



Interactive effects of body size and environmental gradient on the trophic ecology of sea stars in an Antarctic fjord

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ABSTRACT: Antarctic sea stars can occupy different trophic niches and display different trophic levels, but, while the impacts of their body size and environmental features on their trophic niches are potentially important, they are presently understudied. Here we assessed the trophic ecology in relation to the size and habitat of sea stars in a fjord on King George Island (South Shetland Islands) using stable isotope values of carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and sulphur ($\delta^{34}\text{S}$). The disc radius influenced $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, whereas more limited changes in $\delta^{13}\text{C}$ or $\delta^{34}\text{S}$ values were related to arm length. Specifically, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were linked to disc radius in generalist species (*Diplasterias brandti* and *Odontaster validus*), which could indicate ontogenetic diet shifts, while this relationship occurred less frequently in more specialised species (*Bathybiaster loripes*, *Notasterias bongraini*, and *Perknaster sladeni*). *O. validus* had a smaller isotopic niche size in the inner than the outer fjord. The niche overlap between *D. brandti* and *O. validus* was low in the inner fjord. Low resource availability within the fjord, linked to higher turbidity, could induce trophic niche constriction and interspecific resource segregation. This could represent a mechanism for competition avoidance in a resource-limited system. Conversely, higher resource availability could allow *O. validus* to expand and share its isotopic niche with *D. brandti* in the outer fjord with a limited risk of competition. This trophic plasticity will likely influence how *O. validus* copes with the present and future modification of environmental conditions induced by climate change.

KEY WORDS: Ontogenetic shifts · Resource availability · Trophic interaction · Sea stars · Southern Ocean · Stable isotopes

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1. INTRODUCTION

The trophic ecology of organisms is influenced by both intrinsic biological features (i.e. life cycle, physiology, morphology, and phylogeny) and environmental constraints (e.g. prey availability and pres-

ence of competitors). Intrinsic biological features can include morphological attributes that change during growth, which induce ontogenetic changes in dietary habits and influence the range of the trophic niche (Scharf et al. 2000, Frédérick et al. 2012, Sánchez-Hernández et al. 2019). The ontogenetic trajectories

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of diet are highly taxon specific. For example, ontogenetic diet changes may result from metamorphosis, which induces the development and/or regression of morphological features that allow major habitat and prey changes (Hourdry et al. 1996, Nunn et al. 2012, Calado & Leal 2015, Lejeune et al. 2018). By contrast, the retention of larval traits (i.e. paedomorphosis) permits adults to continue to exploit the same habitat and prey as larvae (Lejeune et al. 2018). Direct growth from juvenile to adult size is also characterised by ontogenetic dietary shifts in predators, as their ability to handle larger prey depends on the size of their feeding structures, which is correlated with body size (Keppeler & Winemiller 2020). Therefore, increasing body size can result in the consumption of larger prey (Scharf et al. 2000, Sainte-Marie & Chabot 2002, Fernandez et al. 2017) and an increase in trophic position, as larger taxa usually occupy higher trophic levels in aquatic environments (Potapov et al. 2019).

Ontogenetic diet shifts during direct development have primarily been studied in aquatic predatory vertebrates, while few studies have been conducted on invertebrates. However, ontogenetic changes in prey type (Viherluoto et al. 2000, Sainte-Marie & Chabot 2002) and prey size (Sainte-Marie & Chabot 2002, Campos & van der Veer 2008) have been observed within several invertebrate taxa. In particular, ontogenetic habitat changes and increases in prey diversity (Manzur et al. 2010), mean size, and size range (Baeta & Ramón 2013, Fernandez et al. 2017) have been observed in sea stars. These ontogenetic shifts may result from specific feeding behaviours and/or changes in the size of feeding structures rather than global body size. In particular, disc size influences the maximum area within which sea stars can feed, as they do not evert their stomach beyond the edges of their disc, to prevent it being damaged (Lawrence 2012). Overall, sea stars may provide an adequate model taxon to study the occurrence and mechanisms of ontogenetic diet shifts in invertebrates.

Sea stars (Echinodermata, Asteroidea) are a key group of Southern Ocean benthos (McClintock 1994). Detailed investigations of sea star diets in the Southern Ocean, although relatively scarce, have indicated that they belong to different feeding guilds: suspension or sediment feeders, predators of mobile or sessile prey, scavengers, and omnivores (reviewed by Dearborn 1977, McClintock 1994). Some species consume a wide range of prey types and sizes, such as *Odontaster validus* (Pearse 1965, Dayton et al. 1974), but others are more specialised, such as *Perknaster fuscus*, which is known to exclu-

sively consume sponge tissues (Dayton et al. 1974). Many sea star species co-occur in the coastal Antarctic and are frequently sampled together in food web function investigations (e.g. Gillies et al. 2012, 2013, Wing et al. 2012, 2018, Michel et al. 2019). This co-existence may result in different trophic interactions depending on habitat characteristics and subsequent resource availability.

Environmental constraints influencing the trophic ecology of organisms can include prey availability (composition and abundance) or the presence of other organisms with similar trophic ecology that influence competition intensity. Sufficient prey availability allows for the consumption of the same prey type by all organisms without competitive interaction (Pool et al. 2017, Costa-Pereira et al. 2019). However, limited resource availability induces changes in trophic behaviours to limit competition, such as adding new prey items to the diet, which increases the range of the trophic niche (optimal foraging; Stephens & Krebs 1986, Cardona 2001, Svanbäck & Bolnick 2007) or, by contrast, causes specialisation for unshared resources, resulting in niche constriction and partitioning (Schoener 1974, Mason et al. 2008, Juncos et al. 2015, Pool et al. 2017). The global negative relationship between productivity and the degree of niche segregation between teleosts in lakes (Comte et al. 2016) suggests that trophic niche partitioning in cases of low resource availability is the most common phenomenon. As a result, niche overlap theory predicts that niche overlap between species decreases as the potential for competition increases (Pianka 1974). Intrinsic biological features and environmental constraints may also interact in shaping the trophic niche of organisms, as demonstrated by the ontogenetic changes of habitat that may induce changes in the diet, since prey taxonomic composition may differ between areas occupied by juveniles and adults (Frédérich et al. 2012, Sánchez-Hernández et al. 2019).

Polar fjords have spatially variable environmental conditions because of glacial meltwater inputs. Furthermore, meltwater inputs in the inner fjords provide high quantities of freshwater and inorganic suspended matter, resulting in spatial gradients in temperature, salinity, turbidity, and bottom sediment characteristics (Munoz & Wellner 2016, Meslard et al. 2018). Freshwater discharge might cause an osmotic shock to marine taxa, which could be responsible for removing 15% of the standing zooplankton biomass of the fjord. Dead sinking zooplankton constitutes an important food source for scavenging benthic fauna (Zajaczkowski & Legeżyńska 2001). Additionally,

high turbidity can reduce light transmission to the sea bottom, dilute organic matter, and clog the feeding structures of suspension feeders (Thrush et al. 2004, Donohue & Garcia Molinos 2009), preventing the development of photosynthetic and suspension feeding organisms. This can result in spatial gradients of primary production (Hoffmann et al. 2019, Holding et al. 2019) and benthos characteristics (Włodarska-Kowalczyk & Pearson 2004, Włodarska-Kowalczyk et al. 2005, Sahade et al. 2015), and then of resource availability. Consequently, fjords provide an adequate model ecosystem for investigating the effects of different levels of prey and resource availability on the trophic interactions between co-occurring organisms.

Stable isotope compositions of carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and sulphur ($\delta^{34}\text{S}$) are commonly used trophic markers for food web studies to identify the primary production sources of the food web (with $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values) and trophic levels of organisms (with $\delta^{15}\text{N}$ values; Michener & Kaufman 2007). The relationship of these stable isotope values with body size indicates changes in habitat use, resource selection, and trophic level throughout growth. Similarly, spatial variations in the stable isotope composition of an organism may be useful to highlight the use of different resources, especially in sedentary or poorly motile organisms, such as sea stars, which are often dependent on the closest or most easily available carbon sources. Finally, stable isotopes allow comparison of the size and overlap of the isotopic niches (i.e. as a proxy for trophic niches) of various organisms (Jackson et al. 2011, Skinner et al. 2019).

In this study, we used stable isotope trophic markers to investigate how intrinsic and extrinsic factors drive the trophic ecology of Antarctic sea stars. Ezcurra Inlet, a fjord in Admiralty Bay, King George Island (South Shetland Islands), was our model ecosystem, as the turbidity presented a natural gradient of habitat and resource availability. Specifically, we focussed on 2 questions: (1) Do ontogenetic diet shifts occur in Antarctic sea stars, and if so, what drives them? We hypothesised that such shifts existed as a result of an increase in body size, as well as an increase in the size of feeding structures. Moreover, we hypothesised that the feeding guild and behaviour of the different sea star species could impact the importance of ontogenetic diet shifts. (2) Can small-scale habitat variations influence trophic interactions between sea stars through resource availability and diversity? We hypothesised that in areas with lower food availability, sea stars would constrict their trophic niche and decrease their trophic niche over-

lap. This study aimed to explore how ontogenetic niche shifts and trophic plasticity could shape Antarctic sea star feeding ecology, influence their role in coastal food webs, and help them cope with their rapidly changing environments.

2. MATERIALS AND METHODS

2.1. Study site

The Ezcurra Inlet is part of Admiralty Bay, King George Island (South Shetland Islands, ca. $62^{\circ} 10' \text{ S}$, $58^{\circ} 33' \text{ W}$; Fig. 1). The Ezcurra Inlet is a fjord with tide-water glaciers in its inner parts (Braun & Gossmann 2002). Inflows of glacial meltwater from glaciers lead to decreases in salinity, temperature, and dissolved organic matter content and increases in pH, dissolved oxygen content, and inputs of inorganic terrestrial matter in surface waters in the vicinity of glaciers (Szafranski & Lipski 1982, Jonasz 1983, Osińska et al. 2021). These surface waters are transported out of the fjord by wind-generated currents (Pruszek 1980), resulting in suspended inorganic matter concentration, and thus turbidity, decreasing from the inner to the outer fjord (Pęcherzewski 1980b). Diatom blooms in summer are prevented by katabatic winds and turbidity but may occur if weak winds allow inflow of oceanic water into Admiralty Bay (Wasiłowska et al. 2015). Low cell numbers, with a significant contribution of benthic and periphyton species and occasional occurrence of freshwater diatoms provided by terrestrial runoff, were observed in Ezcurra Inlet but limited

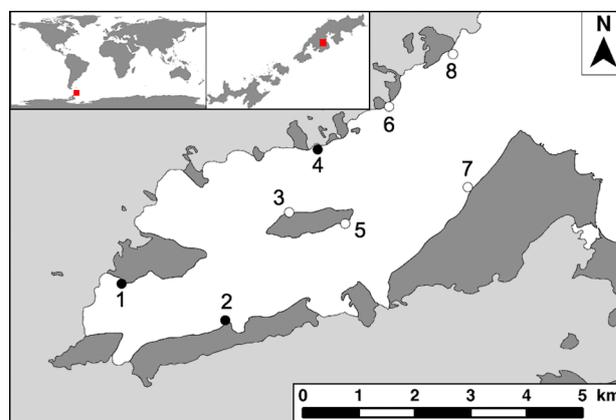


Fig. 1. Location of sampling stations in the Ezcurra Inlet, South Shetland Islands. Sampling stations with sufficient ($n \geq 5$) sample numbers of both *Diplasterias brandti* and/or *Odontaster validus* are shown as open circles; other stations are represented by filled circles. Ice-covered (light grey) and ice-free (dark grey) landmasses are also depicted

changes of phytoplankton abundance, chlorophyll concentration, and particulate organic carbon were recorded from the inner to the outer fjords (Pęcherzewski 1980a, Ligowski 1986, Rakusa-Suszczewski 1995, Wasilowska et al. 2015). However, concentration of dissolved organic carbon increased from the inner to the outer fjords (Pęcherzewski 1980a). The benthos characteristics are impacted by turbidity and differ between the inner and outer fjords. The innermost areas are characterised by bottom sediments made up of silt, clay, and mud (Rodrigues et al. 2010, Berbel & Braga 2014), a poorly diversified benthic fauna with low biomass dominated by polychaetes (Pabis et al. 2011, Siciński et al. 2011), and an absence of benthic vegetation (Zieliński 1990). By contrast, the outer fjord is characterised by coarser sediment (Rodrigues et al. 2010, Berbel & Braga 2014) and higher zoobenthic diversity and biomass, with suspension feeders being a main component of the benthos (Pabis et al. 2011, Siciński et al. 2011, Krzeminska & Kuklinski 2018) and a macroalgae community in shallow areas (Zieliński 1990).

2.2. Sampling and sample preparation

Sea stars were collected ($n = 286$, 8 species, Table 1) by scuba divers from 6 to 23 December 2010, at 8 stations in Ezcurra Inlet, at depths ranging between 6 and 30 m (Fig. 1). Sampled sea stars were fixed with 4% formaldehyde and then stored in 90% ethanol. Laboratory work started in 2017. Sea stars were identified to the species level. For each individual sea star, the arm length (distance from the mouth to the tip of the longest arm) and disc radius (distance from the mouth to the interradial margin, i.e. the point separating 2 arms) were recorded, and, depending on the sea star size, one or several arms were separated from the central disc to obtain enough material for stable isotope analyses. Internal organs and podia were removed from each arm. The arms were then washed with distilled water and oven dried at 50°C for 48 h. All samples were then homogenised into powder using a mixer mill (MM301, Retsch).

2.3. Stable isotope analysis

Carbonates in the endoskeleton are more enriched in ^{13}C than other tissue components, and their composition is not directly related to diet (DeNiro & Epstein 1978). Consequently, subsamples were exposed to 37% hydrochloric acid (HCl) vapour for 48 h to

remove carbonates (Hedges & Stern 1984). The presence of remaining carbonates was tested with 'Champagne tests' (Jaschinski et al. 2008). Namely, a small amount of the acidified sample was dropped in HCl. No effervescence resulting from the reaction of carbonates with HCl was observed, indicating sufficient carbonate removal. Acidified subsamples were then kept at 60°C until further sample preparation. They were then precisely weighed (ca. 2.5–3 mg) in 5×8 mm tin cups with ca. 3 mg of tungsten trioxide and analysed with an elemental analyser (vario MICRO Cube, Elementar) coupled to a continuous-flow isotope-ratio mass spectrometer (IsoPrime100, Elementar). Stable isotope ratios of carbon, nitrogen, and sulphur were expressed in δ notation ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$) and in ‰ values relative to international references (Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$, N_2 in atmospheric air for $\delta^{15}\text{N}$, and Canyon Diablo troilites for $\delta^{34}\text{S}$) according to the following formula:

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

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 $(X/x)_{\text{sample}}$ and $(X/x)_{\text{standard}}$ are the ratios of both stable isotopes in the sample and the standard, respectively.

Certified reference materials from the International Atomic Energy Agency (IAEA, Vienna, Austria), IAEA N-1 (ammonium sulphate; $\delta^{15}\text{N} = 0.4 \pm 0.2\text{‰}$), IAEA C-6 (sucrose; $\delta^{13}\text{C} = -10.8 \pm 0.5\text{‰}$), and IAEA S-1 (silver sulphide; $\delta^{34}\text{S} = -0.3\text{‰}$) were used as primary standards. Secondary standards included sulphanilic acid (Sigma-Aldrich; $\delta^{13}\text{C} = -25.6 \pm 0.4\text{‰}$; $\delta^{15}\text{N} = -0.1 \pm 0.4\text{‰}$; $\delta^{34}\text{S} = 5.9 \pm 0.5\text{‰}$; means \pm SD) and 2 sea stars sampled for other research work ($\delta^{13}\text{C} = -21.2 \pm 0.2\text{‰}$, $\delta^{15}\text{N} = 15.1 \pm 0.3\text{‰}$, $\delta^{34}\text{S} = 18.2 \pm 0.5\text{‰}$ for the first sample; $\delta^{13}\text{C} = -15.1 \pm 0.3\text{‰}$, $\delta^{15}\text{N} = 12.2 \pm 0.2\text{‰}$, $\delta^{34}\text{S} = 15.5 \pm 0.4\text{‰}$ for the second sample).

Preservation in formaldehyde and ethanol may induce alterations in stable isotope values that need to be corrected before data analysis. These impacts are both taxon (Le Bourg et al. 2020) and tissue specific (Sweeting et al. 2004). To date, no studies on the impact of preservation on stable isotope values in tissues of Antarctic sea stars have been conducted. Consequently, we corrected stable isotope values using the results of an experiment on the impact of preservation on stable isotope values of the temperate sea star *Marthasterias glacialis* (Le Bourg et al. 2020), as it is the most closely related taxon to the Antarctic sea stars and because stable isotope values were analysed in the tegument in this experiment as

Table 1. Sea star species, number of individuals collected, ranges of the arm length and disc radius, and mean \pm SD values of carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and sulphur stable isotope values ($\delta^{34}\text{S}$) at each station in the Ezcurra Inlet. NA: not available. Empty cells indicate that sea stars of a given species were not found in a given station. For station locations, see Fig. 1

		1	2	3	4	5	6	7	8	All stations	
<i>Bathybiaster loripes</i>	n	8	3		1					12	
	Range arm length (cm)	5.3–8.1	5.4–6.6		8.4						5.3–8.4
	Range disc radius (cm)	1.4–1.9	1.3–1.6		2.1						1.3–2.1
	$\delta^{13}\text{C}$ (‰)	-15.2 ± 1.0	-16.5 ± 1.3		-14.4						-15.5 ± 1.2
	$\delta^{15}\text{N}$ (‰)	11.7 ± 0.6	11.2 ± 1.4		11.5						11.6 ± 0.8
	$\delta^{34}\text{S}$ (‰)	15.8 ± 0.9	17.0 ± 0.6		15.2					16.0 ± 1.0	
<i>Diplasterias brandtii</i>	n			16	21	6	11	30	18	102	
	Range arm length (cm)			0.7–10.5	1.2–10.8	1.4–8.0	1.1–8.7	0.9–12.8	0.7–5.7		0.7–12.8
	Range disc radius (cm)			0.1–1.4	0.1–0.8	0.1–1.6	0.1–1.2	0.1–1.4	0.1–0.9		0.1–1.6
	$\delta^{13}\text{C}$ (‰)			-15.1 ± 1.2	-15.4 ± 0.8	-15.5 ± 1.5	-17.5 ± 1.7	-17.8 ± 1.3	-17.4 ± 1.4		-16.6 ± 1.7
	$\delta^{15}\text{N}$ (‰)			9.0 ± 0.5	9.3 ± 0.4	8.9 ± 0.5	9.3 ± 0.4	9.4 ± 0.5	9.0 ± 0.6		9.2 ± 0.5
	$\delta^{34}\text{S}$ (‰)			17.3 ± 0.8	17.4 ± 0.8	17.4 ± 0.8	17.1 ± 0.6	17.3 ± 0.6	17.0 ± 0.9		17.2 ± 0.7
<i>Labidiaster annulatus</i>	n							2		2	
	Range arm length (cm)							NA–21.2		NA–21.2	
	Range disc radius (cm)							NA–2.9		NA–2.9	
	$\delta^{13}\text{C}$ (‰)							-21.1 ± 2.4		-21.1 ± 2.4	
	$\delta^{15}\text{N}$ (‰)							12.3 ± 1.6		12.3 ± 1.6	
	$\delta^{34}\text{S}$ (‰)						17.3 ± 0.8			17.3 ± 0.8	
<i>Notasterias bongraini</i>	n		1			1	6	13		21	
	Range arm length (cm)		10.2			8.9	5.1–6.8	1.2–8.1		1.2–10.2	
	Range disc radius (cm)		1.9			0.9	0.6–1.0	0.2–1.2		0.2–1.9	
	$\delta^{13}\text{C}$ (‰)		-22.1			-22.8	-22.6 ± 0.5	-23.3 ± 1.1		-23.0 ± 1.0	
	$\delta^{15}\text{N}$ (‰)		8.4			6.6	6.8 ± 0.4	7.3 ± 0.6		7.1 ± 0.6	
	$\delta^{34}\text{S}$ (‰)		18.9			16.4	18.0 ± 0.5	17.8 ± 1.2		17.8 ± 1.0	
<i>Odontaster meridionalis</i>	n					2				2	
	Range arm length (cm)					2.1–3.6				2.1–3.6	
	Range disc radius (cm)					0.9–1.4				0.9–1.4	
	$\delta^{13}\text{C}$ (‰)					-21.1 ± 1.5				-21.1 ± 1.5	
	$\delta^{15}\text{N}$ (‰)					9.5 ± 1.2				9.5 ± 1.2	
	$\delta^{34}\text{S}$ (‰)					18.6 ± 1.8				18.6 ± 1.8	
<i>Odontaster validus</i>	n		3	19	1	11	9	62	24	129	
	Range arm length (cm)		2.7–3.6	0.8–3.9	1.2	1.2–4.3	1.4–2.7	0.3–3.9	0.8–4.6	0.3–4.6	
	Range disc radius (cm)		1.1–1.7	0.2–1.7	0.4	0.4–1.8	0.6–1.4	0.1–1.9	0.2–1.6	0.1–1.9	
	$\delta^{13}\text{C}$ (‰)		-14.4 ± 1.0	-17.0 ± 0.9	-20.5	-17.1 ± 1.0	-16.1 ± 2.0	-18.3 ± 1.7	-17.3 ± 1.9		-17.6 ± 1.8
	$\delta^{15}\text{N}$ (‰)		10.6 ± 0.9	9.0 ± 0.4	8.2	9.1 ± 0.5	8.8 ± 0.7	9.4 ± 0.7	9.3 ± 0.7		9.3 ± 0.7
	$\delta^{34}\text{S}$ (‰)		17.6 ± 0.6	17.7 ± 0.8	16.3	18.1 ± 0.6	17.2 ± 0.8	17.4 ± 1.2	17.3 ± 1.3	17.5 ± 1.1	
<i>Perknaster sladeni</i>	n						2		15	17	
	Range arm length (cm)						1.1–7.5		0.6–3.9	0.6–7.5	
	Range disc radius (cm)						0.3–1.9		0.1–1.2	0.1–1.9	
	$\delta^{13}\text{C}$ (‰)						-19.3 ± 3.6		-18.6 ± 1.5	-18.7 ± 1.7	
	$\delta^{15}\text{N}$ (‰)						9.4 ± 1.1		9.2 ± 1.4	9.2 ± 1.3	
	$\delta^{34}\text{S}$ (‰)						17.8 ± 0.8		17.1 ± 1.4	17.2 ± 1.4	
<i>Psilaster charcoti</i>	n				1					1	
	Range arm length (cm)				7.0					7.0	
	Range disc radius (cm)				1.7					1.7	
	$\delta^{13}\text{C}$ (‰)				-17.7						-17.6
	$\delta^{15}\text{N}$ (‰)				10.5						10.5
	$\delta^{34}\text{S}$ (‰)				16.8					16.8	
All species	n	8	7	35	24	20	28	107	57	286	
	Range arm length (cm)	5.3–8.1	2.7–10.2	0.7–10.5	1.2–10.8	1.2–8.9	1.1–8.7	0.3–21.2	0.6–5.7		NA–21.2
	Range disc radius (cm)	1.4–1.9	1.1–1.9	0.1–1.7	0.1–2.1	0.1–1.8	0.1–1.9	0.1–2.9	0.1–1.6		0.1–2.9
	$\delta^{13}\text{C}$ (‰)	-15.2 ± 1.0	-16.4 ± 2.9	-16.2 ± 1.4	-15.6 ± 1.3	-16.9 ± 2.0	-18.2 ± 3.0	-18.8 ± 2.3	-17.6 ± 1.7		-17.7 ± 2.4
	$\delta^{15}\text{N}$ (‰)	11.7 ± 0.6	10.5 ± 1.4	9.0 ± 0.5	9.3 ± 0.7	8.9 ± 0.7	8.6 ± 1.1	9.1 ± 1.0	9.2 ± 0.9		9.2 ± 1.1
	$\delta^{34}\text{S}$ (‰)	15.8 ± 0.9	17.5 ± 0.8	17.5 ± 0.8	17.2 ± 1.0	17.8 ± 0.8	17.4 ± 0.7	17.4 ± 1.0	17.1 ± 1.2		17.3 ± 1.0

in our current study. Furthermore, this study investigated the long-term impact (2 yr) of preservation on stable isotope values and reported that stable isotope values remained stable following the initial change after 1 mo (formaldehyde) and 9 mo (ethanol) of preservation. Consequently, we considered it unlikely that stable isotope values would be further altered after 7 yr of preservation (this study). 0.2‰

was added to $\delta^{13}\text{C}$ values to account for the effects of both formaldehyde (+0.8‰) and ethanol (−0.6‰), while 1.5‰ was added to $\delta^{34}\text{S}$ values to account for the effects of formaldehyde. By contrast, no correction factors were added to $\delta^{15}\text{N}$ values, as no significant impact of formaldehyde and ethanol on $\delta^{15}\text{N}$ values were observed in the tegument of *M. glacialis* (Le Bourg et al. 2020).

2.4. Data analysis

All data analyses were performed using R 3.6.0 (R Core Team 2017).

The species *Labidiaster annulatus*, *Odontaster meridionalis*, and *Psilaster charcoti* were discarded from statistical analyses due to their low numbers (Table 1).

The influences of the species, sampling station, and the 2 covariates (disc radius and arm length) on $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ values were assessed using type III analyses of covariance (ANCOVA). First-order interactions between the factor species and the 2 covariates were included in the models. Non-significant interactions were progressively removed from the models, and post-hoc Scheffé analyses were performed on the station factor. These analyses were conducted only on *Diplasterias brandti* and *O. validus* and at stations where sufficient numbers ($n \geq 5$) of both species were available (i.e. Stns 3, 5, 6, 7, and 8), as the other species were unevenly sampled across Ezcurra Inlet. More specifically, *Bathyiaster loripes* was sampled in inner Stns 1, 2, and 4, while *Notasterias bongraini* was mostly sampled in outer Stns 6 and 7, and *Perknaster sladeni* was mostly sampled in outer Stn 8 (Table 1, Fig. 1).

The relationships between stable isotope values and disc radius and arm length were further assessed for both *D. brandti* and/or *O. validus*, as well as for *B. loripes*, *N. bongraini*, and *P. sladeni* with Pearson's correlation coefficients. This analysis was conducted using data from all sampling stations. However, significant differences in stable isotope values between the sampling stations exclude the possibility of pooling stations to study the relationship between stable isotope values and size variables. Pooling the sampling stations with different mean stable isotope and size values results in an increase in variability and thus an underestimation of the correlation between stable isotope values and size variables (see Supplement 1 at www.int-res.com/articles/suppl/m674p189_suppl1.pdf). The effect of the sampling station on stable isotope values and covariates was preliminarily corrected for each species separately. Consequently, for each species, the stable isotope values and the covariates were mean corrected for each station according to the following formula:

$$\text{cor}X_{ijk} = X_{ijk} - (\bar{X}_{jk} - \bar{X}_j) \quad (2)$$

where X_{ijk} is the value of the variable X for the individual i belonging to species j at station k . \bar{X}_{jk} is the mean of the variable X for all individuals i of species j at station k . \bar{X}_j is the mean of the variable X for all

individuals i of species j . Further details are provided in Supplement 1. Pearson's correlation coefficients between the mean-corrected variables were then computed for each species.

For *D. brandti* and *O. validus* and at each station where both species were sufficiently sampled ($n \geq 5$), the size of the isotopic niche was estimated using the methodology of Skinner et al. (2019) by estimating the volumes of the standard ellipsoids generated with $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ values for each species at each station. We computed the sample size corrected standard ellipsoid volume (SEV_C) and used a Bayesian approach to estimate the standard ellipsoid volume (SEV), based on 10^5 successive iterations (SEV_B), to quantify uncertainty in SEV estimates. Relative ellipsoid overlaps between *D. brandti* and *O. validus* were also computed for each station with a Bayesian approach as a measure of isotopic niche partitioning between both species. To do so, ellipsoids were approximated in 3-dimensional meshes for each iteration. The intersection between the meshes of both species were then approximated into a third mesh, which was the overlapping volume between the 2 previous meshes. At each station, the ratio between the overlapping volume and the ellipsoid volume (i.e. Overlap_B) for a given species indicates which proportion of its isotopic niche is covered by the other species. R functions for estimating SEV_C , SEV_B , and Overlap_B are provided in Skinner et al. (2019).

Pairwise comparisons of SEV_B and Overlap_B between species for each station and between stations for each species were performed by calculating the percentage of the estimated SEV that differed between each pair of standard ellipses. This percentage (P) indicates the probability that a given standard ellipse has a larger or smaller SEV or overlap than another. If P was lower than 5% or exceeded 95%, the probability that 2 ellipses had different SEV or overlap values was higher than 95%. In that case, the differences between the compared SEVs or overlaps were considered meaningful. A P higher than 50% was transformed into $(1 - P)$. The 'orderPvalue' function in the 'agricolae' package in R (de Mendiburu 2020) was used to order the P and $(1 - P)$ values according to the SEV_B or Overlap_B modes and sort ellipses in groups of ellipses with a similar SEV_B or Overlap_B .

3. RESULTS

The ANCOVA results indicated that $\delta^{13}\text{C}$ values were higher in *Diplasterias brandti* ($-17.0 \pm 1.7\%$

[SD]) than in *Odontaster validus* ($-17.6 \pm 1.8\%$, $F_{1,190} = 19.411$, $p < 0.001$). For both species, $\delta^{13}\text{C}$ values also differed between sampling stations ($F_{4,190} = 3.635$, $p = 0.007$) and tended to decrease from the inner to the outer Ezcurra Inlet. Post hoc analysis highlighted 4 groups of stations with similar $\delta^{13}\text{C}$ values. The first group contained inner Stn 3 with the highest $\delta^{13}\text{C}$ values ($-16.2 \pm 1.4\%$, Fig. 1). The second group contained Stns 5 ($-16.5 \pm 1.4\%$) and 6 ($-16.8 \pm 1.9\%$) and had intermediate $\delta^{13}\text{C}$ values between inner Stn 3 and outer Stn 8 ($-17.3 \pm 1.7\%$). The last group contained a southern outer station, Stn 7, which had the lowest $\delta^{13}\text{C}$ values ($-18.1 \pm 1.6\%$). Furthermore, $\delta^{13}\text{C}$ values were influenced more by the disc radius ($F_{1,190} = 28.960$, $p < 0.001$) than by arm length ($F_{1,190} = 5.970$, $p = 0.015$). Moreover, the interaction of the station with the disc radius ($F_{4,190} = 4.965$, $p < 0.001$) and arm length ($F_{4,190} = 4.192$, $p = 0.003$) influenced $\delta^{13}\text{C}$ values. When analysing relationships between $\delta^{13}\text{C}$ values and size variables in 5 species, $\delta^{13}\text{C}$ values appeared to be linked with disc radius and arm length in most species but higher slopes were observed for disc radius than for arm length (Table 2). *D. brandti* and *O. validus* had similar $\delta^{15}\text{N}$ values ($F_{1,198} = 0.229$, $p = 0.633$), and $\delta^{15}\text{N}$ values differed between sampling stations ($F_{4,198} = 3.336$, $p = 0.011$). Nevertheless, the spatial gradient of $\delta^{15}\text{N}$ values was less pronounced than for $\delta^{13}\text{C}$ values. The post hoc analysis highlighted 3 groups of stations, with inner Stn 3 having the lowest $\delta^{15}\text{N}$ values ($9.0 \pm 0.5\%$) and outer Stn 7 having the highest $\delta^{15}\text{N}$

values ($9.4 \pm 0.7\%$; Table 1, Fig. 1), while other stations displayed intermediate values. The disc radius also influenced $\delta^{15}\text{N}$ values ($F_{1,198} = 9.348$, $p = 0.003$). Station-corrected $\delta^{15}\text{N}$ values increased with the station-corrected disc radius for *Bathybiaster loripes* ($2.5\% \text{ cm}^{-1}$), *D. brandti* ($0.7\% \text{ cm}^{-1}$), and *O. validus* ($0.7\% \text{ cm}^{-1}$), but no relationship was found for *Notasterias bongraini* or *Perknaster sladeni* (Table 2a).

$\delta^{34}\text{S}$ values were lower in *D. brandti* ($17.2 \pm 0.7\%$) than in *O. validus* ($17.5 \pm 1.1\%$, $F_{1,193} = 6.835$, $p = 0.010$). Sampling station had no effect on $\delta^{34}\text{S}$ values ($F_{4,193} = 1.770$, $p = 0.136$), whereas arm length had a significant effect on $\delta^{34}\text{S}$ values ($F_{1,193} = 4.989$, $p = 0.027$), and the correlation tests between station-corrected $\delta^{34}\text{S}$ values and station-corrected arm length were significant for *D. brandti* ($0.1\% \text{ cm}^{-1}$) and *N. bongraini* ($0.3\% \text{ cm}^{-1}$; Table 2b).

Estimation of SEV_B showed that the isotopic niches of *O. validus* were larger at 3 outer stations (6, 7, and 8) than at 2 inner stations (3 and 5) and that these outer niches were larger than those of *D. brandti*, which had the same volume from the inner to the outer Ezcurra Inlet (Figs. 2 & 3a). Isotopic niche overlap varied between stations. The overlap was low at inner Stns 3, 5, and 6 but high at outer Stns 7 and 8 (Figs. 2 & 3b). *D. brandti* had ca. 72 and ca. 88 % of its isotopic niche covered by that of *O. validus* at Stns 7 and 8, respectively. *O. validus* had ca. 25 % of its isotopic niche covered by that of *D. brandti* at Stns 7 and 8.

Table 2. Relationships (Pearson's correlation coefficients and p-values; slopes and intercepts were also computed for significant results) between (a) station-corrected disc radius and stable isotope values and (b) station-corrected arm length and stable isotope values for 5 sea star species in the Ezcurra Inlet

a	n	Disc radius— $\delta^{13}\text{C}$				Disc radius— $\delta^{15}\text{N}$				Disc radius— $\delta^{34}\text{S}$			
		r	p	Slope	Intercept	r	p	Slope	Intercept	r	p	Slope	Intercept
<i>Bathybiaster loripes</i>	12	-0.008	0.981			0.612	0.035	2.52	7.5	0.084	0.796		
<i>Diplasterias brandti</i>	102	0.288	0.003	1.08	-17.2	0.442	<0.001	0.68	8.8	0.252	0.013	0.55	16.9
<i>Notasterias bongraini</i>	21	-0.415	0.061			-0.264	0.248			-0.175	0.461		
<i>Odontaster validus</i>	129	0.424	<0.001	1.73	-19.2	0.419	<0.001	0.70	8.6	-0.007	0.938		
<i>Perknaster sladeni</i>	17	-0.795	<0.001	-3.44	-17.4	-0.213	0.411			0.238	0.393		
b	n	Arm length— $\delta^{13}\text{C}$				Arm length— $\delta^{15}\text{N}$				Arm length— $\delta^{34}\text{S}$			
		r	p	Slope	Intercept	r	p	Slope	Intercept	r	p	Slope	Intercept
<i>Bathybiaster loripes</i>	12	-0.023	0.945			0.511	0.089			0.409	0.187		
<i>Diplasterias brandti</i>	102	0.229	0.021	0.11	-17.2	0.484	<0.001	0.10	8.7	0.368	<0.001	0.11	16.7
<i>Notasterias bongraini</i>	21	-0.670	0.001	-0.45	-20.3	-0.403	0.070			0.447	0.048	0.33	15.9
<i>Odontaster validus</i>	129	0.387	<0.001	0.72	-19.3	0.372	<0.001	0.28	8.6	-0.015	0.867		
<i>Perknaster sladeni</i>	17	-0.727	0.001	-0.87	-17.3	-0.138	0.598			0.294	0.287		

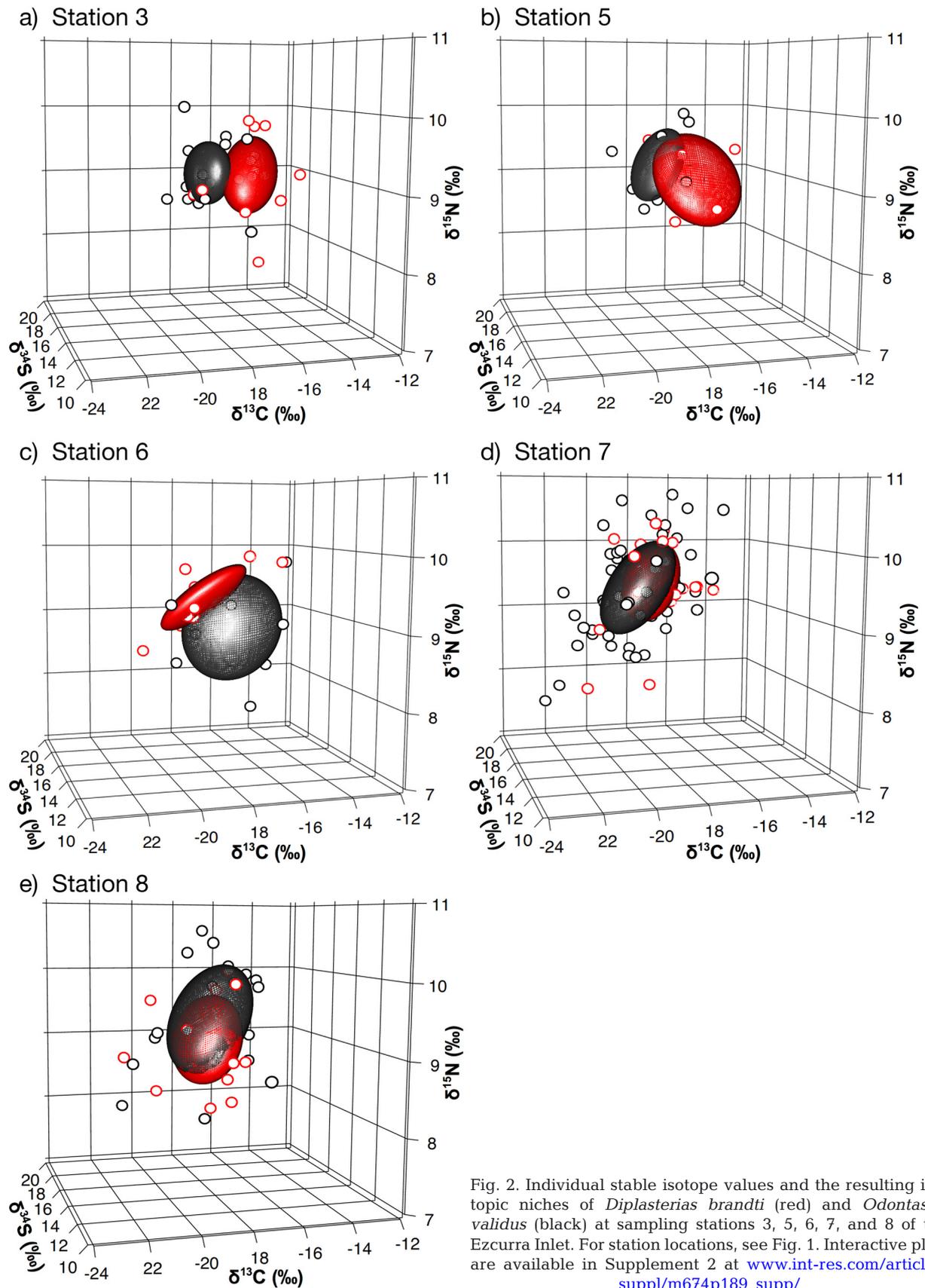


Fig. 2. Individual stable isotope values and the resulting isotopic niches of *Diplasterias brandti* (red) and *Odontaster validus* (black) at sampling stations 3, 5, 6, 7, and 8 of the Ezcurra Inlet. For station locations, see Fig. 1. Interactive plots are available in Supplement 2 at www.int-res.com/articles/suppl/m674p189_supp/

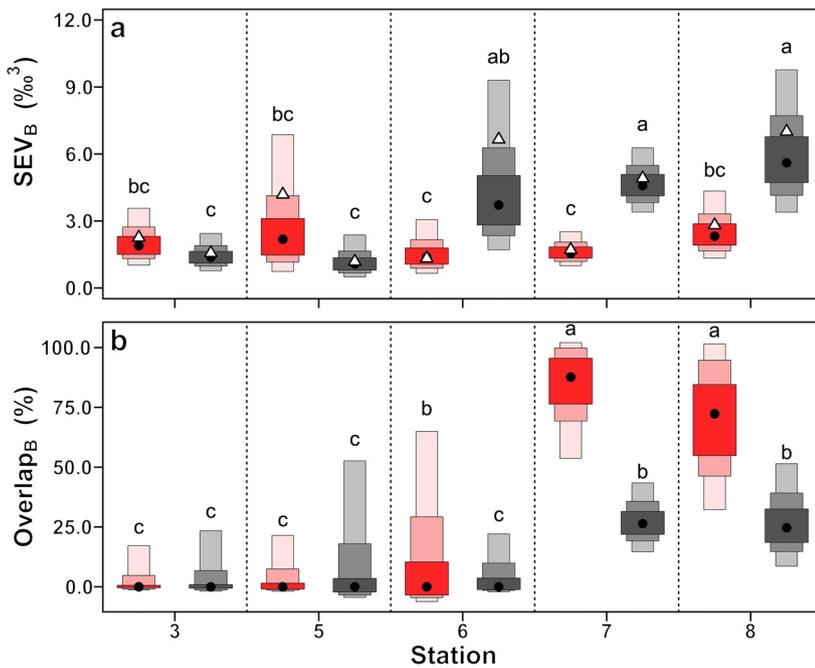


Fig. 3. Density plots depicting the Bayesian estimation of the standard ellipsoid (a) volumes (SEV_B) and (b) overlap for *Diplasterias brandtii* (red) and *Odontaster validus* (black) at sampling stations 3, 5, 6, 7, and 8 in the Ezcurra Inlet. Black dots are the modes. Shaded boxes represent the 50, 75, and 95% confidence intervals. White triangles are standard ellipsoid volumes corrected for sample size (SEV_C). Letters over density boxes are groups of ellipsoids with similar SEV_B and overlap. For station locations, see Fig. 1

4. DISCUSSION

4.1. Size-related variations of the trophic ecology of sea stars: importance of species identity

Stable isotope compositions of sea stars were influenced by their size, with disc radius influencing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and arm length influencing $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values. However, the disc radius may have more influence on $\delta^{13}\text{C}$ values than the arm length, as a 5-fold higher F -value was computed for the disc radius than for the arm length in ANCOVA. Similarly, the relationship between $\delta^{15}\text{N}$ values and the disc radius is highly informative and could be explained by the importance of the disc function in sea star feeding. Indeed, except for species from the order Paxillostida, such as *Bathybiaster loripes*, sea stars evert their stomach to feed but never beyond the edges of their disc to prevent damage. A larger disc may therefore allow sea stars to extend their stomach over a larger area, resulting in the capacity to feed on larger prey, or on larger surfaces when consuming biofilms or encrusting organisms (Lawrence 2012). Consequently, increasing disc size likely improves the ability of sea

stars to handle larger prey throughout growth, resulting in the consumption of small prey by smaller sea stars and the consumption of larger (Baeta & Ramón 2013, Fernandez et al. 2017) and/or more carnivorous (Himmelman & Dutil 1991) prey by larger individuals. Finally, the $\delta^{34}\text{S}$ values correlated with arm length in *Diplasterias brandtii* but not in *Odontaster validus* despite the ANCOVA results highlighting the relationship between arm length and $\delta^{34}\text{S}$ values. Consequently, the relationship between stable isotope values and arm length is likely less informative than the relationship with the disc radius. $\delta^{34}\text{S}$ are usually used in studies on marine food webs to refine the discrimination between primary producers or between benthic and pelagic sources (Fry et al. 1982, Machás & Santos 1999, Connolly et al. 2004), as pelagic sulphates with high $\delta^{34}\text{S}$ values are the main source of inorganic sulphur for both phytoplankton and phytobenthos at the baseline of food webs (Giordano & Raven 2014), whereas sulphides with low $\delta^{34}\text{S}$ values are present in sediment as

a result of the activity of sulphate-reducing bacteria (Fry et al. 1982). Consequently, limited ontogenetic shifts of $\delta^{34}\text{S}$ values may indicate limited changes in feeding habitat.

Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values increased with disc radius in *D. brandtii* and *O. validus*. *O. validus* is a highly generalist feeder that consumes prey of diverse sizes, ranging from diatoms to other echinoderms, and also scavenges on carrion (Pearse 1965, Dayton et al. 1974, Brueggeman 1998). A similar generalist behaviour may be expected for *D. brandtii*, as its congener *D. brucei* appears to feed on various prey from microorganisms (Michel et al. 2019) to macroorganisms (Dayton et al. 1974, Rauschert 1991). The increasing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with disc radius for these species may indicate the progressive replacement of small prey with low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values by larger (Baeta & Ramón 2013, Fernandez et al. 2017) and/or more carnivorous (Himmelman & Dutil 1991) benthic prey in the diet during growth. Lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in smaller prey could result from smaller prey usually occupying lower trophic levels in communities (Potapov et al. 2019) but also from these prey being growing juvenile

organisms with low trophic enrichment factors. Indeed, trophic enrichment factors tend to be negatively linked to growth rates (Lefebvre & Dubois 2016). Faster turnover in juveniles investing resources into growth than in adults investing into maintenance may explain this pattern. Small trophic enrichment factors should also be expected in juvenile sea stars themselves and could further contribute to their low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Finally, consumption by juveniles of pelagic diatoms sinking to the bottom, as suggested by the observation of diatoms in the stomach content of *O. validus* (Pearse 1965), could further contribute to their low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. By contrast, adults would have high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values due to the larger trophic enrichment factors in their tissues and/or due to the consumption of large adult organisms also having high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values thanks to their larger trophic level and the higher trophic enrichment factor in their tissues.

In other species with less generalist diets, or in non-predators, disc size was less frequently linked to their isotopic composition, suggesting that ontogenetic diet shifts are less marked for these species. *Notasterias bongraini* may feed on plankton or suspension feeding organisms throughout its life, as suggested by its large dorsal pedicellariae (Koehler 1911, Fisher 1940), which play a role in capturing planktonic prey (Emson & Young 1994). Its congener *N. armata* was also observed feeding on bivalves (Dearborn 1977, Brueggeman 1998). Similarly, *Perknaster sladeni* may have a spongivore diet both as a juvenile and an adult, similar to its congener *P. fuscus* (Dayton et al. 1974).

Nevertheless, $\delta^{15}\text{N}$ values increased with disc radius for *B. loripes*. This species likely feeds on sediment, as suggested by the observation of mud in its stomach (Dearborn 1977) and its low $\delta^{34}\text{S}$ values (influenced by sediment sulphides). The increasing $\delta^{15}\text{N}$ values in *B. loripes* could indicate that this species exhibits a more predatory behaviour by consuming larger prey buried in sediment while growing. Alternatively, larger individuals could gain access to more degraded organic matter, displaying higher $\delta^{15}\text{N}$ values, as bacterial degradation and fractionation may induce high $\delta^{15}\text{N}$ values in residual organic matter (Saino & Hattori 1980, Wada 1980, Mintenbeck et al. 2007).

4.2. Spatial variations in the trophic ecology of sea stars and their link to habitat characteristics

The trophic ecology of sea stars varied spatially in the Ezcurra Inlet. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values differed

among sampling stations, with $\delta^{13}\text{C}$ values decreasing from the inner to the outer stations and $\delta^{15}\text{N}$ values differing between the innermost station and one of the outermost stations, while other stations had intermediate $\delta^{15}\text{N}$ values. The pattern of decreasing $\delta^{13}\text{C}$ values from the inner to the outer Ezcurra Inlet was also observed in the organic carbon from surface sediment (Deflandre et al. 2013). A similar pattern was observed in Kongsfjorden, an Arctic fjord in Svalbard, where it was hypothesised that sedimentary organic matter derived from benthic meiofauna and ^{13}C -enriched diatoms in the inner fjord and from plankton in the outer fjord (Bourgeois et al. 2016). Higher importance of matter of terrestrial origin and freshwater diatoms provided by glacier meltwater in inner stations versus autochthonous production in outer stations (Pęcherzewski 1980b, Jonasz 1983, Ligowski 1986) may also help explain this pattern.

Fjords, including the Ezcurra Inlet, are characterised by turbidity gradients (Pęcherzewski 1980b, Munoz & Wellner 2016, Meslard et al. 2018) because of sediment discharge by melting glaciers in their inner basins. This results in gradients of primary production (Zieliński 1990, Hoffmann et al. 2019, Holding et al. 2019) and benthos characteristics (Włodarska-Kowalczyk et al. 2005, Pabis et al. 2011, Sahade et al. 2015), which induce changes in ecosystem functions. These differences in community characteristics may result in the presence of different species of sea stars with specific feeding behaviours along the fjord and explains the uneven sampling for several species from this study. For example, *B. loripes* is likely a sediment feeder (Dearborn 1977) and was mostly sampled in the inner stations, while *N. bongraini* and *P. sladeni* may feed on suspension feeders and were sampled in the outer area where this type of prey is more abundant (Pabis et al. 2011, Siciński et al. 2011, Krzeminska & Kuklinski 2018). However, higher turbidity is not necessarily associated with reduced trophic diversity in areas affected by ice disturbance (Pasotti et al. 2015b, Włodarska-Kowalczyk et al. 2019).

D. brandti and *O. validus* appeared to have slightly overlapping isotopic niches in the inner Ezcurra Inlet but largely overlapping isotopic niches in the outer fjord. According to competition and niche overlap theory (Pianka 1974), despite a lower diversity and biomass of resources, higher trophic resource segregation occurred between the 2 species in the inner fjord. We also observed an isotopic niche constriction for *O. validus* in the inner basin.

In the inner area of the Ezcurra Inlet, reduced benthos diversity and biomass resulted from high

turbidity and muddy bottoms (Pabis et al. 2011, Siciński et al. 2011), which would only allow the presence of predators or omnivores that could adapt their diet to low resource availability. The dietary plasticity of *D. brandti* and *O. validus* could allow them to adapt to such environmental conditions, and our observations confirm the prediction based on ecological niche theory. In the outer fjord, higher prey availability could allow the exploitation of the same prey by the 2 species, resulting in diet similarities and overlap.

Nevertheless, dietary plasticity seemed to be species specific. *O. validus* had a larger isotopic niche in the outer fjord than in the inner one. Conversely, the isotopic niche of *D. brandti* did not change much from the inner to the outer section of Ezcurra Inlet despite an increase in prey diversity. *O. validus* is a highly generalist omnivore that feeds on various prey (Pearse 1965, Dayton et al. 1974). Larger isotopic niches would be expected for *O. validus* in the outer Ezcurra Inlet, as enlargement of its isotopic niche is likely due to intraspecific specialisation (i.e. all individuals did not feed exactly on the same items and diverged more in the outer fjord than the inner fjord). Similar niche variation was anticipated for *D. brandti*, as its congener *D. brucei* was also observed feeding on various prey (Dayton et al. 1974, Rauschert 1991, Michel et al. 2019). Nevertheless, its isotopic niche size did not increase in the outer fjord. This could suggest, on the one hand, a more limited trophic plasticity for this species than for *O. validus*. On the other hand, it may indicate that individuals probably feed on more similar prey, resulting in less individual isotopic differences.

4.3. Conclusion and perspectives

Because of climate change, terrestrial glaciers are receding worldwide (Cook et al. 2005, Mernild et al. 2012), including on King George Island (Braun & Gossmann 2002, Rückamp et al. 2011). In fjords, increased glacial melting causes short-term increases in terrestrial runoff and then in turbidity (Sahade et al. 2015), sedimentation rates (Boldt et al. 2013), and mud contribution to the bottom sediment (Munoz & Wellner 2016). Considering the impact of high turbidity on the benthos (Thrush et al. 2004, Donohue & Garcia Molinos 2009), glacier retreat may thus contribute to a short-term reduction of the diversity and abundance of the benthic communities already impacted by turbidity (Sahade et al. 2015). As a result, modifications of the trophic ecology of gener-

alist sea stars such as *O. validus* are expected to occur. Moreover, reduced glacier surface could diminish terrestrial inputs and open new areas for benthic colonisation in the long term, leading to more diverse benthic assemblages (Pasotti et al. 2015a) and subsequent modifications of the trophic ecology of sea stars. The ultimate consequences of these changes for benthic communities will likely be a trade-off between environmental stress (Sahade et al. 2015), opening of new areas for colonisation (Pasotti et al. 2015a) and changes in the metabolic balance of benthic communities, which will influence the carbon balance and food webs (Braeckman et al. 2021). Here, we demonstrated that ontogenetic niche shifts and trophic plasticity drive sea star feeding ecology and that their effects were species specific. Therefore, the 2 mechanisms are likely to influence the way in which these key benthic organisms cope with present and future environment-induced changes in resource availability.

Data availability. Data used in this manuscript are part of the dataset 'Stable isotope ratios of C, N, and S in Southern Ocean sea stars (1985–2017)' (expedition ZA) available at the Global Biodiversity Information Facility (GBIF, <https://doi.org/10.15468/p8gcpe>).

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