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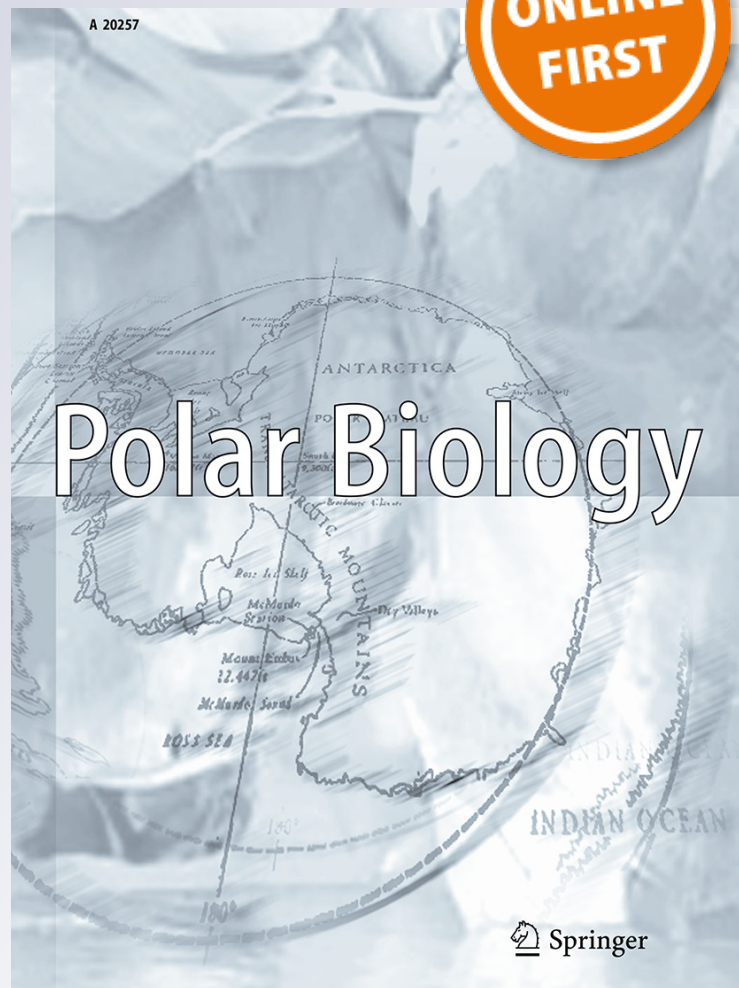
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Trophic plasticity of Antarctic echinoids under contrasted environmental conditions

Loïc N. Michel¹  · Bruno David² · Philippe Dubois³ · Gilles Lepoint¹ · Chantal De Ridder³

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Abstract Echinoids are common members of Antarctic zoobenthos, and different groups can show important trophic diversity. As part of the ANT-XXIX/3 cruise of RV Polarstern, trophic plasticity of sea urchins was studied in three neighbouring regions (Drake Passage, Bransfield Strait and Weddell Sea) featuring several depth-related habitats offering different trophic environments to benthic consumers. Three families with contrasting feeding habits (Cidaridae, Echinidae and Schizasteridae) were studied. Gut content examination and stable isotopes ratios of C and N suggest that each of the studied families showed a different response to variation in environmental and food conditions. Schizasteridae trophic plasticity was low, and these sea urchins were bulk sediment feeders relying on sediment-associated organic matter in all regions and/or depth-related habitats. Cidaridae consumed the most animal-derived material. Their diet varied according to the considered area, as sea urchins from Bransfield Strait relied mostly on living and/or dead animal material, while specimens from Weddell Sea fed on a mixture of dead animal material and other detritus. Echinidae also showed

important trophic plasticity. They fed on various detrital items in Bransfield Strait, and selectivity of ingested material varied across depth-related habitats. In Weddell Sea, stable isotopes revealed that they mostly relied on highly ¹³C-enriched food items, presumably microbially reworked benthic detritus. The differences in adaptive strategies could lead to family-specific responses of Antarctic echinoids to environmental and food-related changes.

Keywords Antarctic · Echinoids · Feeding behaviour · Stable isotopes · Ecological plasticity · Diet shift

Introduction

The capability to make use of various food sources represents an adaptive advantage for polar animals coping with drastic environmental fluctuations induced by seasonality, sea ice cover, etc. Echinoids are recurrent members of benthic communities throughout the Southern Ocean (David et al. 2005; Gutt 2007; Gutt et al. 2013). This ecological “success” is at least partly related to their diverse and versatile feeding habits, made possible by exploitation of epifaunal and infaunal habitats (Saucède et al. 2006). The regular echinoids are epifaunal browsers using the teeth of their Aristotle’s lantern to rasp or bite living sessile organisms or carrions. They are, to some extent, opportunistic, but usually confined to a limited range of food types, some species preferring vegetal or animal food items, some others being true generalists (De Ridder and Lawrence 1982; Lawrence et al. 2013). Diets can vary according to food availability, and feeding plasticity is then observed when seasonal or accidental variations occur in the environment (Lawrence and Sammarco

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1982; Norkko et al. 2007; Hughes et al. 2012). The situation is different for irregular echinoids (usually infaunal) as most of them are microphagous, usually swallowing bulk sediment to feed on the associated particulate organic matter (e.g., De Ridder et al. 1985).

In Antarctic waters, food nature and availability are influenced by sea ice conditions, and omnivore benthic animals can shift their diet accordingly. For instance, in the Ross Sea, the regular sea urchin *Sterechinus neumayeri* can use the detritus pathway when living in permanent sea ice conditions, detritus replacing the fresh algal material ingested by the animals when living in more sea ice-free waters (Norkko et al. 2007). In the Weddell Sea, although displaying distinct diets, Cidaridae and Echinidae ingest sediment together with other food material (Jacob et al. 2003). These observations underline that detritus and sediment are commonly used as food sources by Antarctic regular echinoids. By exploring the shelf from the outer side of the South Shetland Islands to the Northern part of the Antarctic Peninsula, the ANT-XXIX/3 expedition offered the opportunity to collect echinoids in three neighbouring areas following a north–south gradient: (1) a zone found north of South Shetland Islands, in the Drake Passage; (2) the Bransfield Strait; and (3) an area located east of Antarctic Peninsula, in the Weddell Sea. These three regions differ not only in terms of primary productivity and sea ice cover (Bracher and Huntemann 2015; Dorschel et al. 2015; Table 1) but also seafloor topography and currents, which is reflected in benthic community structure and food availability (Glover et al. 2008; Lockhart and Jones 2008). In this context, our aim was to visualize whether and to what extent feeding plasticity occurs among representative taxa of Antarctic echinoids in response to environmental changes (i.e. different sea ice conditions and food availability). Three families exhibiting contrasting feeding habits were investigated: (1) Cidaridae, regular echinoids which prefer animal food items; (2) Echinidae, regular echinoids which are true generalists; and (3) Schizasteridae, irregular echinoids

which feed on sediment. To assess trophic plasticity in the studied echinoids, two complementary methods were applied. First, gut contents were examined to identify the main food items. Second, stable isotope ratios of C and N were analysed. These trophic markers have proven particularly useful to unravel trophic interactions in Antarctic benthic food webs (Nyssen et al. 2002), but also to identify food sources of sympatric regular echinoids from other regions when gut contents look alike (Wangenstein et al. 2011).

Materials and methods

Sampling

Echinoid samples were collected using Agassiz trawls between 10/02 and 12/03/2013, during the PS81 (ANT-XXIX/3) expedition of RV Polarstern. Itinerary, stations list and details on trawling are given in the cruise report (Gutt 2013). According to the bottom topography of the studied regions, five depth-related habitats were considered (Fig. 1): “bank” (all regions, depth 0–250 m), “upper slope” (all regions, depth 250–350 m), “lower slope” (Drake Passage and Bransfield Strait only, depth 350–550 m), “canyon” (Bransfield Strait only, depth 550–800 m) and “deep depression” (Weddell Sea only, depth 350–500 m). Eleven species (4 Cidaridae, 2 Echinidae and 5 Schizasteridae; Table 2) were sampled. After collection, specimens were dissected on board and selected tissues or organs prepared for subsequent analysis.

Gut content observation

Gut contents of 101 specimens (15 Cidaridae, 52 Echinidae and 34 Schizasteridae; Table 2) were examined. For irregular echinoids (Schizasteridae), the observations were made on board, directly after dissection. For regular echinoids (Echinidae and Cidaridae), stomach contents (i.e.

Table 1 Chlorophyll A concentrations (averaged over the last 5 years prior to the cruise) and sea ice cover (averaged over the last 5 years prior to the cruise and over the last 30 days and the actual

Area	[Chlorophyll A] (2008–2012, mg m ⁻³)	Sea ice cover (2008–2012, area%)	Sea ice cover (30 days before sampling, area%)
Drake Passage	0.47–0.52	7–8	0–0
Bransfield Strait	0.23–0.35	27–29	0–0
Weddell Sea	0.67–1.53	54–63	67–94

day when the sampling took place) for each of the sampled areas (data from Bracher and Huntemann 2015)

Fig. 1 Map of the sampled stations. *Red* bank, *orange* upper slope, *yellow* lower slope, *green* canyons, *blue* deep depressions. *Grey line* 200 m isobath. (Color figure online)

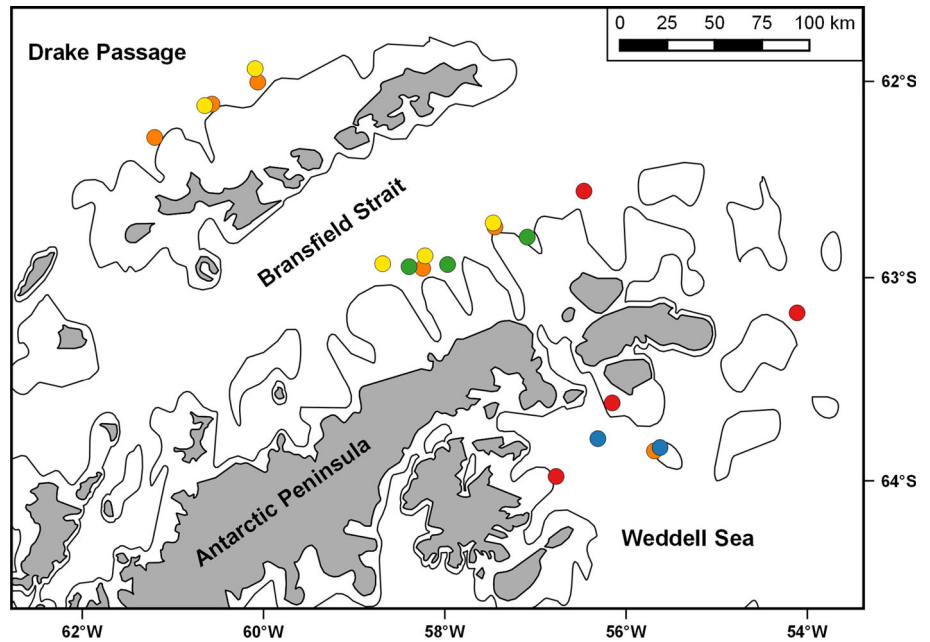


Table 2 Number of specimens (*n*) analysed for gut content examination (GC) and C and N stable isotope ratios (SI)

Area	Habitat	Family	Species	Sample numbers (<i>n</i>)		
				GC	SI	
Drake Passage	Upper slope	Cidaridae	<i>Ctenocidarid gigantea</i>	1	1	
		Schizasteridae	<i>Abatus cavernosus</i>	1	1	
			<i>Amphipneustes similis</i>	3	3	
	Lower slope	Schizasteridae	<i>Amphipneustes rostratus</i>	1	1	
			<i>Amphipneustes similis</i>	1	1	
Bransfield Strait	Upper slope	Cidaridae	<i>Notocidarid gaussiensis</i>	1	2	
			<i>Notocidarid mortenseni</i>	7	7	
		Echinidae	<i>Sterechinid antarcticus</i>	12	12	
			<i>Sterechinid neumayeri</i>	5	5	
	Lower slope	Schizasteridae	<i>Amphipneustes similis</i>	11	11	
		Echinidae	<i>Sterechinid antarcticus</i>	10	10	
		Schizasteridae	<i>Amphipneustes rostratus</i>	1	1	
	Canyon		Schizasteridae	<i>Brachyternaster chesheri</i>	2	2
			Cidaridae	<i>Aporocidarid eltaniana</i>	5	9
			Echinidae	<i>Sterechinid antarcticus</i>	2	3
			<i>Sterechinid neumayeri</i>	3	2	
Weddell Sea	Bank	Schizasteridae	<i>Amphipneustes similis</i>	5	5	
		Cidaridae	<i>Ctenocidarid gigantea</i>	1	4	
		Echinidae	<i>Sterechinid neumayeri</i>	11	16	
	Upper slope	Schizasteridae	<i>Amphipneustes similis</i>	6	6	
		Echinidae	<i>Sterechinid neumayeri</i>	8	8	
	Deep	Echinidae	<i>Sterechinid neumayeri</i>	1	7	
		Schizasteridae	<i>Abatus cavernosus</i>	3	3	
	Total				101	120

material present in the first digestive loop) were kept in 70 % ethanol. These contents were examined through qualitative microscopic observations and food items were

classified into three main categories: (1) pieces of animal preys or carrion resulting from bites (fleshy, usually non-decayed food fragments), (2) detritus (decaying fragments

and particles), and (3) sediment. When possible, food fragments were further identified (phylum or class level).

Stable isotope analysis

A hundred and twenty sea urchins were selected for stable isotope analysis (Table 2). Following recommendations of Mateo et al. (2008), animals were dissected to separate soft, non-metabolically active tissues. Due to differences in echinoids morphology, analyses were performed on the peristome for Echinidae, the stomach caecum for Schizasteridae and the spine muscles for Cidaridae. Echinidae peristomes and Schizasteridae stomach caecum walls consist of a connective tissue sandwiched between two epithelia. Since epithelial and connective tissues are also associated to spine musculature of Cidaridae, the structure of the three sampled organs is comparable. Samples were kept frozen ($-20\text{ }^{\circ}\text{C}$) before further treatments once back from the expedition. They were subsequently oven-dried at $60\text{ }^{\circ}\text{C}$ for 72 h and then ground to a homogeneous powder using mortar and pestle. Inorganic carbon present in samples can be a source of bias in C stable isotope ratio analysis. Preliminary “champagne tests” were therefore run to check whether tissues contained carbonates. These tests consist in dropping a small amount of sample powder in 10 % HCl. Effervescence indicates presence of carbonates, while the lack of visible bubbling suggests that no significant amount of carbonates is present in the tissues (Jaschinski et al. 2008). Here, champagne tests indicated that Schizasteridae caeca did not contain carbonates and did not require acidification. Echinidae peristomes and Cidaridae spine muscles contained significant yet moderate amounts of carbonates and were acidified by exposing them to HCl vapours for 48 h in an airtight container (Hedges and Stern 1984). After acidification, a second series of “champagne tests” were run. They indicated that the procedure successfully removed all carbonates from samples.

Stable isotope ratios measurements were performed via continuous flow-elemental analysis-isotope-ratio mass spectrometry (CF-EA-IRMS) at University of Liège, using a Vario Micro Cube elemental analyser (Elementar Analysensysteme GmbH, Hanau, Germany) coupled to an Isoprime 100 mass spectrometer (Isoprime, Cheadle, UK). Since acidification is known to alter N isotopic ratios (Mateo et al. 2008), acidified samples were analysed twice: once for C isotopic ratios, using decarbonated material, and once for N isotopic ratios, using native material. Isotopic ratios were expressed using the widespread δ notation (Coplen 2011). Sucrose (IAEA-C6, $\delta^{13}\text{C} = -10.8 \pm 0.5\text{ }‰$, mean \pm SD) and ammonium sulphate (IAEA-N2, $\delta^{15}\text{N} = 20.3 \pm 0.2\text{ }‰$, mean \pm SD) were used as certified reference materials (CRM). Both of these CRM are

calibrated against the international isotopic references, i.e. Vienna Pee Dee Belemnite (VPBD) for carbon and atmospheric air for nitrogen. Standard deviations on multi-batch replicate measurements of laboratory standards (amphipod crustacean muscle) analysed interspersed among the samples were 0.1 ‰ for $\delta^{13}\text{C}$ and 0.2 ‰ for $\delta^{15}\text{N}$.

Inter-region and/or inter-depth habitat differences of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were tested using hypothesis-based comparison procedures. D’Agostino and Pearson and Shapiro–Wilk normality tests revealed that several datasets did not follow a Gaussian distribution. Nonparametric procedures (Mann–Whitney U test when two groups were compared, Kruskal–Wallis one-way analysis of variance followed by Dunn’s post hoc test when three groups were compared) were therefore applied. All statistical analyses were conducted using Prism 6.05 (GraphPad Software, La Jolla, USA).

Results

Gut content examination

Cidaridae, Echinidae and Schizasteridae displayed distinct feeding behaviours. All investigated Schizasteridae had homogenous gut contents that consisted of sediment whatever their habitats and regions. In contrast, for regular echinoids (Cidaridae and Echinidae), various food items were filling the gut. Cidaridae and Echinidae displayed, respectively, “typical” gut contents, with no obvious differences between species within families. However, for the two families, differences were observed between regions and habitats (Table 3).

Cidaridae fed on animals (living or dead), the food items being scattered and free within the gut lumen. Sediment was conspicuous in the gut of the Weddell Sea specimen, while it was scattered or absent in the gut of the Bransfield and Drake specimens. Bransfield Strait appeared to offer the wider variety of animal remains compared to Weddell Sea and Drake Passage. In Bransfield Strait, Cidaridae collected on the slopes (all from the genus *Notocidaris*, Table 2) fed on carrion or preys, mostly sponges. In the canyons, Cidaridae (*Aporocidaris eltaniana*; Table 2) fed on carrion and detritus. Data from the Weddell Sea and Drake Passage are each based only on one specimen of *Ctenocidaris gigantea*, both collected on the slope. Their gut content consisted of carrion (Weddell Sea) and degraded detritus; as said above, the specimen from Weddell Sea had a conspicuous amount of sediment within its gut.

In Echinidae, food was packed into mucus-coated pellets. Gut contents consisted of a variety of detritus originating from animals and occasionally macroalgae (Table 3). Sediment was scattered or absent in samples

Table 3 Feeding behaviour and main food items of echinoids according to gut content analysis

	Drake Passage		Bransfield Strait		Weddell Sea	
	Upper slope	Lower slope	Upper + lower slope	Canyons	Bank + upper slope	Deep
Echinidae	–	–	Selective detritus feeders Diverse finely particular detritus (sponges, bryozoans, crustaceans, polychaetes, unidentified particles), fragments of macroalgae	Detritus feeders Detritus (unidentifiable organic matter, fragments of sponges, cnidarians and bryozoans, foraminiferans)	Detritus feeders Detritus (unidentifiable organic matter, fragments of cnidarians, crustaceans, and bryozoans)	Detritus feeders Detritus (unidentifiable organic matter)
			Scattered sediment	Sediment	Sediment	Sediment
Schizasteridae	Bulk sediment feeders	Bulk sediment feeders	Bulk sediment feeders	Bulk sediment feeders	Bulk sediment feeders	Bulk sediment feeders
	Sediment	Sediment	Sediment	Sediment	Sediment	Sediment
Cidaridae	Selective detritus feeders	–	Carnivores/scavengers	Scavengers	Scavengers/detritus feeders	–
	Unidentified granular and fibrous material, bryozoan remains		Bites of animal preys (sponges), carrion (sponges, bryozoans, cnidarians), detritus (bryozoans, polychaetes tubes, crustaceans)	Carrion (sponges, molluscs), detritus (polychaetes tubes, crustaceans, unidentifiable organic matter)	Carrion (sponges, ascidians), detritus (unidentifiable organic matter)	
	No sediment		Scattered sediment	No sediment	Sediment grains	

collected on the slopes of Bransfield Strait. It occurred conspicuously in all samples from Weddell Sea (slopes + deep) and in the samples collected in the canyons of Bransfield Strait. For the samples collected on the slopes of Bransfield Strait, numerous and diverse detrital items were observed associated with scattered sediment grains. The detrital items were usually identifiable and consisted of sponge spicules, bryozoan, anthozoan, crustacean and polychaete fragments, decaying diatoms and foraminiferans; macroalgae fragments were also occasionally observed. These detrital items were typically here in the form of fine particles relatively homogenous in size and densely packed within the food pellets. The gut of Echinidae collected in canyons contained detrital particles mixed with sediment within the food pellets. Most detrital particles were unidentifiable, while the other ones consisting mostly of sponges, cnidarians, bryozoans and foraminiferans remain. In Weddell Sea, sediment and detritus (usually in advanced stages of decay) were the main particles found within the food pellets.

Stable isotope analysis

Inter-region differences in the isotopic composition of *S. neumayeri* (Figs. 2a, 3) were present for carbon (Bransfield

Strait: $\delta^{13}\text{C} = -21.60 \pm 0.46 \text{‰}$; Weddell Sea: $\delta^{13}\text{C} = -16.51 \pm 1.13 \text{‰}$; Table 4) and, to a lesser extent, for nitrogen (Bransfield Strait: $\delta^{15}\text{N} = 8.47 \pm 0.56 \text{‰}$; Weddell Sea: $\delta^{15}\text{N} = 7.64 \pm 0.84 \text{‰}$; Table 4). In Bransfield Strait, isotopic ratios of *S. neumayeri* and *S. antarcticus* (Figs. 2a, 3) were similar, both for carbon (*S. neumayeri*: $\delta^{13}\text{C} = -21.60 \pm 0.46 \text{‰}$; *S. antarcticus*: $\delta^{13}\text{C} = -21.04 \pm 1.52 \text{‰}$; Table 4) and nitrogen (*S. neumayeri*: $\delta^{15}\text{N} = 8.47 \pm 0.56 \text{‰}$; *S. antarcticus*: $\delta^{15}\text{N} = 8.95 \pm 0.58 \text{‰}$; Table 4).

In each region, $\delta^{13}\text{C}$ of Schizasteridae (Figs. 2b, 3) was different (Table 4). The trend was similar to that observed for *S. neumayeri*, with values becoming less negative following a North–South gradient (Drake Passage: $\delta^{13}\text{C} = -24.91 \pm 1.03 \text{‰}$; Bransfield Strait: $\delta^{13}\text{C} = -22.31 \pm 1.33 \text{‰}$; Weddell Sea: $\delta^{13}\text{C} = -20.22 \pm 0.29 \text{‰}$), but was less marked (Fig. 3). $\delta^{15}\text{N}$ of Schizasteridae also differed among locations (Table 4). In this case, $\delta^{15}\text{N}$ of sea urchins from Drake Passage ($\delta^{15}\text{N} = 8.04 \pm 0.64 \text{‰}$) was significantly higher than $\delta^{15}\text{N}$ of sea urchins from Weddell Sea ($\delta^{15}\text{N} = 7.17 \pm 0.52 \text{‰}$; Table 4), but specimens from Bransfield Strait formed an intermediary group ($\delta^{15}\text{N} = 7.67 \pm 0.88 \text{‰}$) that was not different from either Drake Passage or Weddell Sea (Table 4). The distinctions among regions prevail, and no clear species-related effects were observed (Fig. 2b).

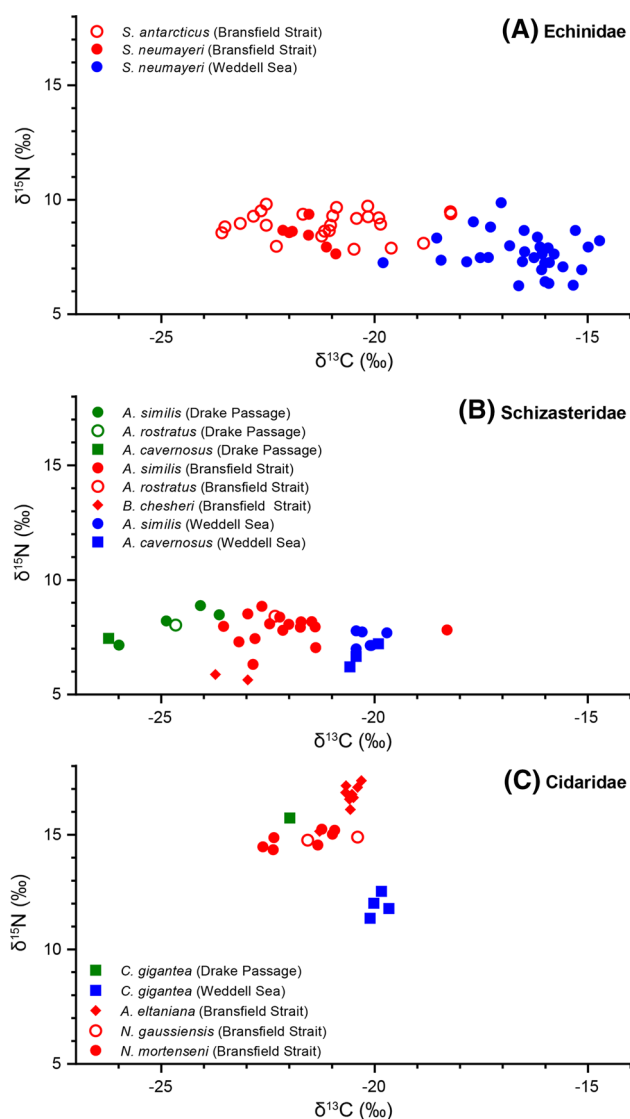


Fig. 2 Full range of $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) values of sea urchins. (Color figure online)

Cidaridae $\delta^{15}\text{N}$ (Figs. 2c, 3) varied widely across groups (Table 4). It was higher for the *A. eltaniana* sampled in the canyons of Bransfield Strait ($\delta^{15}\text{N} = 16.62 \pm 0.66$ ‰) than for the *Notocidarid* spp. sampled on the continental slopes the same region ($\delta^{15}\text{N} = 14.82 \pm 0.31$ ‰; Table 4). Both groups from Bransfield Strait were more ^{15}N -enriched than the *C. gigantea* from Weddell Sea ($\delta^{15}\text{N} = 11.92 \pm 0.49$ ‰; Table 4). The $\delta^{15}\text{N}$ of the single *C. gigantea* from Drake Passage was more comparable with values measured in Bransfield Strait than in Weddell Sea ($\delta^{15}\text{N} = 15.73$ ‰, Fig. 3). $\delta^{13}\text{C}$ also differed between Cidaridae groups (Figs. 2c, 3; Table 4). The *Notocidarid* spp. sampled on the continental slopes of Bransfield Strait ($\delta^{13}\text{C} = -21.54 \pm 0.76$ ‰) were significantly more ^{13}C -depleted than *C. gigantea* individuals from Weddell Sea ($\delta^{13}\text{C} = -19.91 \pm 0.19$ ‰; Table 4). Bransfield canyons,

A. eltaniana had $\delta^{13}\text{C}$ intermediate between those two groups ($\delta^{13}\text{C} = -20.62 \pm 0.28$ ‰) and not significantly different from either of them (Table 4). Finally, the only *C. gigantea* from Drake Passage that could be analysed was found in the same range than other Cidaridae from Bransfield Strait (Fig. 2; $\delta^{13}\text{C} = -21.99$ ‰).

Discussion

Stable isotope ratios of animals are influenced by many ecological, physiological, and environmental factors (Boecklen et al. 2011). Among those, factors involving (1) differences in consumer foraging ecology and trophic resource exploitation and (2) baseline shifts and variation in primary producers and/or organic matter pool isotopic composition are likely to have strong effects on consumer isotopic composition. Here, Schizasteridae carbon isotopic ratios showed inter-location variation, with increasing (i.e. less negative) $\delta^{13}\text{C}$ following a north–south gradient. On the one hand, sea urchins could feed on different sources in each zone, favouring more ^{13}C -depleted items in Drake Passage than in Bransfield Strait or in Weddell Sea. However, gut content analyses suggested that Schizasteridae show similar trophic behaviour and feed on sediment and associated organic matter in all three regions. On the other hand, the isotopic composition of sediment-associated organic matter (hereafter SOM) in these three regions is likely to vary. These three regions are indeed characterized by widely different environmental conditions, and notably by increasing presence of sea ice from north to south (Bracher and Huntemann 2015; Dorschel et al. 2015; Table 1). Organic matter associated with Antarctic sea ice is very rich in ^{13}C , and sea ice inputs to sediment can cause an increase in SOM $\delta^{13}\text{C}$ (Gibson et al. 1999). Higher SOM $\delta^{13}\text{C}$ in locations where sea ice is more present could in turn cause higher sea urchin $\delta^{13}\text{C}$. Elevated $\delta^{13}\text{C}$ values have indeed been recorded for meiobenthic copepods and nematods from Lazarev Sea locations heavily influenced by sea ice (Veit-Köhler et al. 2013). Settling this issue would require precise knowledge of isotopic composition of SOM in each sampling location. However, combination of insights drawn from gut content examination and stable isotope analysis suggest that Schizasteridae feeding habits are similar in Drake Passage, Bransfield Strait and Weddell Sea, and that they are bulk sediment feeders relying on SOM. The variability in their isotopic composition (Fig. 2) is likely related to baseline shifts in SOM isotopic composition rather than actual inter-regions differences in feeding habits.

$\delta^{13}\text{C}$ showed less variation in Cidaridae than in the two other families. $\delta^{15}\text{N}$, on the other hand, was much more variable than in Echinidae or Schizasteridae. Although

Fig. 3 Mean values (\pm SD) of $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) of sea urchins. (Color figure online)

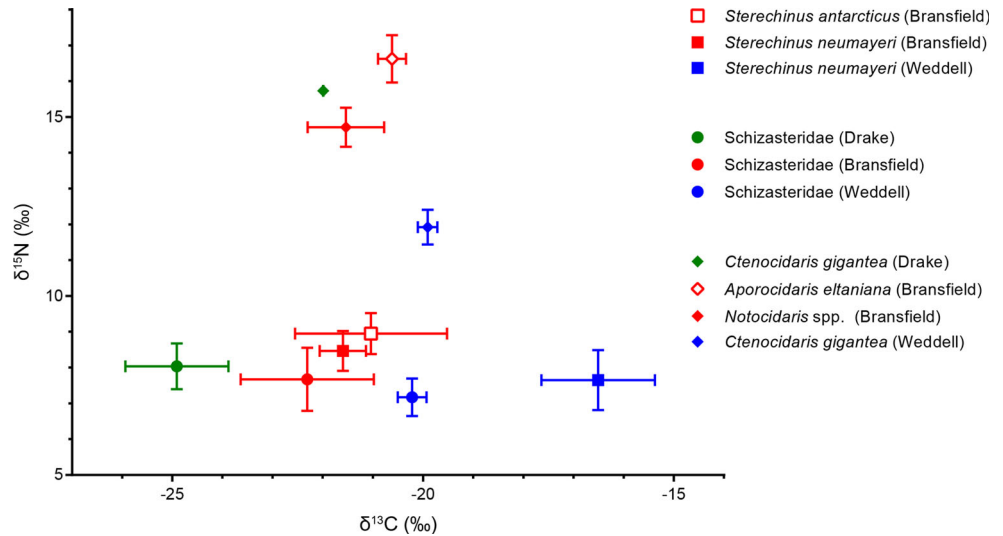


Table 4 Results of stable isotope ratios statistical analyses

	Variable	Test	Statistics	<i>p</i>
<i>Echinidae</i>				
<i>S. neumayeri</i> Weddell versus <i>S. neumayeri</i> Bransfield	$\delta^{13}\text{C}$	MW	$U = 0.00$	<0.0001*
	$\delta^{15}\text{N}$	MW	$U = 42.50$	0.0108*
<i>S. neumayeri</i> Bransfield versus <i>S. antarcticus</i> Bransfield	$\delta^{13}\text{C}$	MW	$U = 62.00$	0.2498
	$\delta^{15}\text{N}$	MW	$U = 45.50$	0.0555
<i>Schizasteridae</i>				
All species Weddell versus all species Bransfield versus all species Drake	$\delta^{13}\text{C}$	KW	$H2 = 22.82$	<0.0001*
All species Weddell versus all species Bransfield	$\delta^{13}\text{C}$	DPH	MRD = -12.79	0.0045*
All species Weddell versus all species Drake	$\delta^{13}\text{C}$	DPH	MRD = -24.67	<0.0001*
All species Bransfield versus all species Drake	$\delta^{13}\text{C}$	DPH	MRD = -11.88	0.0325*
All species Weddell versus all species Bransfield versus all species Drake	$\delta^{15}\text{N}$	KW	$H2 = 7.73$	0.0210*
All species Weddell versus all species Bransfield	$\delta^{15}\text{N}$	DPH	MRD = 9.21	0.0668
All species Weddell versus all species Drake	$\delta^{15}\text{N}$	DPH	MRD = 13.33	0.0322*
All species Bransfield versus all species Drake	$\delta^{15}\text{N}$	DPH	MRD = 4.12	>0.9999
<i>Cidaridae</i>				
<i>A. eltania</i> Bransfield versus <i>Notocidaris</i> spp. Bransfield versus <i>C. gigantea</i> Weddell	$\delta^{13}\text{C}$	KW	$H2 = 14.14$	<0.0001*
<i>A. eltania</i> Bransfield versus <i>Notocidaris</i> spp. Bransfield	$\delta^{13}\text{C}$	DPH	MRD = 6.67	0.0881
<i>A. eltania</i> Bransfield versus <i>C. gigantea</i> Weddell	$\delta^{13}\text{C}$	DPH	MRD = -7.67	0.1481
<i>Notocidaris</i> spp. Bransfield versus <i>C. gigantea</i> Weddell	$\delta^{13}\text{C}$	DPH	MRD = -14.33	0.0007*
<i>A. eltania</i> Bransfield versus <i>Notocidaris</i> spp. Bransfield versus <i>C. gigantea</i> Weddell	$\delta^{15}\text{N}$	KW	$H2 = 14.14$	<0.0001*
<i>A. eltania</i> Bransfield versus <i>Notocidaris</i> spp. Bransfield	$\delta^{15}\text{N}$	DPH	MRD = 8.56	0.0156*
<i>A. eltania</i> Bransfield versus <i>C. gigantea</i> Weddell	$\delta^{15}\text{N}$	DPH	MRD = 15.28	0.0003*
<i>Notocidaris</i> spp. Bransfield versus <i>C. gigantea</i> Weddell	$\delta^{15}\text{N}$	DPH	MRD = 8.72	0.0255*

MW Mann–Whitney test, KW Kruskal–Wallis test, DPH Dunn’s post hoc test, MRD mean rank difference

* Significant differences ($p < 0.05$)

some of this variation may come from the fact that regions and/or depth-related habitats were represented by different species (Table 2; Fig. 2), some trends were quite clear. In

all regions, Cidaridae were markedly more ^{15}N -enriched than all the other sea urchins. This is consistent with their preference towards animal food items (Jacob et al. 2003),

since $\delta^{15}\text{N}$ is well known for showing a stepwise increase with increasing trophic level (DeNiro and Epstein 1981).

In Bransfield Strait, $\delta^{15}\text{N}$ of Cidaridae was high, ranging from 13.47 ‰ to as much as 17.36 ‰ (Fig. 2c). These values are comparable with $\delta^{15}\text{N}$ of predator and/or scavenger invertebrates and fishes sampled in Antarctic benthic ecosystems (Nyssen et al. 2002; Mincks et al. 2008). Moreover, differences were also recorded within this region and Cidaridae sampled in the canyons (*A. eltaniana*) had higher $\delta^{15}\text{N}$ than specimens from the continental slope (*Notocidaris* spp.). This elevated $\delta^{15}\text{N}$ could be linked with scavenging behaviour, since scavengers often feed on carrion originating from high-trophic-level consumers that could not be consumed while alive (Nyssen et al. 2002). This is supported by examination of gut contents, whose animal fraction was a mixture of prey eaten alive and carrion in Cidaridae from the slopes of Bransfield Strait, but only carrion in those sampled in canyons (Table 3). This prevalent scavenging behaviour in deep habitats could be linked with comparatively lower live prey availability in Bransfield Strait canyons. Alternatively, Cidaridae could undergo starvation due to low prey availability, as starvation can lead to ^{15}N enrichment (Fantle et al. 1999).

In Weddell Sea, $\delta^{15}\text{N}$ of Cidaridae (*C. gigantea*, Table 2), although still higher than that of Echinidae and Schizasteridae, was significantly lower than in Bransfield Strait. This suggests a more mixed diet and reliance on animal prey (living or dead) as well as detrital items and/or organic matter. Gut content of the single Cidaridae that could be analysed from this area supported this hypothesis, as it contained more detrital items than in Bransfield, and it was also the only Cidaridae gut content showing conspicuous amounts of sediment. This view is also consistent with a previous study indicating that, in Weddell Sea, Cidaridae ingested a mixture of bryozoans, hydrozoans, sponges and various sediment-associated items (Jacob et al. 2003). The $\delta^{15}\text{N}$ of the only *C. gigantea* from Drake Passage was much higher than values recorded from Weddell Sea, and rather comparable to values of other Cidaridae from Bransfield. Although this hypothesis is supported by a single observation, and caution is therefore advised, this might point out that the scavenging/detritus feeding behaviour of Cidaridae is associated to the Weddell Sea. This behaviour could be explained by lower prey availability and/or palatability of prey in this region.

Gut contents and stable isotopes both suggested that feeding habits of *S. neumayeri* and *S. antarcticus* were similar. These results are in accordance with a previous study that highlighted trophic niche overlap between those two species (Jacob et al. 2003). Differences in depth distribution could limit interspecific competition, as *S. neumayeri* prefers shallower zones, while *S. antarcticus* is

most commonly found in deeper ones (Brey and Gutt 1991). Contrastingly, $\delta^{13}\text{C}$ of *Sterechinus* spp. were very different between Weddell Sea and Bransfield Strait. Variation in carbon stable isotopic ratios was much more marked than for Schizasteridae and Cidaridae (Figs. 2, 3). This important variation is unlikely to be caused only by changes in isotopic composition of the food web baseline, but probably rather reflects strong trophic plasticity in Echinidae. *S. neumayeri* from Weddell Sea indeed showed very important ^{13}C enrichment, with $\delta^{13}\text{C}$ ranging from -19.8 to -14.72 ‰ (Fig. 2a). Such values are striking, as they are markedly more positive than most food items available to sea urchins in these areas of Weddell Sea and Antarctic Peninsula, including suspended particulate organic matter, plankton, phytodetritus, bulk surface and subsurface sediments and even, to some extent, sea ice-associated algae (Rau et al. 1991; Mincks et al. 2008). High $\delta^{13}\text{C}$ values have already been reported for other consumers of the Antarctic Peninsula, although ^{13}C enrichment was not as strong as here. Those consumers include deposit-feeding Holothuroidea *Molpadia musculus* and *Ypsilocucumis turricata* ($\delta^{13}\text{C} = -18.35 \pm 0.87$ ‰ and -18.88 ± 0.28 ‰, respectively; Mincks et al. 2008) and suspension-feeding Anthozoa ($\delta^{13}\text{C}$ up to -16 ‰; Nyssen et al. 2002). Important ^{13}C enrichment of benthic consumers, including bivalves and sea urchins, has also been recorded in Arctic ecosystems (Hobson and Welch 1992; Lovvorn et al. 2005). This phenomenon is usually linked with direct or indirect assimilation of detrital organic material reworked by sediment microorganisms and/or meiofauna. The Antarctic Peninsula shelf undergoes seasonal deposition of high amounts of phytodetritus coming from fast-sinking sea ice algae aggregates (Riebesell et al. 1991) and from post-sea ice retreat summer phytoplankton blooms (Smith et al. 2008). This material accumulates in sediments, where it constitute persistent “food banks” that are available to benthic consumers all year round (Mincks et al. 2005, 2008). Here, data from stations sampled during the PS81 cruise accordingly suggested that over the 2008–2012 period, both average sea ice cover and surface primary productivity were higher in Weddell Sea than in the other areas (Bracher and Huntemann 2015; Dorschel et al. 2015; Table 1). Weddell Sea was also the only sampled region to still show presence of sea ice during the sampling (i.e. late austral summer; Table 1). In this context, high $\delta^{13}\text{C}$ of Echinidae from Weddell Sea could come from assimilation of microbe-reworked detrital organic matter present among sediment “food banks”. This is consistent with common presence of highly decayed detritus in gut contents of those animals (Table 3). Furthermore, bacterial metabolism taking place inside digestive pellets (De Ridder and Foret 2001) could strengthen this effect, leading to the high $\delta^{13}\text{C}$ measured here.

Previous food web structure studies also suggested important spatial- and depth-related variations in *Sterechinus* spp. feeding habits. In shallow zones of the Antarctic Peninsula, sea urchins in general (Dunton 2001) and *S. neumayeri* in particular (Brand 1976; Corbisier et al. 2004) apparently feed mostly on macroalgae. Here, these did not seem to be a major food item, as macroalgal fragments were rarely found in *Sterechinus* spp. guts (less than 10 % of individuals). This is most likely linked with low availability of macroalgae at the sampled depths and/or locations. In deeper zones around the Antarctic Peninsula, *Sterechinus antarcticus* has been suggested to feed on a mixture of benthic detritus and macrofaunal organisms (Mincks et al. 2008). Diet of both *S. antarcticus* and *S. neumayeri* sampled in Bransfield Strait in this study seem consistent with these findings. Comparison of *Sterechinus* spp. carbon and nitrogen stable isotope ratios with literature data points SOM, benthic detritus and various sessile or vagile invertebrates as feasible food items (Dunton 2001; Corbisier et al. 2004; Mincks et al. 2008). Gut contents of Echinidae from the continental slope of Bransfield Strait contained many unidentifiable detrital items as well as fragments originating from various benthic invertebrates, but little to no sediment, suggesting that they are selective detritus feeders (or “gourmet” detritus feeders, sensu Plante et al. 1990). In Bransfield Strait canyons, sediment was more conspicuous in the guts, suggesting inter-depth habitat trophic variability.

In Weddell Sea, *S. antarcticus* and *S. neumayeri* seem to depend on food availability and benthic-pelagic coupling (Jacob et al. 2003). They frequently ingest considerable amounts of bryozoans, as well as detritus and sediment. However, in some instances, large amounts of diatoms can deposit on the seafloor, forming thick layers of “fluff”. When diatoms are available, both species predominantly feed on them over any other food source, likely by collecting them from the sediment surface (Jacob et al. 2003). Our hypothesis that Weddell Sea Echinidae rely on highly decayed detritus stored in “food banks” is coherent with those results. Diatom fluffs and microbially reworked benthic detritus could indeed represent two different states of material originating from the water column.

Each of the studied families showed a different response to variation in environmental and food conditions. Schizasteridae trophic plasticity was low, and these sea urchins were bulk sediment feeders relying on SOM in all regions and/or depth-related habitats. The animal-based inputs in the diet of Cidaridae changed both in importance (lower animal fraction in diet in Weddell Sea than in Bransfield Strait) and in nature (mixture of live and dead material on the slopes of Bransfield Strait vs. mostly dead material in the canyons of this region). Nitrogen stable isotopes clearly showed that Cidaridae were the only group to occupy different trophic

levels in different regions or habitats. Finally, feeding behaviour of Echinidae seemed to change according to depth in Bransfield Strait (greater selectivity on the slopes than in the canyons). Carbon stable isotope ratios also revealed that main food items of this group were different in Bransfield Strait and Weddell Sea, where sea urchins seem able to exploit heavily microbially reworked detrital matter. These differences in trophic plasticity could be important in the current context of environmental changes occurring in the studied area. The Antarctic Peninsula is indeed one of the most quickly warming regions of the world, and as a result, sea ice cover in this area shows an important decrease (Turner et al. 2005; Parkinson and Cavalieri 2012). These changes will undoubtedly in turn modify sea urchin trophic environment, and warmer temperatures notably cause a decrease in the amount of material available to benthic consumers in “food banks” (Mincks et al. 2005). While sea urchin responses to such changes are difficult to predict, our results suggest that differences in adaptive strategies could lead to different effects on each of the studied families’ feeding habits, biology and, ultimately, distribution in the Southern Ocean.

Data accessibility

In accordance with guidelines of the Scientific Committee on Antarctic Research and the Belgian Science Policy Office, all data supporting this article are openly available at doi:10.6084/m9.figshare.1591834.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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