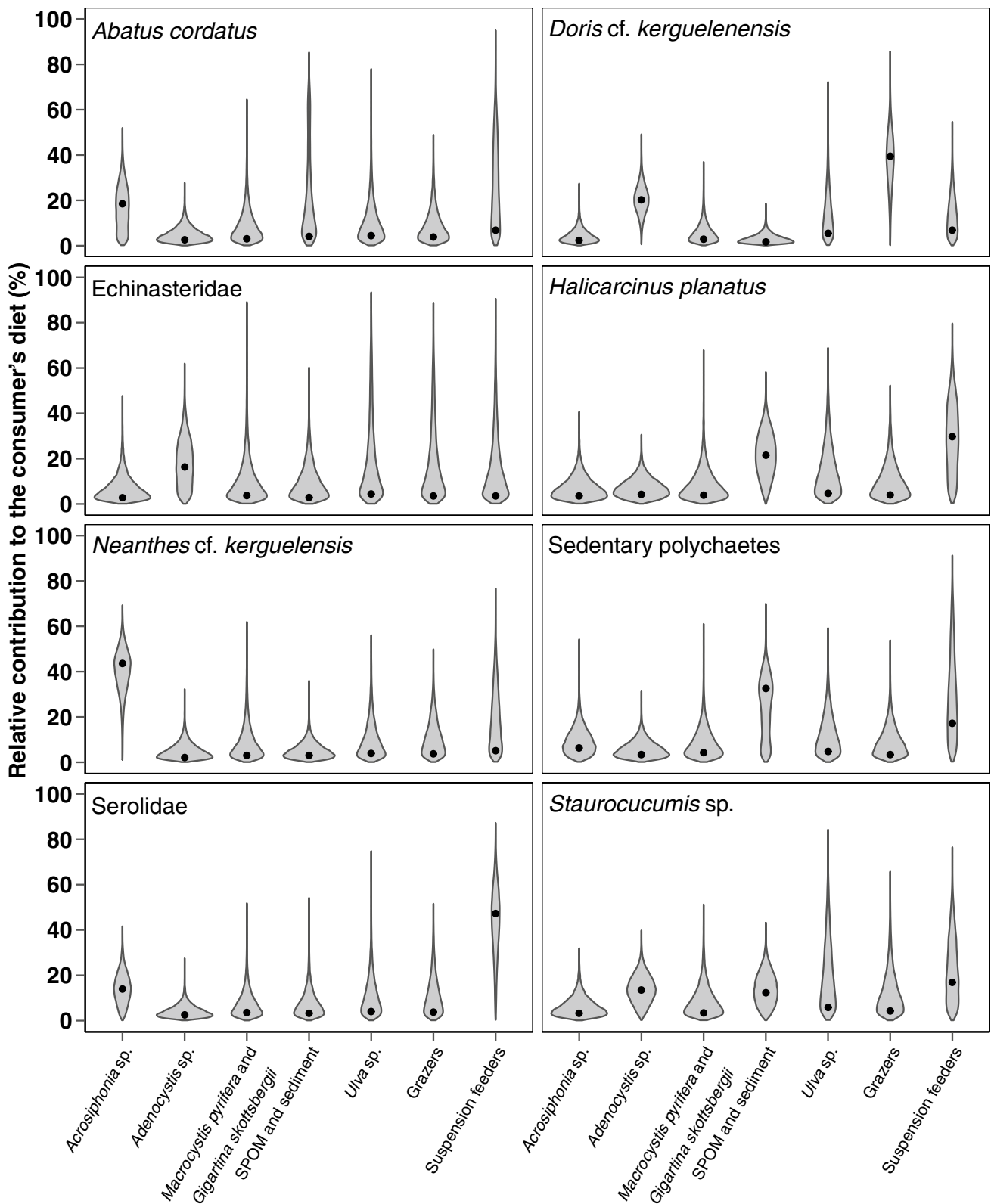
Fig. 3 Percentages of the relative contributions of primary producers and/or organic matter sources and low-δ¹⁵N consumers to the diet of each intermediate-δ¹⁵N consumer group determined by a Bayesian mixing model. Violin plots are the full distribution of the estimated contributions to the diet. The black dots are the modes
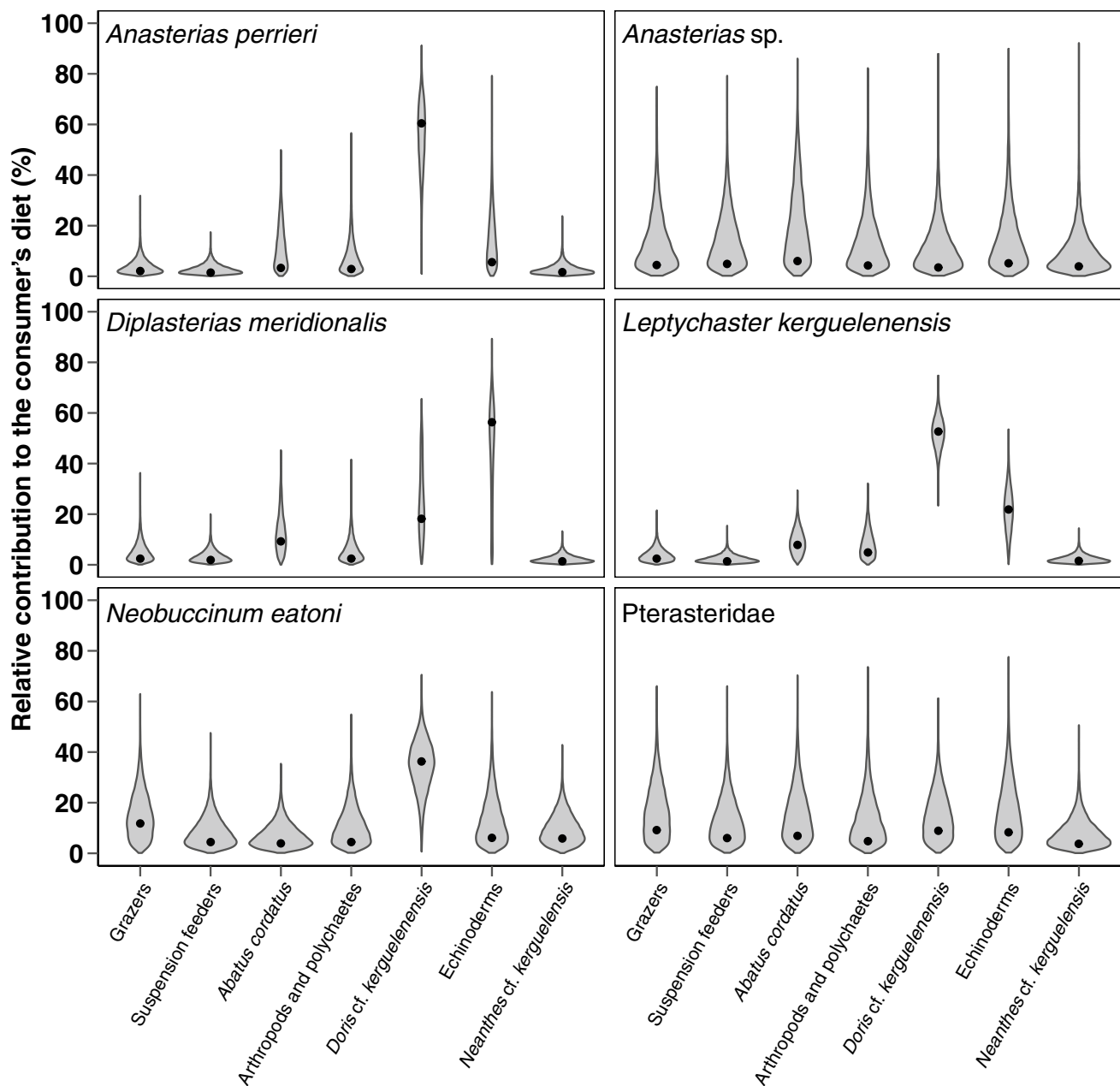
Fig. 4 Percentages of the relative contributions of low-δ^{15}N and intermediate-δ^{15}N consumers to the diet of each high-δ^{15}N consumer group determined by a Bayesian mixing model. Violin plots are the full distribution of the estimated contributions to the diet. The black dots are the modes

High-δ^{15}N consumers

Most of the high-δ^{15}N consumers were shown to feed on the nudibranch *D.* cf. *kerguelenensis* (Fig. 4). The nudibranch was indeed the main prey item for *A. perrieri* (mode = 60.8%, CI$_{95}$ = 28.3–76.7%), *L. kerguelenensis* (mode = 52.6%, CI$_{95}$ = 39.5–63.9%) and *N. eatoni* (mode = 36.2%, CI$_{95}$ = 13.0–52.2%). Furthermore, although the modal contribution of *D.* cf. *kerguelenensis* to the diet of *D. meridionalis* did not exceed 20% (mode = 16.7%,

CI$_{95}$ = 3.5–54.2%), it could still be considered a secondary food source for this species.

The main prey of *D. meridionalis* appeared to be echinoderms (mode = 56.8%, CI$_{95}$ = 3.9–72.1%). Echinoderms also appeared as a secondary food source for *L. kerguelenensis* (mode = 21.2%, CI$_{95}$ = 5.4–38.3%). Finally, the mixing model did not highlight major and/or secondary food sources for *Anasterias* sp. and the Pterasteridae, as no food source had a modal contribution to the diet higher than 10% for these two species.

Discussion

Food web structure of the nearshore kelp forests of the Kerguelen Islands

Our analysis highlighted the presence of two major energetic pathways in the kelp forest of Port-aux-Français: a bentho-pelagic pathway based on the consumption of both benthic (including detritus) and pelagic sources; and a phytobenthos pathway primarily based on the macrophytobenthos (Fig. 5).
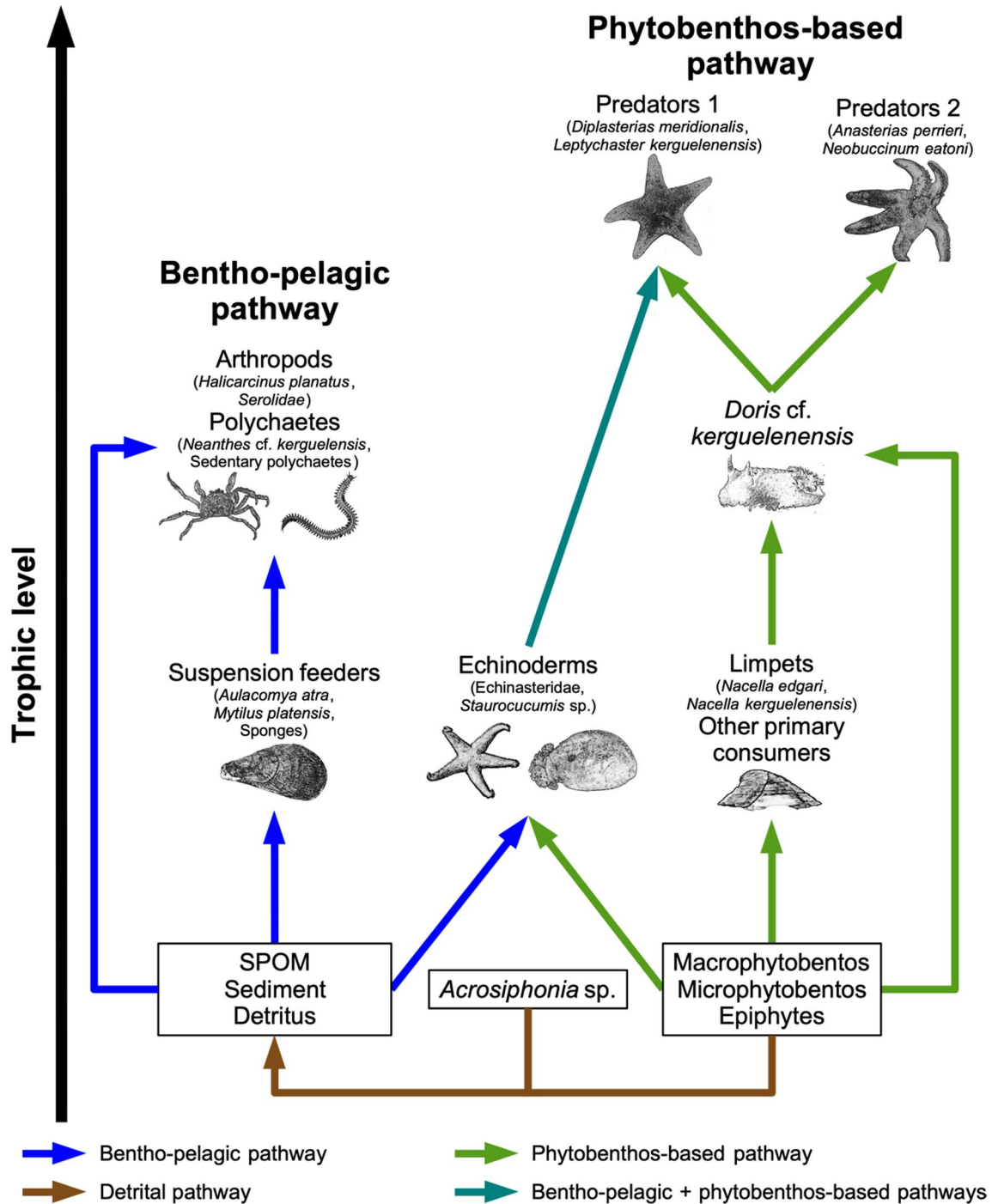

Fig. 5 Conceptual food web of the shallow subtidal benthic community of Port-aux-Français, Kerguelen Islands. Each arrow indicates a carbon transfer between two consecutive organism groups

The bentho-pelagic pathway

The present mixing models identified two groups of primary consumers. The first group contained the suspension feeders that consumed SPOM, sediment, and the seaweed *Acrosiphonia* sp. It is unlikely that bivalves and sponges consume *Acrosiphonia* sp. directly; rather it is more probable that they consume it as detritus. The consumption, selection, and assimilation of macrophytobenthos-derived particles, including kelp, by bivalves has already been observed in former studies (Stuart et al. 1982; Renaud et al. 2015). The result showing *Acrosiphonia* sp. as a food source for suspension feeders may also be explained by the selection of specific elements of the SPOM characterized by depleted $\delta^{13}C$ ratios compared to the bulk surface SPOM. These elements would result from pelagic production as pelagic SPOM is typically more depleted in ^{13}C than resuspended SPOM. Suspension feeders may specifically select some elements of the phytoplankton or specific particle size classes (Stuart and Klumpp 1984; Ribes et al. 1999; Levinton et al. 2002) characterized by distinct stable isotope ratios compared to bulk SPOM (Rau et al. 1990; Hansman and Sessions 2016; Hunt et al. 2017). The mixing models run for the intermediate-$\delta^{15}N$ consumers indicated that SPOM and sediment are important food sources for the crab *H. planatus* and the sedentary polychaetes. Similarly, suspension feeders appeared to be important food sources for *H. planatus*, as well as for the Serolidae isopods. *H. planatus* is known to feed on a wide range of items, including diatoms, phytobenthos, copepods, and polychaetes (ref. in Vinuesa et al. 2011), while the Serolidae isopods consume both amphipods and polychaetes (Luxmoore 1985). *N.* cf. *kerguelensis* may also be considered a component of the bentho-pelagic pathway, as it was modeled to feed mostly upon *Acrosiphonia* sp., which is mostly associated with the bentho-pelagic pathway. *N.* cf. *kerguelensis* may consume detritus of *Acrosiphonia* sp. This is in line with the knowledge that Nereididae polychaetes may display either deposit (Tsuchiya and Kurihara 1979; Fong 1987) or suspension feeding behaviors (Costa et al. 2006; Toba and Sato 2013), although they may also display predatory behaviors (Costa et al. 2006). Sedentary polychaetes appeared to feed mostly on SPOM and resuspended sediment. These results suggest that both polychaete groups may occupy a lower trophic level than initially suggested by their $\delta^{15}N$ ratios indicating a higher trophic level than suspension feeders. Analyzing stable isotopes in whole organisms instead of in a selected tissue may bias $\delta^{15}N$ ratios toward higher values (Mateo et al. 2008). However, this does not explain the results as gut content evacuation was conducted after the sampling. This can instead be explained by the consumption of degraded organic matter, as bacterial degradation and fractionation may lead to high $\delta^{15}N$ ratios in residual organic matter (Saino and Hattori 1980;

Wada 1980). High $\delta^{15}N$ values in polychaetes may also be explained by the consumption of zooplankton or organisms buried in sediments that were not specifically sampled in this study.

Suspension feeders, arthropods and polychaetes did not represent major food sources for the higher trophic consumers analyzed in this study by the third mixing model, suggesting a lower reliance of predators on the bentho-pelagic pathway than on the pathway based on macrophytobenthos. Nevertheless, the bentho-pelagic pathway may still provide food sources to several predators, as some high-$\delta^{15}N$ ratios consumers may consume prey that may potentially exploit both the bentho-pelagic pathway described here and the second energetic pathway based on the phytobenthos exclusively (see below).

The phytobenthos-based pathway

The second group of low-$\delta^{15}N$ values consumers identified by the mixing model contained both limpet species, with *N. edgari* mostly feeding on the Phaeophyceae *Adenocystis* sp., and *N. kerguelenensis* feeding on *Adenocystis* sp. as well as on the Chlorophyceae *Ulva* sp. and *Acrosiphonia* sp. *Adenocystis* sp. has already been observed in the gut contents of *Nacella* species by Rosenfeld et al. (2018), but it was a minor contributor to their diet. Species from the genus *Nacella* are generalist grazers that consume the most common resources available, which usually include micro- and macrophytobenthos (Blankley and Branch 1985; Andrade and Brey 2014; Rosenfeld et al. 2018). In particular, microphytobenthos, which was not sampled because of low organic matter content in sediment and lack of biofilm on kelp, usually has higher $\delta^{13}C$ ratios than most seaweeds in temperate (Riera and Richard 1996; Rigolet et al. 2014) and Antarctic food webs (Dunton 2001; Corbisier et al. 2004). Microphytobenthos is notably a key food source for the Antarctic limpet *Nacella concinna* (Dunton 2001; Corbisier et al. 2004). The microphytobenthos is therefore likely an important food source for both the *N. edgari* and *N. kerguelenensis* species at Port-aux-Français. However, the two species may still occupy distinct trophic niches, as the mixing model suggested that *N. kerguelenensis* had a higher reliance on *Ulva* sp. and *Acrosiphonia* sp. than *N. edgari*.

The nudibranch *D.* cf. *kerguelenensis* appeared as the single and major consumer of limpets according to the mixing model. It was also modeled to feed on the seaweed *Adenocystis* sp. This result was unexpected as *D.* cf. *kerguelenensis* is known to be a specialized sponge consumer (McDonald and Nybakken 1997), and its small size and highly specialized feeding organ (i.e., radula with similar, hook-shaped and smooth teeth, Troncoso et al. 1996), which functions as a rasp on the outer cell layers of sponges (Forrest 1953), is unlikely suited for limpet predation. A possible explanation

could be that *D.* cf. *kerguelensis* consumes sessile fauna that do not rely on particulate matter from pelagic origin for nutrition and that was not specifically sampled because of low abundance.

High-δ^{15}N values consumers, such as the sea stars *A. perrieri* and *L. kerguelenensis* and the gastropod *N. eatoni*, appeared to feed mostly on *D.* cf. *kerguelenensis*, but they probably also feed on other consumers depending more on the benthic than on the pelagic compartment for their diet. Previous studies on the ecology of sea stars of the genus *Anasterias* in subtidal benthic ecosystems of the Southern Ocean showed that these species are major predators of limpets (Blankley 1984), and may feed in clusters on them when they are too large for a single individual (Blankley and Branch 1984). Other preys include the crab *H. planatus*, polychaetes and isopods (Blankley 1984; McClintock 1985). The consumption of *D.* cf. *kerguelenensis* and the previously reported predation on grazing limpets suggest that predators are an important component of the phytobenthos-based pathway.

Potential trophic links between the phytobenthos-based and bentho-pelagic pathways

No major food sources were highlighted by mixing models for echinoderms from the intermediary level group. However, their role in the food web's functioning can be inferred based on former ecological studies and a cautionary interpretation of the present model outputs. Several food sources had a modal contribution higher than 10% for each organism group.

A small contribution of *Acrosiphonia* sp. to the diet of the sea urchin *A. cordatus* was highlighted. However, this species is a deposit feeder and sediment swallower (Poulin and Féral 1995; Pascal et al. 2021). The species distribution in medium to fine sand and muddy sediments (Poulin and Féral 1995) and narrow ecological niche (Saucède et al. 2017) suggest that *A. cordatus* has a specialized and partially selective deposit feeding strategy. In particular, comparison of ingested and surrounding sediments by metabarcoding and stable isotope ratios has shown that this species do not consume meiofauna buried in sediment but partially selects organic particles with distinct stable isotope compositions instead (Pascal et al. 2021). This hence suggests that *A. cordatus* is a primary consumer, and does not occupy a higher trophic level, as initially suggested by its high values of δ^{15}N compared to those of suspension feeders and grazers. Rather, its high δ^{15}N ratios may indicate consumption of enriched organic matter due to bacterial degradation (Saino and Hattori 1980; Wada 1980). The selective consumption of enriched degraded particles of the sediment would then explain why the direct trophic pathway between sediments and *A. cordatus* was not detected by the mixing models,

considering that stable isotopes were analyzed in bulk sediments. The large presence of *A. cordatus* in the subtidal communities of the Kerguelen Islands may, then, suggest the existence of another trophic pathway based on detritus within sediments.

The model also highlighted a small contribution of *Adenocystis* sp. to the diet of Echinasteridae sea stars. The known diet of several Echinasteridae species includes sponges, bryozoans, SPOM and biofilms (Jangoux 1982; Sheild and Witman 1993), which would explain why the group appeared to have intermediate lower δ^{15}N values than other sea stars. Similarly, the model indicated low contributions of *Adenocystis* sp., along with low contributions of SPOM, sediment, and suspension feeders to the diet of the Holothuroidea *Staurocucumis* sp. Subantarctic Holothuroidea preferentially feed on phytoplankton, as well as on different benthic organisms (e.g., seaweed, sponges, copepods, amphipods, ostracods, bryozoans and foraminiferans) when available (McClintock 1994). Consequently, Echinasteridae and *Staurocucumis* sp. would be supported by both the bentho-pelagic and the phytobenthos-based pathways. Therefore, these echinoderms represent the link between the two pathways, a link that is also supported by the fact that these organisms are consumed by the sea stars *L. kerguelenensis* and *D. meridionalis*, which may also exploit the phytobenthos-based pathway. Links between suspension feeders, algivores and detritivores were hypothesized in kelp forests of Patagonia (Castilla 1985; Adami and Gordillo 1999) although they resulted from the predation by sea stars of all trophic guilds instead of the existence of organisms feeding on multiple carbon sources.

How efficiently do our trophic models represent the Kerguelen Islands coastal food webs?

Mixing models showed that at least two main types of food sources support the subtidal food web at Port-aux-Français. However, the interpretation of the isotopic results proved difficult due to small mode values for all prey and large 95% confidence intervals not revealing preferred prey for many species (i.e., the urchin *A. cordatus*, the starfish *Anasterias* sp. and of the families Echinasteridae and Pterasteridae, and the Holothuroidea *Staurocucumis* sp.). This can result from organisms feeding on items that were not included in the models because they were not sampled. This leads to the question of whether a sufficiently diverse set of organisms were sampled. Scarce quantitative studies on coastal communities from Kerguelen Islands combined to constraining sampling logistics prevented a targeted sampling that likely ignored several food web components. Yet, stable isotope data were retrieved from wide set of invertebrate taxa belonging to the main functional groups reported by Arnaud (1974), and contributed to highlight at least two

interconnected food chains. Furthermore, the results for the organisms for which no major prey were highlighted may indicate the existence of supplementary trophic pathways, like the potential detrital pathway within sediments on which *A. cordatus* seems to rely, or another one used by the sea star *Anasterias* sp., which showed the highest $\delta^{13}C$ ratios of the study and was outside the mixing polygon delimited by the sampled food items. Like the bentho-pelagic and phytobenthos-based pathways, these supplementary trophic pathways may be connected to other trophic pathways. Consequently, hard-to-interpret mixing model outputs might be the reflection of a complex food web featuring multiple trophic interactions, sources and pathways that stable isotope analyses of selected elements on a limited number of groups cannot depict exactly.

Kelps as a carbon source in subantarctic food webs

The kelp *M. pyrifera* did not appear as a major food source in the diet of all investigated consumers in the subtidal food web of Port-aux-Français, and hence seems unlikely to constitute a major organic matter source for consumers in the food web analyzed. This could contrast with Kaehler et al. (2000; 2006) who suggested that kelp-derived detritus was an important food source for communities associated with kelp forests from Prince Edward Islands. However, contrary to the present study, Kaehler et al. (2000; 2006) did not sample any species of the macrophytobenthos other than *M. pyrifera* and could not take into account their potential importance in the functioning of coastal food webs. Therefore, they may have overestimated the importance of *M. pyrifera* as a food source. Nevertheless, we cannot exclude the contribution of detrital *M. pyrifera* to the detritus pool contained in sediment. The measured isotopic composition of this sediment is indeed a mix of the isotopic composition of many seaweeds, and it is likely that *M. pyrifera* largely contribute to this pool and hence enters the food web via the brown food chain. Our data indicated that it probably does not contribute much to the green food chain or to the brown food chain as macrophytodetritus.

M. pyrifera did not appear as a major food source for grazers (herbivores or detritivores) such as limpets. Instead, grazers consumed other seaweed species. Similarly, with the exception of a specialized consumer, grazers of temperate kelp forests may preferentially consume seaweed species other than *Laminaria digitata* (Schaal et al. 2010). Local variations in the consumption of *L. digitata* may occur and were linked to its nutritive values (Schaal et al. 2009). Consequently, one can conclude that none of the investigated consumers may have a major, direct impact on large kelp densities and abundance and that overgrazing of *M. pyrifera* seems unlikely in kelp forests from the Kerguelen Islands in their current state. This varies greatly from temperate and Patagonian *M. pyrifera* forests, emphasizing the fact that this widespread ecosystem differs in its associated biodiversity but also in its functioning.

Conclusions

In this study, two main energetic pathways were identified in the nearshore subtidal ecosystem of Port-aux-Français, in the Kerguelen Islands, using mixing models. The first pathway is characterized by suspension feeders and polychaetes exploiting both pelagic SPOM and possibly resuspended macrophytobenthos detritus as a secondary food source. The second pathway was characterized by grazers feeding on micro- and macrophytobenthos. The two food chains were interconnected through trophic links mediated by Echinasteridae sea stars and the Holothuroidea *Staurocucumis* sp., which are, in turn, prey for higher predators of the phytobenthos-based pathway.

Mixing models did not highlight major prey for several sampled organisms. One explanation to these results was that these organisms exploit other trophic pathways in addition to the two ones highlighted in this study. Kelp forests from Kerguelen Islands may then be complex ecosystems supporting a variety of trophic pathways and further research is hence necessary to identify all trophic pathways and their potential connections.

Living kelp did not appear to be a significant contributor to the diet of the sampled organisms, indicating that the kelp forests near the Port-aux-Français scientific station are unlikely to be impacted by overgrazing in their current state. This can be the result of one or several predators effectively controlling a population of potential grazers.

Author contributions BLB, TS, GL and LNM developed the questions investigated in the manuscript. TS and LNM designed the sampling protocol and conducted the fieldwork. BLB, AC and GL designed the analysis protocol and collected the data. BLB and AC analyzed the data. BLB, TS, AC, GL and LNM wrote the manuscript.

Data availability statement The raw data underlying this article are freely available at the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/dataset/28120c52-2b34-4db4-b348-812ee1eaf958). Data from sea stars are also part of the dataset "Stable isotope ratios of C, N, and S in Southern Ocean sea stars (1985–2017)" available at https://doi.org/10.15468/p8gcpe (data subset: expedition PROTEKER-2016).

Declarations

Conflict of interest The authors declare that they have no conflict of interests.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed and all necessary approvals have been obtained.

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