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Trophic ecology of three echinoderms in deep waters of the Weddell Sea (Antarctica)

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ABSTRACT In the Southern Ocean, the trophic ecology of deep-sea communities is probably one of the most neglected fields in the discipline. In the present study, the trophic position and energy storage-mobilization of 3 different deep-sea echinoderms living in the Weddell Sea (around 1500 m depth) were investigated with indirect tools (i.e. stable isotopes, carbohydrate-lipid-protein balance, and free fatty acid [FFA] contents). The stalked crinoid *Dumetocrinus antarcticus*, the holothurian *Rhipidothuria racovitzai*, and the ophiuroid *Ophiura carinifera* were sampled in spring 2003 during a Polarstern cruise. We found that stable isotopes were in line with previous results of other species ($\delta^{13}C$ ranging from –24.3‰ to –26.5‰; $\delta^{15}N$ ranging from 6.8‰ to 7.9‰), showing similarities in the trophic position of the 3 echinoderms. The capability to store energy by these 3 organisms is conspicuous and different, e.g. from 18 to 45% of the organic matter (OM) consists of lipids. The capability to mobilize energy in the form of carbohydrates and FFAs among species was also very different (e.g. biomolecules ranging from 9 to 22 µg carbohydrates $mgOM^{-1}$ and from 4 to 39 µg FFA $mgOM^{-1}$). It is suggested that even if the trophic level is similar in the 3 echinoderms, the strategies to invest the energy inputs in these deep-sea organisms in polar environments may be quite different.

KEY WORDS: Suspension feeders · Deposit feeders · Fatty acids · Stable isotopes · Energy storage · Antarctica · Biomarkers · Deep sea

INTRODUCTION

An important part of the seasonal primary productivity in Antarctic waters (up to 90% at the beginning of the blooms in polar waters; Wassmann et al. 1991) arrives almost intact to the benthic communities, forming food banks (Gutt & Starmans 1998, Mincks et al. 2005, Isla et al. 2006a,b). This organic matter fuels the overall system for weeks or months (Holm-Hansen 1985, Clarke 1988, Piepenburg et al. 1997). In the euphotic zone, twenty to forty intense blooms a year (produced between late spring and early autumn; Isla et al. 2009) produce a huge amount of particulate organic matter (POM) that is rapidly transferred to the benthic communities (Lampitt et al. 1993, Cattaneo-Vietti et al. 1999, Rossi et al. 2013, Gutt et al. 2017). This phenomenon

produces a tight benthic–pelagic coupling in Antarctic waters (Ambrose & Renaud 1997, Clough et al. 2005).

The highly diverse Antarctic bottoms (Arntz et al. 1994, Gili et al. 2001, Gili et al. 2006a, Gutt et al. 2017) hold a huge biomass in which suspension and deposit feeders have a prominent role. Among these organisms, echinoderms are very abundant and taxonomically diverse, capturing particles by actively intercepting the main currents, or by detecting and consuming the primary productivity and its associated microbial and metazoan community from the ocean floor (Gutt 1991, McClintock 1994, O'Loughlin et al. 2011, Ambroso et al. 2016). In general, information on the trophic ecology of benthic organisms in Antarctic waters is scarce (Orejas et al. 2001, Jacob et al. 2003; Gili et al. 2006b, Elias-Piera et al. 2013). Most trophic studies to date have been carried out in the Antarctic Peninsula and on the Weddell Sea continental shelf (150–2000 m depth) (McClintock 1994, Dahm 1999, Jacob et al. 2003, Purinton et al. 2008, Corsolini & Borghesi 2017), thus trophic ecology information for the deep-sea areas of the Weddell Sea is still very scarce (Jacob et al. 2003).

These deep areas may also have an important presence of benthic suspension or deposit feeders (Brandt et al. 2007a,b; Gutt et al. 2017), but the trophic ecology of these organisms can only be guessed at, because very few studies have been made to date (see Frutos et al. 2017, Gutt et al. 2017). During the ANT XXI-2 'Polarstern' cruise (2003–2004), 3 different echinoderms were observed forming quite dense patches at 1500 m depth: the stalked crinoid *Dumetocrinus antarcticus* (Bather, 1908), the holothurian *Rhipidothuria racovitzai* (Hérouard, 1901), and the ophiuroid *Ophiura (Ophiuroglypha) carinifera* (Koehler, 1901). This suggests that primary productivity may also reach these deep zones in sufficient quantity to fuel these communities.

The stalked crinoid is a suspension feeder, fixed on the substrate (Macurda & Meyer 1974). Its body shape and morphology indicates that this animal is adapted to intercept particles from the water column, as in other suspension-feeding species (Orejas et al. 2001). Like other suspension feeders, it therefore depends on the quantity and quality of the water column seston particles to feed (Gili & Coma 1998). Other echinoderms may actively search for food in the food banks ('green carpets'; Mincks et al. 2005), which may be sparse in different areas. We do not have precise information about the trophic ecology of the holothurian, but it may be a deposit feeder, detecting and feeding on these degrading phytoplankton carpets present in the sediment (Gutt 1991, McClintock et al. 1994). Ophiuroids can be considered intermediate strategists between suspension feeding and deposit feeding (Gutt et al. 2017): they may be highly concentrated in soft bottoms where detritus is available, filtering the resuspended material (Piepenburg et al. 1997), and actively moving from patch to patch of detritus, taking advantage of the asymmetric distribution of organic matter (OM) in the soft bottom substrates (Piepenburg & Juterzenka 1994).

In areas like the deep Antarctic benthos which are logistically difficult to access, direct tools (e.g. stomach contents, feeding experiments) are not a practical method to obtain a complete picture of the energy fluxes (Gili et al. 2006b). However, indirect methods, such as the integration of results for multiple biomarkers (e.g. stable isotopes, biochemical balance, and fatty acids) assessed in combination, have proven very useful in elucidating the trophic ecology of benthic organisms (e.g. Gori et al. 2012, Elias-Piera et al. 2013, Viladrich et al. 2017). The use of identifiable molecular biomarkers, which pass from food sources to the consumer, is also useful to detect soft-bodied microscopic prey, such as bacteria, phytoplankton, ciliates and flagellates (Rossi et al. 2006c). Using such indirect tools allows identification of food sources, trophic

position of the organisms, the ecosystem's capability to store energy, or even the effects of environmental changes integrated over time (Viladrich et al. 2016a,b). For example, the proportions of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes may vary with nutrient source and trophic level of consumers. Stable isotope analysis has been successfully used to elucidate food source partitioning, and food web dynamics (Jacob et al. 2005, Mincks et al. 2008, Søreide et al. 2008, Elias-Piera et al. 2013). Also, overall fatty acid (FA) composition and specific FAs used as trophic markers can help to elucidate trophic relationships in food webs and quantify available mobilisable lipids (free fatty acids [FFAs]; Viladrich et al. 2016a,b). Finally, many organisms commonly use energy storage to cope with seasonal food shortages: protein, carbohydrate, and lipid levels may reflect food shortages in benthic aquatic organisms (Rossi et al. 2006a,b). Benthic–pelagic coupling processes may be thus studied using these indirect tools (Rossi et al. 2017).

Improving knowledge of the trophic ecology of deep-sea organisms, especially in Antarctic waters, will help in the understanding of biodiversity and ecosystem functioning in this remote area. In the present study, the 3 abovementioned echinoderm species were collected and analysed for stable isotopes, FFAs and biochemical balance (protein, lipid and carbohydrate content) to explore their trophic ecology in late spring Antarctic conditions. In this time of the year, food banks are almost depleted (Isla et al. 2011) and the cycle of primary productivity starts again. The study will be a key point to understand future changes in the trophic ecology of these considered important contributors of the biomass in Antarctica (Brey & Gerdes 1998) in a fast-changing area.

MATERIALS AND METHODS

Sampling area and sampled species

The sampling area was located in the southwestern Weddell Sea, around 1500 m depth (Fig. 1; 70°7.88'S; 11°21.56'W).

The 3 echinoderm species sampled belong to 3 different classes: *Rhipidothuria racovitzai* is a holothurian, *Dumetocrinus antarcticus* is a crinoid, and *Ophiura carinifera* is an ophiuroid. In a bottom trawl made using an Agassiz Trawl, these were among the more abundant species found in the deep platform, and the only 3 echinoderm species found at that time in this sampling (Arntz & Brey 2005). Also, the camera used in the Multi-Box Core (Arntz & Brey 2005) recorded the presence of these 3 echinoderms as the more abundant species (D. Gerdes & W. E. Arntz pers. comm.). Once collected, the animals (10–20 per species) were immediately frozen (–80°C) and freeze-dried (at –110°C and a pressure of 5 mbar), and then stored at –20°C pending biochemical analysis.

Stable isotope analysis

Four replicates of freeze-dried holothurian tissue, ophiuroid and crinoid arms were weighed with a microbalance (Mettler Toledo, model XS3DU). Around 0.50 to 0.60 mg of freeze dried samples were used for this analysis.

The samples were slightly acidified with 10% HCl to remove carbonates, which can bias $\delta^{13}C$ signatures (Jacob et al. 2005), following protocols from McConnaughey & McRoy (1979), Hobson & Welch (1992) and Jacob et al. (2005).

The $\delta^{13}C$ and $\delta^{15}N$ stable isotope analyses were performed with a mass spectrometer (Flash EA 1112 HT O/H-N/C), following the same procedure as previously described in Elias-Piera et al. (2013). Isotopic ratios are expressed as parts per thousand (‰) (difference from a standard reference material) according to the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 10^3$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. $R_{standard}$ values for ^{13}C and ^{15}N are from PeeDee Belemnite (PDB) and atmospheric N_2, respectively.

Organic matter content and biochemical balance

The OM content and the lipid analysis were calculated by sub-sampling 35 to 50 mg of holothurian tissue, ophiuroid and crinoid arms (10 per species). Samples were combusted at 500°C for 4 h in a muffle furnace (Relp 2H-M9). The remaining inorganic ash was weighed. The difference between dry weight (DW) and ash weight gave the OM content (ash-free dry weight) (Slattery & McClintock 1995, Rossi et al. 2006a,b).

The lipid analyses were performed spectrophotometrically and were quantified according to Barnes & Blackstock (1973) in 10 samples per species. Around 11 mg DW of holothurian tissue, around 35 mg DW of crinoid arms, and around 66 mg DW of ophiuroid arms were homogenised in 3 ml of chloroform–methanol (2:1 v/v), using cholesterol as a standard (absorbance vs. concentration). Results are presented in µg lipid (Lip) $mgOM^{-1}$ (Rossi et al. 2006a, Elias-Piera et al. 2013).

Protein and carbohydrate analyses were performed applying spectrophotometric methodologies (10 samples per species and analytical procedure): 8 to 11.5 mg tissue DW was weighed in a microbalance (precision: ± 0.01 mg) for each analysis (Rossi et al. 2006a, Elias-Piera et al. 2013). The Lowry et al. (1951) method was followed for protein analysis. The tissue was homogenised in 1 ml, 1 N NaOH, using albumin as a standard (absorbance vs. concentration). Carbohydrate content of tissues was analysed and quantified following Dubois et al. (1956). Each tissue was weighed and homogenised in 3 ml of double distilled water, using glucose as a standard (absorbance vs concentration). Results are presented in µg protein (Prot) $mgOM^{-1}$ and µg carbohydrate (CHO) $mgOM^{-1}$.

Fatty acid analysis

Holothurian tissue, ophiuroid and crinoid arms were analysed with gas chromatography to identify and quantify FFAs. Around 11 and 15 mg DW of 4 replicates of holothurian arms, 4 of ophiuroid arms and 6 of crinoid arms were extracted with dichloromethane–methanol (3:1). An internal standard (250 µl of 2-octyldodecanoic acid, 5β-cholanic acid, 2-nonadecanone and hexatriacontane) was added. The extract was re-dissolved in 0.5 ml of chloroform and passed through a 500 mg aminopropyl mini-column (Waters Sep-Pak® Cartridges). The FFA fraction was dried with nitrogen flux and then methylated using a solution of methanol/BF_3 (20% of BF_3 diluted in methanol) heated at 90°C for 1 h. Subsequently, 4 ml of Milli-Q water saturated with NaCl was added and FAs were recovered as fatty acid methyl esters (FAMEs). FAMEs were analysed by gas chromatography (GC; Agilent 5890 Series II instrument equipped with a flame ionization detector and a splitless injector) and were identified by retention time in comparison with standard FAs (37 FAME compounds, Supleco® Mix C_4–C_{24}). FA quantification was

performed through peak area integration in the GC traces (Chromquest 4.1 software). Results are presented in µg FFA $mgOM^{-1}$.

The present protocol, with slight changes, has been previously used with different biological material (Rossi & Fiorillo 2010, Gori et al. 2012, Rossi et al. 2013, Elias-Piera 2014, Viladrich et al. 2016a,b, 2017).

Statistical analyses

Analyses of potential differences in stable isotopic signature ($\delta^{13}C$ and $\delta^{15}N$) and lipid-protein-carbohydrate composition between species were performed with a 1-way ANOVA test (R-language function 'aov') and a post-hoc Tukey test (R-language function 'TukeyHSD') with a significance level of $p < 0.05$. Data were previously analysed by the Shapiro-Wilk ($p = 0.1$) and Levene's Test ($p = 0.05$) (R language function 'Shapiro.test' and 'LeveneTest') to test normality and homogeneity of variances, respectively. Data met the criteria for parametric analysis after logarithmic transformation.

Analysis of similarity (ANOSIM;analogous to 1-way ANOVA) was conducted, and a principal components analysis (PCA) was performed to investigate which FAs were more representative in terms of abundance in the different echinoderms using the R-language function 'rda' (vegan library). The PCA was constructed using logarithmically transformed FA compositional data.

A multi-dimensional scaling (MDS) analysis using the PRIMER software was applied to investigate similarities (Bray-Curtis similarity) between the 3 species according the FAs. A SIMPER analysis using the FFAs was also conducted to evaluate the relative contribution of FAs to the dissimilarity of each species.

RESULTS

Stable isotopes

Fig. 2 shows the stable isotope proportion of the 3 species. The $\delta^{13}C$ values of the 3 echinoderms ranged from –24.3 to –26.5‰, but only the crinoid's value was significantly different from that of the other 2 species ($F_{9,2} = 79.63$, $p < 000.1$). The $\delta^{15}N$ values were similar among species, ranging from 6.8 to 7.9‰. The only difference was between the holothurian and the crinoid ($F_{9,2} = 6.84$, $p = 0.0156$).

Carbohydrates, proteins and lipids

Fig. 3 shows the biochemical balance (carbohydrate, protein and lipid content of the organic matter tissue). In Fig. 3A, carbohydrate concentration values of the 3 species are shown and ranged between 9 and 22 µgCHO $mgOM^{-1}$. The carbohydrate, protein and lipid concentrations in the holothurian tissues were more than twice those of the other 2 studied species, being significantly different from them ($F_{27,2} = 44.35$, $p < 0.001$).

Fig. 3B shows the total protein content of the 3 species: this ranged from 159 to 211 µgProt $mgOM^{-1}$, but none of the differences were significant ($F_{27,2} = 2.98$, $p = 0.0668$).

Values of total lipids are shown in Fig. 3C and range between 179 and 448 µgLip $mgOM^{-1}$. All the echinoderm species had high lipid concentrations, the highest value being

found in the holothurian. Both the holothurian and the crinoid had significantly higher concentrations of total lipids than the ophiuroid ($F_{22,2}$ = 21.14, p < 0.001).

Fatty acid analyses

The total concentration of FFAs was significantly higher in the holothurian than the other 2 studied species (Fig. 4). In fact, the difference is around one order of magnitude higher in this organism than the sessile crinoid and the ophiuroid.

The proportions of the different groups of FFA in the 3 species are shown in Fig. 5. Except for the crinoid, polyunsaturated (PU)FAs were the most prominent FFAs found in this study, while saturated (S)FAs generally showed the lowest proportions of the totals. In the holothurian there was an increasing gradient from SAFA to mono-unsaturated (MU)FA to PUFA. The different FFAs were quite balanced in the sessile crinoid. In the ophiuroid, PUFAs were especially abundant.

In the 3 species, the 20:4(n-6) was the most prominent FFA (Fig. 6). Almost 30% of the FFA in the ophiuroid is 20:4(n-6), being more than 15% in the other 2 echinoderm species. The 16:1(n-9) was abundant in holothurian and crinoid, but almost not present in the ophiuroid. The proportions (in%) of 22:6(n-3) had very asymmetric values among the 3 studied species, being very abundant in holothurian but only slightly above 0% and 5% in the other 2 species. The 22:1(n-9) —derived from the 18:1(n-9)—represents around 10% in the sessile crinoid, but was almost non-existent in the other 2 species. The 24:1(n-9), derived from the 22:1(n-9), was only present in moderate amounts in the holothurian and the crinoid. Long-chain FFAs, e.g. 24:4(n-6) and 24:5(n-3), were especially notable in the ophiuroid.

The 3 species exhibited significant species-specific differences in FA composition (ANOSIM, p < 0.01). The PCA applied to the different FFAs clearly distinguishes the 3 different species (Fig. 7); the same result appears on the MDS analysis taking into account 40% similarity (data not shown). The first 2 principal components (PC1 and PC2) accounted for 34.6% and 40.7% of the FA variation, respectively. For the crinoid and the ophiuroid, the FAs that mainly separate these species were the 20:2 (abundant in the ophiuroid at 11.5%) and the 22:1 (abundant in the crinoid at 9.9%). The holothurians were significantly different from the other 2 species, even though the most abundant FAs were the same in all 3 species: – 20:4(n-6) and 20:5(n-3).

From the SIMPER analysis, there was 80.18% dissimilarity between the holothurian and the crinoid and 89.95% dissimilarity between the holothurian and ophiuroid. The FA 22:6 contributed 10.61 and 10.14% to the dissimilarity, respectively. Other FAs making major contributions to the 2 dissimilarities were 20:4(n-6) (contributing 9.48 and 8.91%, respectively), 16:0 (6.08 and 6.54%), and 16:1 (6.05 and 6.32%). The dissimilarity between crinoid and ophiuroid was 50.95%, mainly due to the FAs 16:0 (9.29% contribution), 20:4(n-6) (8.65%), 16:1 (6.22%) and 22:1 (6.0%).

DISCUSSION

The present study shows that, although the trophic position of the 3 echinoderm species seems to be similar, there are significant differences among the holothurian (*Rhipidothuria racovitzai*), the crinoid (*Dumetocrinus antarcticus*), and the ophiuroid (*Ophiura carinifera*) storage and mobilization of lipids and carbohydrates in spring.

Carbon stable isotopes corroborate the fact that the source of food are the recurrent phytoplankton blooms (Jacob et al. 2006, Mintenbeck et al. 2007, Mincks et al. 2008, Elias-Piera et al. 2013). Such primary productivity may arrive almost intact to the bottom (to the continental platform, 300–400 m depth; Rossi et al. 2013) and possibly in large quantities to the deep sea (Shimanaga & Shiriyama 2000). The trophic position of the 3 organisms is quite similar to other suspension-feeding organisms (e.g. Antarctic gorgonians), having similar diets (Elias-Piera et al. 2013). The mixture of phytoplankton and reworked material (in which rotifers, copepods, ciliates and other fauna may be living) could be responsible for the elevated $\delta^{15}N$ values. These high values are also present in holothurians of shallow warm temperate seas (Grall et al. 2006, Carlier et al. 2007), and other deep-sea holothurians (Fanelli et al. 2011).

Of the FFAs found in the 3 species, the most dominant is the 20:4(n-6), with the 18:1(n-9) and longer-chained (C_{24}) FAs also non-negligible. These fatty acids have been identified with an omnivorous diet (Graeve et al. 2001, Suhr et al. 2003, Würzberg et al. 2011), which is in line with the $\delta^{15}N$ values. The omnivore/carnivore diet is also evidenced by the 20:1 and 22:1 (Drazen et al. 2008). This seems to confirm that these organisms feed not only on the microalgae found in the food banks, but also on the associated biota – i.e.micro-organisms (Howell et al. 2003). The 20:4 and 20:5 FAs are abundant in various species of echinoderms (Ginger et al. 2000, Graeve et al. 2001, Howell et al. 2003, Drazen et al. 2008, Galloway et al. 2013, Corsolini & Borghesi 2017), being typical compounds of membrane lipids in marine organisms (Corsolini & Borghesi 2017).

The amount of energy stored (in the form of lipids) is high or very high in the 3 species compared to other echinoderms in deep sea areas (Drazen et al. 2008). These values demonstrate a high capability to accumulate high quality energetic molecules that will be used to face starvation or/and reproductive periods in a highly seasonal environment. The capability to store energy will depend on the different life cycles and the different trophic guilds, which, in this case, can be considerably different between the 3 groups.

Reproduction features are, in fact, one of the key points in understanding energy storage in marine invertebrates (Rossi et al. 2017). The lower values of lipids found in *O. carinifera* (in the present study) compared with the holothurian may be partly explained by investment in the gonadal output of large eggs during this period. Interestingly, gamete production in this ophiuroid species takes a considerable amount of time, and is different depending on the year cycle considered (Grange et al. 2004). We suggest that brittle stars mainly invest energy stored after the window of primary production as reproductive output. The large amount of PUFA may also be an indicative marker, as these fatty acids are related to the development of membranes, nervous tissues and early stage development, transferred from mother to the offspring (Bell & Sargent 1996, Viladrich et al. 2017). Sessile and low mobility animals living in deep waters may adjust their growth and reproduction according to temporally and spatially variable food availability (Yasuda et al. 2016). Organisms in the deep sea can thus exhibit temporal and spatial changes in the diet and in reproductive patterns depending on the presence of food banks (Galley 2003, Galley et al. 2008).

Mobility to search for food to achieve the energy storage needed for movement and reproduction is an important quality for at least the ophiuroid and the holothurian. The eurybathymetry of *O. carinifera* allows this species to inhabit both shallow areas and deep zones (Brey & Gerdes 1998, Sands et al. 2013, Ambroso et al. 2016). The same species in different Weddell Sea areas may display very different lipid concentrations, depending on the

environmental conditions (Elias-Piera et al. 2013). For example, the FA markers in King George Island and Larsen area A (Antarctic Peninsula) were very similar, and these 2 sites have a strong seasonal pattern of primary productivity blooms (Elias-Piera 2014, Sañé et al. 2011). However, in the Larsen areas B and C, the amounts of energy stored (and markers of diatom origin) were represented in higher amounts, demonstrating a link between food source and potential accumulation at higher trophic levels, as well as a differential capability to store energy within a single species (Elias-Piera 2014).

R. racovitzai has not only the highest amount of total lipids, but that its carbohydrate and FFAs stores are also significantly higher than in the other 2 echinoderms. Carbohydrates are labile molecules that can be readily incorporated into the Krebs cycle to satisfy metabolic energy demand. A high concentration of carbohydrates in suspension feeders is related to periods in which there is a high metabolic demand (Rossi et al. 2006b). This is interesting, since we find that the FFAs also have a higher concentration in this species than the other 2 echinoderms. Most lipid components that can be considered energy reserves may be oxidised to obtain FFAs (Gurr et al. 2002); those FFAs can be beta-oxidised providing highly efficient energy sources (i.e. a high ATP/FA relationship; Sargent et al. 1988). This means that, among the 3 studied echinoderms, the holothurian seems to be the more metabolically active during the spring period studied (both carbohydrates and FFAs are significantly higher). In this time of the year (and in this area), sediments are quite poor in labile organic material (Isla et al. 2011). We suggest that holothurians are capable of moving, locating, and grazing directly on fresh (and patchily distributed) new green carpets, produced during the first spring blooms, and on the chlorophyll *a* (primary productivity) below the sediment surface. However, this movement has a metabolic cost in terms of respiration and energy mobilization. Thus, the difference in energy storage, but especially in mobilizable molecules, may be thus partly explained because of this behaviour. In deep waters, holothurians may digest up to 63% of the biopolymeric carbon found in the surrounding sediments (especially proteins, but also lipids and carbohydrates) (Amaro et al. 2010), so the transfer of organic matter is quite efficient. The deposit feeder can select, ingest and assimilate the available organic matter (Hudson et al. 2004) using foraging and digestion strategies, which can involve 2 cases: a particle selection where the animal chooses food-rich matter during the capture of particles and ingestion (Levin et al. 1997, Billett et al. 2001, Purinton et al. 2008) or a selective assimilation where the animal digests and/or assimilates a subset of organic matter in its gut (Penry & Jumars 1990, Purinton et al. 2008). In *Protelpidia murrayi*, *Bathyplotes bongraini* and *Molpadia musculus*, the second case occurs, increasing the selective digestion and/or assimilation due to the selectivity of phytodetritus clumps during ingestion (Purinton et al. 2008).

D. antarcticus cannot choose the ingested material, being a sessile suspension feeder. This echinoderm is present in large numbers in the Antarctic Peninsula continental platform (Larsen) and deep areas (Gutt et al. 2011, Eléaume et al. 2012). This crinoid intercepts the particles by expanding its complex branches to the main flux (Macurda & Meyer 1974). The reproduction of these organisms in deep waters is completely unknown: no cycle of gonadal development or gonadal output observation has been made so far. Based on other Antarctic suspension feeding organisms such as gorgonians (Orejas et al. 2007), this strategy may also accumulate large quantities of lipids (Elias-Piera et al. 2013) to produce gametes that will be released in summer–autumn. However, this hypothesis needs to be tested in further research, since we did not observe any sexual product in the *D. antarcticus* collected. The amount of labile macromolecules ready to be mobilised (carbohydrates and FFAs found in the tissues) was low,

and it is possible that the stalked crinoids may simply use the reserves accumulated in summer–autumn and maintained through the resuspension processes in winter, to survive until a new set of phytoplankton blooms bring food to their filter organs.

Interestingly, related to the fact that the samples were collected at the beginning of spring, the 3 echinoderms contained long-chain FFAs. These molecules are considered of high energetic content (Dalsgaard et al. 2003), and may be a key factor to face seasonal (winter) food constraints in benthic suspension feeders in Antarctica (Servetto et al. 2017). The observed lipids and proteins may indicate a clear tendency toward a mechanism of energy accumulation instead of growth (Elias-Piera et al. 2013), which has been demonstrated to be very slow in the few suspension-feeding organisms analysed in Antarctic waters (Martínez-Dios et al. 2016). Deep sea waters in Antarctica are one of the less studied environments worldwide. The strong seasonality also affects these remote areas, in which the abundance of different organisms is not negligible (Brandt et al. 2007a,b). This may be due to an accumulation of labile material that possibly remains intact for months, as mentioned in the 'Introduction'. In the Orleans Submarine Canyon (Brandsfield Strait, Antarctic Peninsula), a high amount of lipids was detected in the sediments, being almost 2 orders of magnitude higher relative to the shallower water sediments (S. Rossi unpubl. data). In fact, downslope flows occur in this area continuously (Baines & Condie 1998), fueling the deeper areas with a high quality of organic matter in productive periods. Deep zones in these areas of the Southern Ocean may thus be richer than other areas of the world in which the primary productivity is high, but the low temperature in deep sea decreases the metabolism of the associated biota and helps to preserve the organic matter (Mincks et al. 2005, Isla et al. 2006b). The quantity of lipids accumulated in Antarctic organisms seems to be, in general, elevated compared to other areas of the world (Gili et al. 2006b, Elias-Piera et al. 2013, Elias-Piera 2014, Servetto et al. 2017). In other cold seas, the response of the organisms to such phytoplankton blooms is similar, the accumulation of lipids being an important factor for their survivorship (Parrish et al. 2009). It is thus not surprising that the 3 studied echinoderms store a high amount of lipids, even at this time of the year, when the sources of food become scarcer (Isla et al. 2011). The high diversification of sea cucumbers in these deep-sea polar waters (O'Loughlin et al. 2011) may be partially explained by this high energetic content and a very stable environment that stimulates diversification and complex interactions between organisms (Gili et al. 2006b). A variable response to a phytoplankton bloom with respect to phenology, even within taxonomic orders, will depend on feeding behavior and gonadogenesis of the species (Parrish et al. 2009).

Climate change is expected to alter the relative contribution of food sources for benthic organisms (Rossi et al. 2017, Gaillard et al. 2017), so it will be essential to understand how expected alterations in available organic matter affect deep-sea communities and their adaptations. The use of indirect tools (biomarkers) may help obtain a clearer picture of what will happen in the coming decades to this rich, pristine but fragile area of the world.

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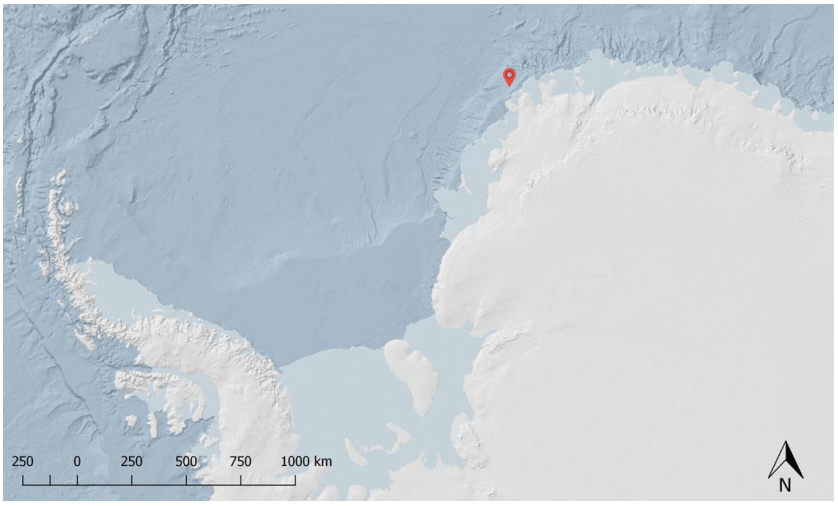

664

665 Fig. 1. Sampling area (red pin at 70°7.88’S, 11°21.56’W) around 1500 m depth in the Weddell
666 Sea (ANT XXI-2 Polarstern cruise)

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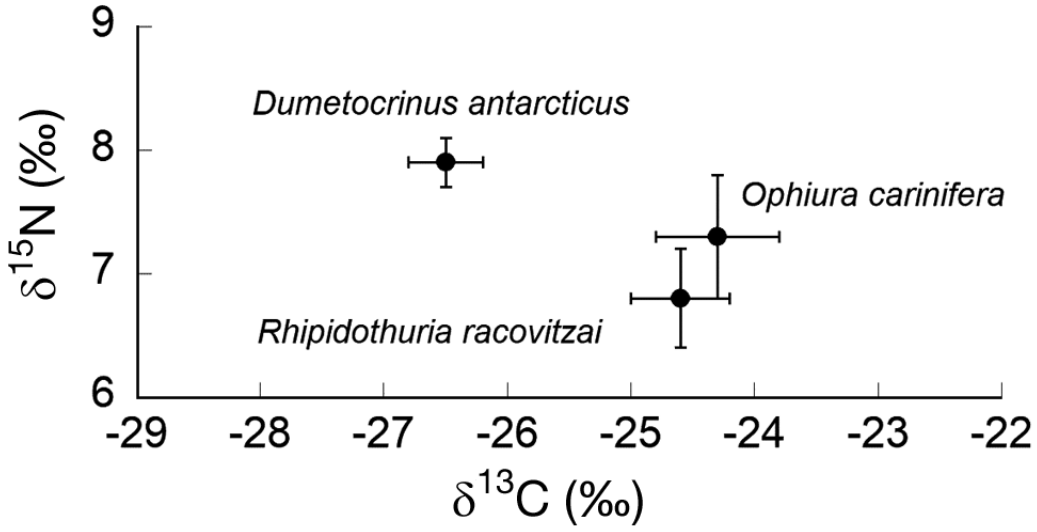

670

671 Fig. 2. Stable isotope values ($\delta^{13}C$ versus $\delta^{15}N$, in ‰) of the 3 species of echinoderms
672 *Rhipidothuria racovitzai*, *Dumetocrinus antarcticus* and *Ophiura carinifera* from the Weddell
673 Sea at 1500 m depth. Data are means ± SD

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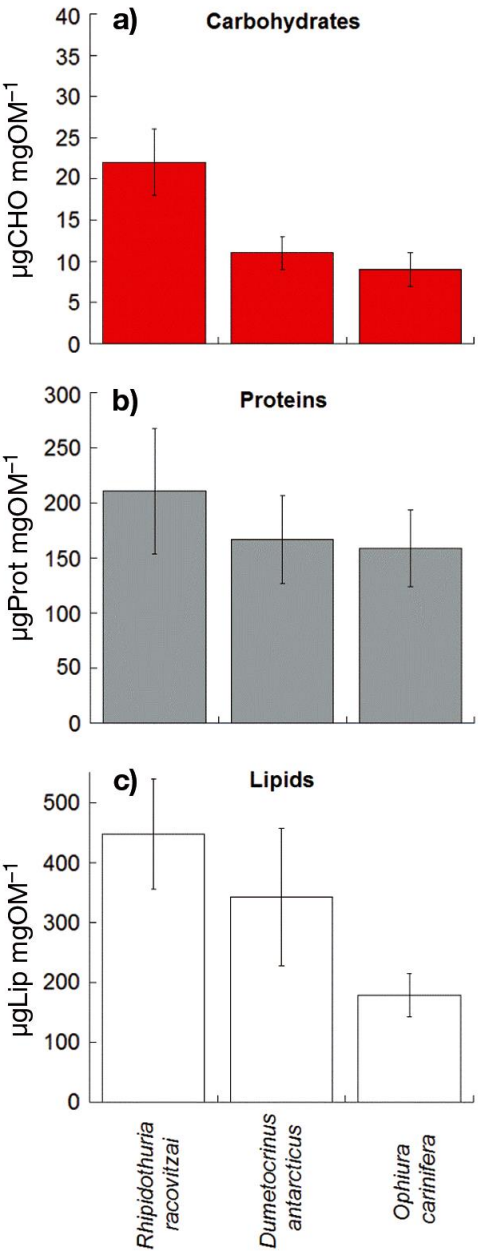

Fig. 3. Biochemical analyses. (a) Carbohydrate (CHO), (b) protein (Prot), and (c) lipid (Lip) content compared to organic matter (µg $mgOM^{-1}$) in the 3 species of echinoderms *Rhipidothuria racovitzai*, *Dumetocrinus antarcticus* and *Ophiura carinifera* from the Weddell Sea at 1500 m depth. Data are means ± SD

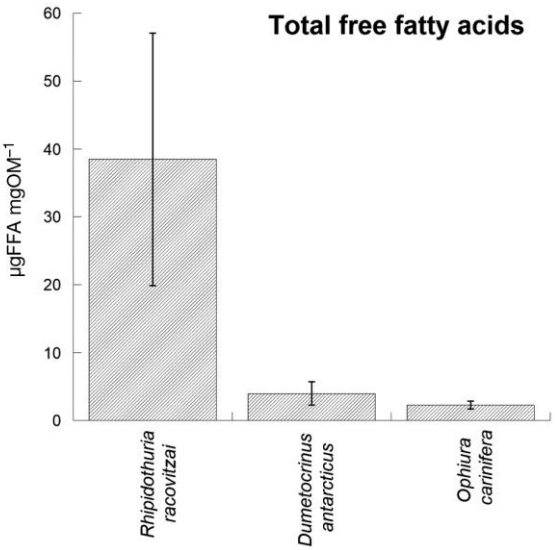

Fig. 4. Total concentration of free fatty acid content compared to organic matter (µgFFA $mgOM^{-1}$) of 3 species of echinoderms *Rhipidothuria racovitzai*, *Dumetocrinus antarcticus* and *Ophiura carinifera* from the Weddell Sea at 1500 m depth. Data are means ± SD

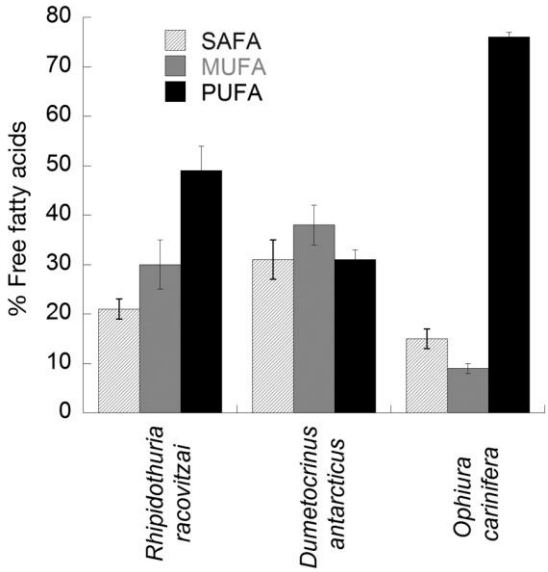

Fig. 5. Proportions (%) of the different groups of free fatty acids (SAFA: saturated; MUFA: mono-unsaturated; PUFA: polyunsaturated) of 3 species of echinoderms *Rhipidothuria racovitzai*, *Dumetocrinus antarcticus* and *Ophiura carinifera* from the Weddell Sea at 1500 m depth. Data are means ± SD

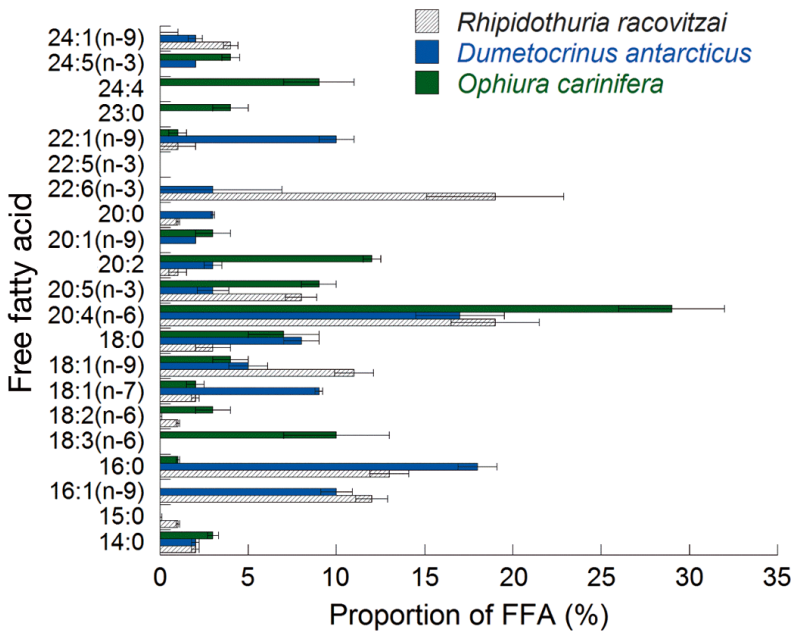

Fig. 6. Free fatty acid (FAA) composition (as a% of the total FFAs) of 3 species of echinoderms *Rhipidothuria racovitzai*, *Dumetocrinus antarcticus* and *Ophiura carinifera* from the Weddell Sea at 1500 m depth. Data are means ± SD

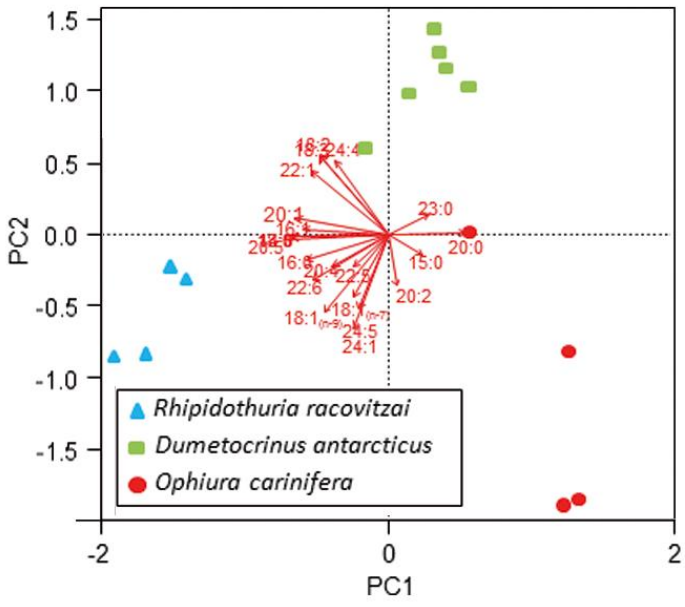

Fig. 7. Principal component analysis (PCA) of the representative fatty acids in the 3 species of echinoderms *Rhipidothuria racovitzai*, *Dumetocrinus antarcticus* and *Ophiura carinifera* from the Weddell Sea at 1500 m depth