

Trophic ecology of seven Antarctic gorgonian species

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ABSTRACT: The trophic ecology of Antarctic anthozoans and their role in benthic–pelagic coupling processes is poorly understood. We studied 7 gorgonian species (*Primnoisis* sp., *Fannyella nodosa*, *Ainigmaptilon antarcticum*, *Notisis* sp., *Primnoella* sp., *Dasystenella* sp. and *Thouarella* sp.) in 2 Antarctic regions: the Eastern Weddell Sea and the Bransfield Strait (Antarctic Peninsula) in austral autumn 2000, a period in which primary productivity drastically decreases. We aimed at finding the main food sources for these gorgonians and to elucidate the strategies of the 7 species in this season, relating the obtained data with their biology and ecology. Stable isotope data of the 7 gorgonian species was virtually the same as that measured in the phytodetritus of the so called ‘green carpets’ and in microzooplankton ($\delta^{13}\text{C}$ from -27.7 to -24.8‰ ; $\delta^{15}\text{N}$ from 4.1 to 7.5‰). A large proportion of the gorgonian’s diet seems to be based on sedimented and resuspended material, which supports the hypothesis that some suspension feeders deal successfully with the Antarctic winter by consuming phytoplankton sedimented in the ‘green carpets’. While stable isotope analysis suggested similar food sources for 7 species, the biochemical balance indicated different energy storage as lipid values (mean \pm SD) ranged from 105.1 ± 99 to 776.4 ± 354.1 μg lipids mg^{-1} organic matter depending on the species. Our results contribute to a better understanding of the trophic ecology of benthic Antarctic gorgonians and their strategies for coping with autumn conditions in this polar environment.

KEY WORDS: Weddell Sea · Benthic–pelagic coupling · Stable isotope · Biochemical balance · Lipids · Energy storage · Octocoral · Passive suspension feeder

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INTRODUCTION

Cnidarians and especially gorgonians are one of the major components of Antarctic benthic communities (Starmans et al. 1999, Gili et al. 2001a, Orejas et al. 2003, Teixidó et al. 2004). These organisms are particularly abundant in some locations of the Weddell Sea and the Antarctic Peninsula (Grebmeier & Barry 1991), contributing to the structure of Antarctic benthic communities (Gutt & Starmans 1998). They add 3-dimensional complexity to the habitat as they are ecosystem engineers

of the so-called ‘animal forest’ (sensu Jones et al. 1994, Rossi et al. 2012).

Despite the abundance of gorgonians in polar regions (Starmans et al. 1999, Gili et al. 2001a), few ecological studies have been conducted on this group (trophic ecology: Orejas et al. 2001, 2003; reproductive ecology and distribution patterns: Orejas et al. 2002, 2007). The 2 studies by Orejas et al. (2001, 2003) provide first insights into the feeding ecology of these organisms, but there are still important gaps to cover, as for instance the influence of seasonality on the feeding habits of gorgonians and

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their strategies for coping with the autumn and winter periods.

Benthic suspension feeders are directly (sinking) or indirectly (through re-suspension and lateral transport) dependent on the food input from surface water in spring and summer to cover their energy demands (Thiel et al. 1988, Campos-Creasey et al. 1994). In Antarctic waters, the bloom-derived phytodetritus and zooplankton faecal pellets accumulate on the seafloor and may persist for long periods (Smith et al. 2008), influencing benthic biological processes such as feeding, reproduction and recruitment (Smith et al. 1993, Smith et al. 1996, Thurston et al. 1998, Billett et al. 2001, Gooday 2002).

As benthic suspension feeders, gorgonians depend on suspended particulate organic material (POM) transferred from the surface to the bottom (Gili et al. 2001a). This flow of POM, produced mainly by the phytoplankton, is an important factor in explaining the benthic–pelagic coupling processes in these areas (Wefer et al. 1988, Lampitt et al. 1993, Ducklow et al. 2006).

Trophic ecology studies are difficult, especially in polar areas where sampling is constrained in space and time, and almost all studies are conducted in spring and summer. Few studies have dealt with the predatory effect and benthic–pelagic coupling of cnidarians in Polar waters (Antarctic: Gili et al. 1996, 2006, Orejas et al. 2001, 2003; Arctic: Orejas et al. 2013). These studies are based on gut-content analyses (Gili et al. 1996, Orejas et al. 2001, 2013), and clearance rates under experimentally controlled conditions (Orejas et al. 2001, 2003). Little is known about the capability of Antarctic benthic cnidarians to cope with feeding constraints in the autumn to winter season, a period largely unstudied. One of the few studies conducted in Antarctic shallow waters is that of Barnes & Clarke (1995); these authors recorded the activity of passive and active suspension feeders during a whole annual period, showing that some organisms remain active all year long. Clarke (2003) suggested that, in polar habitats, a large amount of stored energy could be transferred from the water column to the benthic communities to cope with food constraints but also, because of the low metabolic demand in cold seas, to invest in activities other than respiration. Even if food availability is low in areas such as the Weddell Sea or suffers a slow but significant degradation process (Isla et al. 2011), it is clear that benthic suspension feeders in the Antarctic survive the autumn and winter by relying on a metabolic strategy in which energy is adequately stored to face food constraints. It is not yet

clear, however, which mechanisms Antarctic gorgonians use to overcome the Antarctic autumn and winter, when sediments are enriched in lipids, but water column surface productivity is minimal or absent (Isla et al. 2006b).

Analysis of stable isotope composition is a suitable approach to elucidate the trophic level of an organism because it offers precise information on the characteristics of the assimilated food (e.g. Iken et al. 2001, Jacob et al. 2006, Carlier et al. 2007, Mintenbeck et al. 2007, Mincks et al. 2008). This information can be complemented with analysis of the biochemical balance (protein–carbohydrate–lipid levels). The combination of both methods allows us to understand how different organisms invest their energy depending on the environment and available food, integrating the trophic impact depending on the season and their reproductive strategies (Rossi et al. 2006a, Gori et al. 2007, 2012, Rossi & Tsounis 2007).

We studied the trophic ecology of 7 gorgonian species during the Antarctic autumn in 2000 in both the Eastern Weddell Sea and the Bransfield Strait (Antarctic Peninsula). The main aims of this work were (1) to improve our knowledge of the potential energy source for these organisms by analysing their stable isotope composition (^{13}C and ^{15}N), and (2) to understand, by means of biochemical analyses, how gorgonians face a year period in which primary production is very low or absent, planktonic communities are scarce and other energy sources such as sedimented phytodetritus are available for several months.

MATERIALS AND METHODS

Samples of the 7 gorgonian species *Primnoisis* sp., *Fannyella nodosa*, *Ainigmaptilon antarcticum*, *Notisis* sp., *Primnoella* sp., *Dasystenella* sp. and *Thouarella* sp. were collected on board RV 'Polarstern' in austral autumn 2000 (2 to 26 April) during the ANTXVII/3 cruise, as part of the EASIZ III program (Ecology of the Antarctic Sea Ice Zone). The cruise was conducted in the Eastern Weddell Sea (Kapp Norvegia, Four Seasons Bank and Austasen) and the Bransfield Strait (Antarctic Peninsula) (Fig. 1, Table 1). The Eastern Weddell Sea was studied by Voß (1988), who described the dominant presence of sandy bottoms and dense sponge spicule mats, bryozoan debris and stones. A high number of taxa, species diversity and evenness are key characteristics of these Weddell Sea areas (Orejas et al. 2002, 2003, 2007). Kapp Norvegia is a well-studied area with

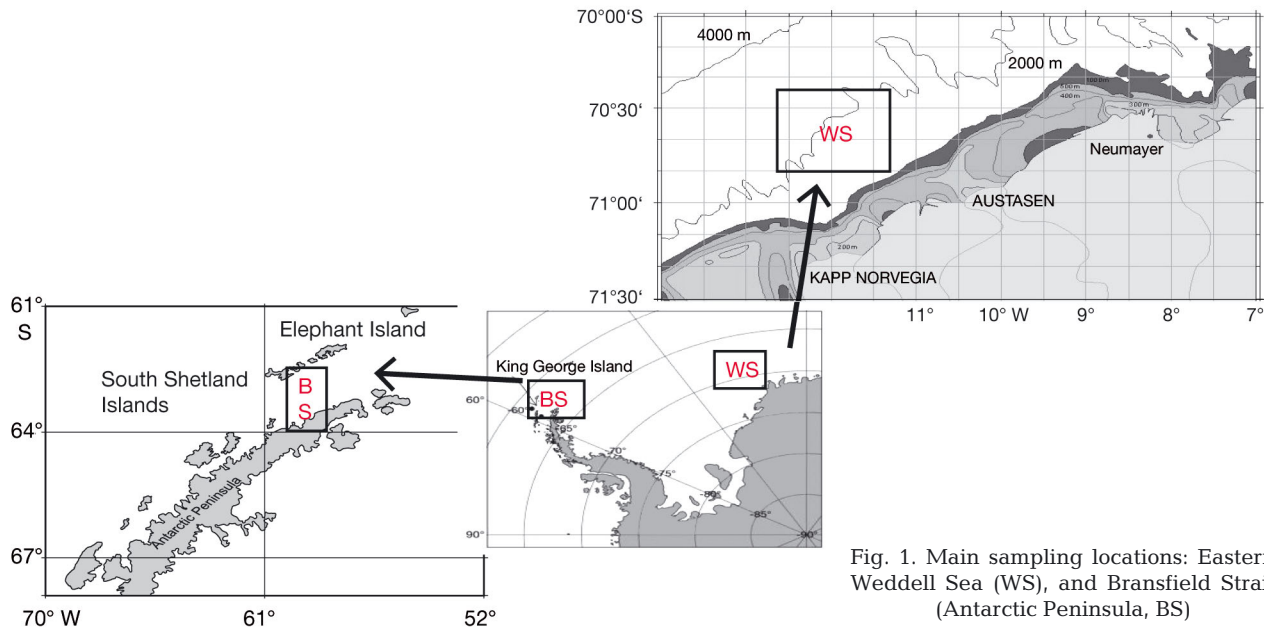


Fig. 1. Main sampling locations: Eastern Weddell Sea (WS), and Bransfield Strait (Antarctic Peninsula, BS)

Table 1. Sampling date (dd.mm.yy), station number, sampling area (WS: Weddell Sea; BS: Bransfield Strait), Zones of WS (KN: Kapp Norvegia; FS: Four Seasons Bank; AU: Austasen), position (latitude and longitude) and depth (m) for the 7 sampled gorgonian species (*A.*: *Ainigmaptilon*; *F.*: *Fannyella*). n: the number of samples collected for each species and at each station for biochemical analyses. For isotopic analyses, 3 samples were collected at each station. At Stn 102, *A. antarcticum* was collected for stable isotope analyses only

| Date | Stn no. | Area | Zone | Lat. (°S) | Long. (°W) | Depth (m) | Species | n |
|----------|---------|------|------|-----------|------------|-----------|-------------------------|----|
| 02.04.00 | 85 | WS | KN | 71°11.30' | 12°15.40' | 309 | <i>Dasystenella</i> sp. | 9 |
| 02.04.00 | 85 | WS | KN | 71°11.30' | 12°15.40' | 309 | <i>Thouarella</i> sp. | 3 |
| 03.04.00 | 102 | WS | KN | 71°11.90' | 12°21.70' | 323 | <i>Primnois</i> sp. | 10 |
| 03.04.00 | 102 | WS | KN | 71°11.90' | 12°21.70' | 323 | <i>A. antarcticum</i> | 0 |
| 03.04.00 | 102 | WS | KN | 71°11.90' | 12°21.70' | 323 | <i>Notisis</i> sp. | 5 |
| 03.04.00 | 102 | WS | KN | 71°11.90' | 12°21.70' | 323 | <i>Dasystenella</i> sp. | 4 |
| 03.04.00 | 102 | WS | KN | 71°11.90' | 12°21.70' | 323 | <i>Thouarella</i> sp. | 15 |
| 04.04.00 | 109 | WS | KN | 71°11.30' | 12°18.50' | 311 | <i>Primnois</i> sp. | 4 |
| 04.04.00 | 109 | WS | KN | 71°11.30' | 12°18.50' | 311 | <i>Notisis</i> sp. | 3 |
| 04.04.00 | 109 | WS | KN | 71°11.30' | 12°18.50' | 311 | <i>Dasystenella</i> sp. | 6 |
| 04.04.00 | 109 | WS | KN | 71°11.30' | 12°18.50' | 311 | <i>Thouarella</i> sp. | 9 |
| 05.04.00 | 111 | WS | FS | 71°07.50' | 11°27.70' | 72 | <i>Primnoella</i> sp. | 5 |
| 05.04.00 | 111-5 | WS | FS | 71°07.50' | 11°27.70' | 66 | <i>Primnoella</i> sp. | 5 |
| 07.04.00 | 119 | WS | AU | 70°50.40' | 10°35.20' | 266 | <i>Primnois</i> sp. | 8 |
| 07.04.00 | 119 | WS | AU | 70°50.40' | 10°35.20' | 266 | <i>A. antarcticum</i> | 7 |
| 07.04.00 | 119 | WS | AU | 70°50.40' | 10°35.20' | 266 | <i>Thouarella</i> sp. | 9 |
| 09.04.00 | 124 | WS | AU | 70°50.60' | 10°35.40' | 247 | <i>Primnois</i> sp. | 10 |
| 09.04.00 | 124 | WS | AU | 70°50.60' | 10°35.40' | 247 | <i>A. antarcticum</i> | 14 |
| 09.04.00 | 124 | WS | AU | 70°50.60' | 10°35.40' | 247 | <i>Thouarella</i> sp. | 15 |
| 10.04.00 | 135 | WS | AU | 70°50.20' | 10°34.70' | 274 | <i>A. antarcticum</i> | 10 |
| 10.04.00 | 136 | WS | AU | 70°50.20' | 10°35.40' | 271 | <i>A. antarcticum</i> | 6 |
| 25.04.00 | 155-7 | BS | | 63°04.85' | 57°31.92' | 96 | <i>F. nodosa</i> | 16 |
| 26.04.00 | 158 | BS | | 63°04.70' | 57°31.60' | 94 | <i>F. nodosa</i> | 10 |

known high primary production rates and current regime, and identified benthic fauna (Gutt & Starman 2001, Isla et al. 2006a,b, 2009). Four Seasons Bank is the shallowest known place in the area with depths <100 m and surrounded by a shelf of ~500 m depth. The Austasen area presents a high density

and transit of icebergs over the shelf, which converts the area into an 'iceberg cemetery' (Gutt 2000, Gutt & Starman 2001). The Bransfield Strait is a highly productive region at all trophic levels (Huntley et al. 1990, Álvarez et al. 2002, Masqué et al. 2002, Zhou et al. 2006). The bottom topography of the Bransfield

Strait consists of a central basin >1000 m deep that is bounded to the northwest by the steep continental margin of the South Shetland Islands (Zhou et al. 2006), consisting of muddy sediments containing gravel or small stones, with communities of sessile epifauna (Troncoso & Aldea 2008). Biogenic sedimentation and glacial deposition act as the main material suppliers (Yoon et al. 1994, Isla et al. 2002).

Samples were collected with bottom trawl (BT) and a TV grab (see Gili et al. 2001b and Table 1 for station list details). Gorgonians were identified on board to the lowest possible taxonomic level, and immediately frozen (−27°C) for laboratory analysis. A total of 186 colonies were preserved for stable isotope composition, organic matter (OM) content and biochemical analysis (Table 1) by freeze-drying subsamples at −110°C and 5 mbar. Freeze-dried samples were stored at −20°C pending analysis.

Stable isotope analysis

Freeze-dried samples of coenenchyme were selected and weighed (0.6 to 1.7 mg) with a microbalance (Mettler Toledo model XS3DU). From each gorgonian species in each station we included 3 replicates (Table 1). Although these octocorals do not have a high inorganic component (Jacob et al. 2005), the tissue was slightly acidified with 10% HCl, in order to remove carbonates, which can bias $\delta^{13}\text{C}$ signatures. The HCl was gently trickled onto each sample. After decalcification, samples were dried in an oven at 60°C and stored in a fridge for 5 h, following protocols from McConnaughey & McRoy (1979), Hobson & Welch (1992) and Jacob et al. (2005).

Stable isotope measurements were performed with a mass spectrometer (Flash EA 1112 HT O/H-N/C). Isotope ratios are expressed as parts per thousand (‰) (difference from a standard reference material) according to the following equation:

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

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

Organic matter content and biochemical analyses

The organic matter (OM) content was calculated by sub-sampling 10 to 15 mg of 'tissue' from each specimen (Table 1). Samples were dried at 80°C for

48 h, weighed and subsequently combusted at 500°C for 4 h. The remaining inorganic ash was then weighed. The difference between dry weight (DW) and ash weight gave the OM content (ash-free dry weight, AFDW) (Slattery & McClintock 1995, Rossi et al. 2006a,b).

The biochemical analyses (i.e. protein, carbohydrate and lipid levels of the OM) were performed spectrophotometrically. The Lowry et al. (1951) method was followed for protein analysis. A tissue sample of 10 to 15 mg was weighed in a microbalance (precision: ± 0.01 mg) and homogenized, grinding the tissue in a crystal potter with 6 ml 1 N NaOH, using albumin as a standard. Carbohydrate content was analysed and quantified following Dubois et al. (1956). A 15 to 20 mg piece of each gorgonian was weighed and homogenized in 6 ml of double-distilled water, using glucose as a standard. Lipids were quantified according to Barnes & Blackstock (1973). A 15 to 20 mg piece of dry tissue was homogenized in 6 ml of chloroform–methanol (2:1 v/v), using cholesterol as a standard. These methods have been successfully applied to other anthozoans (e.g. *Pocillopora damicornis*: Ward et al. 1996, *Heteroxenia fuscescens*: Ben-David-Zaslow & Benayahu 1999, *Paramuricea clavata*: Rossi et al. 2006a,b, *Eunicella singularis*: Gori et al. 2007, *Corallium rubrum*: Rossi & Tsounis 2007). Results are presented as μg protein (P), μg carbohydrate (C) and μg lipid (L) per mg OM.

Statistical design

Differences in stable isotopic signature and biochemical composition between stations (same species compared) and among species were made using 2 different 1-way ANOVA tests. The first ANOVA evaluated the factor 'station' (different stations of the Weddell Sea or the Bransfield Strait) by comparing colonies of the same species between these stations. The second ANOVA compared the different species sampled. Due to the characteristics of the spatial distribution of gorgonians and the haphazard sampling procedure, it was impossible to sample all species at all stations. For statistical significance, a post-hoc Tukey's test was performed, indicating differences between sampling stations (within the same species) or species. The data met the criteria for parametric analysis after logarithmic transformation (Brown-Forsythe test and Levene test, $p = 0.05$, Shapiro-Wilks test, $p = 0.1$), thus permitting the use of an ANOVA test.

RESULTS

Six of the 7 gorgonian species were collected in the Weddell Sea, in 3 different zones: Stns 85 to 109 in Kapp Norvegia (KN), Stns 111 and 111-5 in Four Seasons Bank (FS) and Stns 119 to 136 in Austasen (AU). Only 1, *Fannyella nodosa*, was collected in the Bransfield Strait (BS) (Table 1).

Stables isotopes

All analysed species showed $\delta^{13}\text{C}$ values from -27.7 to -24.8‰ . $\delta^{15}\text{N}$ ranged from 4.1 to 7.5‰ (Fig. 2). All the statistical information of a particular species between stations are summarized in Table 2. There were significant differences within the same species for $\delta^{13}\text{C}$ values in *Primnoisis* sp., *Ainigmaptilon antarcticum*, *Notisis* sp. and *Primnoella* sp., and for $\delta^{15}\text{N}$ in *A. antarcticum* and *Primnoella* sp.

The species-specific ‰ value ranges ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) for the 7 species were as follows: *Primnoisis* sp. (-27.1 to -26.2 and 4.1 to 4.2), *Fannyella nodosa* (-25.1 to -24.7 and 5.5 to 6.3), *Ainigmaptilon antarcticum* (-27.6 to -26.9 and 4.6 to 5.4), *Notisis* sp. (-27 to -26.3 and 5.3 to 6.3), *Primnoella* sp. (-27.1 to -24.8 and 4.2 to 5.9), *Dasystenella* sp. (-26.9 to -26.6 and 6.7 to 7.5), *Thouarella* sp. (-27.2 to -26.2 and 5.1 to 5.6) (Fig. 2).

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among the 7 species differed significantly between *Ainigmaptilon antarcticum* and *Primnoisis* sp. for $\delta^{13}\text{C}$. Statistically significant differences were detected among more species for $\delta^{15}\text{N}$ compared to $\delta^{13}\text{C}$ (Table 3).

Biochemical analyses

Protein, carbohydrate and lipid levels for the 7 species studied are presented in Fig. 3.

Primnoisis sp. presented the lowest protein value ($158.7 \pm 76.9 \mu\text{g protein mg}^{-1}\text{OM}$), whilst *Primnoella* sp. presented the highest protein value with $556.3 \pm 69.4 \mu\text{g protein mg}^{-1}\text{OM}$ (Fig. 3A). The lowest carbohydrate levels were detected in *Fannyella nodosa* with an average value of $12.0 \pm 6.0 \mu\text{g carbohydrate mg}^{-1}\text{OM}$, while the highest value for carbohydrates was found in *Primnoisis* sp. ($80.7 \pm 28.7 \mu\text{g carbohydrate mg}^{-1}\text{OM}$) (Fig. 3B). Finally, lipids showed great variability among species, with the lowest value being detected in *Fannyella nodosa* ($149.0 \pm 108.4 \mu\text{g lipid mg}^{-1}\text{OM}$) and the highest in *Thouarella* sp. ($776.4 \pm 354.1 \mu\text{g lipid mg}^{-1}\text{OM}$) (Fig. 3C).

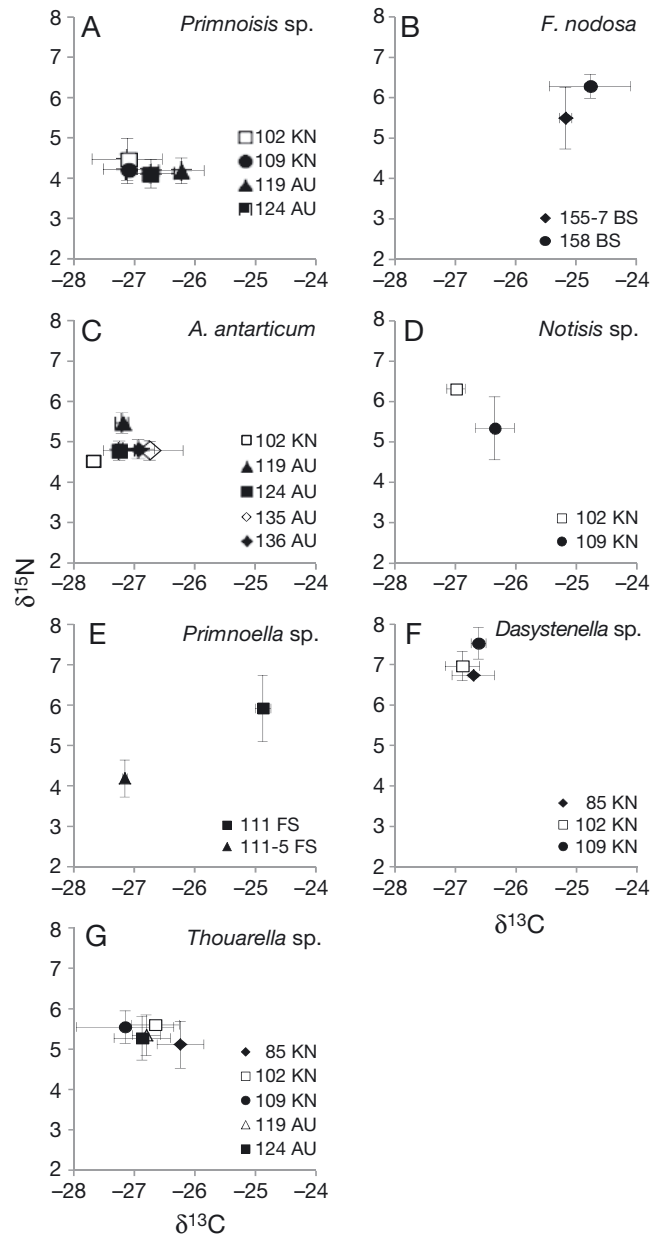


Fig. 2. Stable isotope values ($\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$, in ‰) for the 7 species of gorgonians (A) *Primnoisis* sp., (B) *Fannyella nodosa*, (C) *Ainigmaptilon antarcticum*, (D) *Notisis* sp., (E) *Primnoella* sp., (F) *Dasystenella* sp. and (G) *Thouarella* sp. from Eastern Weddell Sea (stations: Kapp Norvegia: KN; Four Seasons Bank: FS; Austasen: AU) and Bransfield Strait (BS) in autumn 2000 (ANTXVII/3 cruise). Means \pm SD

Table 4 summarizes the significant differences between stations when comparing the biochemical data of the same species: in protein for *Primnoisis* sp., *Fannyella nodosa*, *Ainigmaptilon antarcticum* and *Primnoella* sp.; in carbohydrate levels for *Primnoisis* sp., *A. antarcticum*, *Primnoella* sp. and *Dasystenella* sp., and in lipid levels for: *Primnoella* sp. and *Thouarella* sp.

Table 2. One-way ANOVA for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values comparing *Primnoisis* sp., *Fannyella nodosa*, *Ainigmaptilon antarcticum*, *Notisis* sp., *Primnoella* sp., *Dasystenella* sp. and *Thouarella* sp. between stations. Station codes as in Table 1

| Species | df | $\delta^{13}\text{C}$ | | | $\delta^{15}\text{N}$ | | |
|-------------------------|----|-----------------------|--------|---------------------|-----------------------|-------|--------------------------|
| | | F | p | Difference | F | p | Difference |
| <i>Primnoisis</i> sp. | 11 | 5.32 | 0.006 | 119 \neq 102, 109 | 1.34 | 0.283 | |
| <i>F. nodosa</i> | 5 | 1.11 | 0.353 | | 2.77 | 0.171 | |
| <i>A. antarcticum</i> | 14 | 4.10 | 0.013 | 102 \neq 136 | 5.24 | 0.004 | 119 \neq 102, 124, 135 |
| <i>Notisis</i> sp. | 5 | 9.75 | 0.036 | 102 \neq 109 | 4.56 | 0.099 | |
| <i>Primnoella</i> sp. | 5 | 546.42 | <0.001 | 111 \neq 111-5 | 10.23 | 0.034 | 111 \neq 111-5 |
| <i>Dasystenella</i> sp. | 8 | 0.61 | 0.583 | | 5.65 | 0.052 | |
| <i>Thouarella</i> sp. | 14 | 1.37 | 0.312 | | 0.56 | 0.694 | |

The comparison of species is summarized in Table 5 and revealed significant differences in proteins, carbohydrates and lipids between different species. Lipids were only different between *Dasystenella* sp. and *Thouarella* sp.

DISCUSSION

Main food sources for Antarctic gorgonians in autumn

The overall results obtained from the stable isotope analyses ($\delta^{13}\text{C}$ from -29 to -24‰ ; $\delta^{15}\text{N}$ from 4 to almost 8‰) for the 7 gorgonian species indicate that these octocorals are opportunists and feed on a wide spectrum of suspended particles planktonic organisms, from POM to microzooplankton (Fig. 4). These results agree with previous studies from different regions (Mediterranean: Ribes et al. 1999, 2003, Picciano & Ferrier-Pagès 2007; tropical seas: Ribes et al. 1998; Antarctica: Orejas et al. 2003).

Our finding seem to be confirmed by previous work on the isotopic composition of green carpets, a potential food source during different seasons, because their isotopic values are similar to those of the 7 gorgonian species: In the western Antarctic Peninsula, phytodetritus $\delta^{13}\text{C}$ values range from -25 to -22‰ ($\delta^{15}\text{N}$ from 5.7 to 7.9‰), while surface sediment $\delta^{13}\text{C}$ range from -26 to -24‰ ($\delta^{15}\text{N}$ from 2.8 to 6.4‰), and the $\delta^{13}\text{C}$ of microzooplankton range from -33 to -15‰ ($\delta^{15}\text{N}$ from 3.2 to 7.5‰) (Mincks et al. 2008). In the Weddell Sea where most of the gorgonians of our study were collected, the $\delta^{13}\text{C}$ of POM ranges from -30.4 to -27.3‰ and the $\delta^{15}\text{N}$ from -5.4 to 6.1‰ (Rau et al. 1991). Nyssen et al. (2002) found values of $\delta^{13}\text{C}$ for suspended particulate matter (SPM) ranging from -32 to -28.7‰ , and of $\delta^{15}\text{N}$ from 2.6 to 3.9‰, in agreement with our results (Fig. 4). Our results also agree with previous studies on gorgonians from polar (Jacob et al. 2006) and deep sea areas (Iken et al. 2001, Sherwood et al. 2005). A convergence of deep benthic communities with those of the Antarctic continental shelf has been suggested

Table 3. One-way ANOVA for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values comparing *Primnoisis* sp., *Ainigmaptilon antarcticum*, *Notisis* sp., *Dasystenella* sp. and *Thouarella* sp. between species. Station codes as in Table 1

| Stn no. | df | $\delta^{13}\text{C}$ | | | $\delta^{15}\text{N}$ | | |
|---------|----|-----------------------|-------|--|-----------------------|--------|--|
| | | F | p | Difference | F | p | Difference |
| 85 | 5 | 2.38 | 0.197 | | 23.69 | 0.010 | <i>Dasystenella</i> sp. \neq <i>Thouarella</i> sp. |
| 102 | 14 | 1.48 | 0.257 | | 23.01 | <0.001 | <i>A. antarcticum</i> \neq <i>Notisis</i> sp. and <i>Dasystenella</i> sp. \neq <i>A. antarcticum</i> , <i>Primnoisis</i> sp., <i>Thouarella</i> sp. and <i>Primnoisis</i> sp. \neq <i>Notisis</i> sp., <i>Thouarella</i> sp. |
| 109 | 11 | 2.21 | 0.156 | | 25.57 | <0.001 | <i>Dasystenella</i> sp. \neq <i>Notisis</i> sp., <i>Primnoisis</i> sp., <i>Thouarella</i> sp. and <i>Notisis</i> sp. \neq <i>Primnoisis</i> sp., <i>Thouarella</i> sp. and <i>Primnoisis</i> sp. \neq <i>Thouarella</i> sp. |
| 119 | 8 | 10.88 | 0.004 | <i>A. antarcticum</i> \neq <i>Primnoisis</i> sp. | 19.33 | <0.001 | <i>Primnoisis</i> sp. \neq <i>A. antarcticum</i> , <i>Thouarella</i> sp. |
| 124 | 8 | 6.78 | 0.005 | <i>A. antarcticum</i> \neq <i>Primnoisis</i> sp. | 14.66 | <0.001 | <i>Primnoisis</i> sp. \neq <i>A. antarcticum</i> , <i>Thouarella</i> sp. |

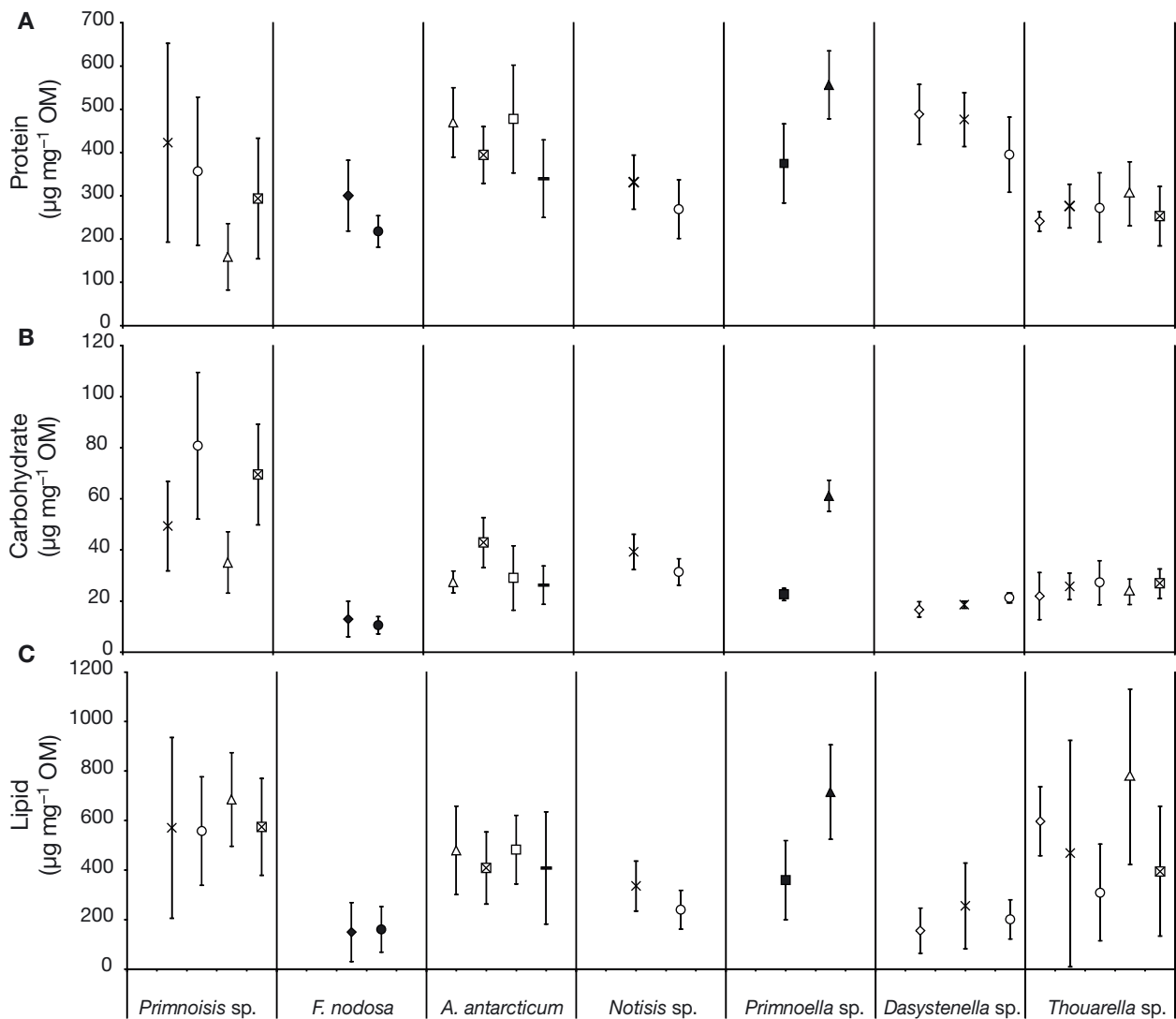


Fig. 3. Biochemical analyses. (A) Protein, (B) carbohydrate and (C) lipid ($\mu\text{g mg}^{-1}$ OM) content in the 7 gorgonian species *Primnoisis* sp., *Fannyella nodosa*, *Ainigmaptilon antarcticum*, *Notisis* sp., *Primnoella* sp., *Dasystenella* sp. and *Thouarella* sp. from Eastern Weddell Sea and Bransfield Strait in autumn 2000 (ANTXVII/3 cruise). Mean \pm SD. Stations: \diamond 85 KN, \times 102 KN, \circ 109 KN, \blacksquare 111 FS, \blacktriangle 111-5 FS, \triangle 119 AU, \boxtimes 124 AU, \square 135 AU, $-$ 136 AU, \blacklozenge 155-7 BS, \bullet 158 BS. Station codes as in Table 1

(Iken et al. 2001), in the sense that both may have suspension feeders with a similar food inputs (Orejas et al. 2003). Our stable isotope values also agree with recent results from Antarctic coastal areas, where the mean $\delta^{13}\text{C}$ signatures for SPM ranged from -25 to -24‰ and the $\delta^{15}\text{N}$ ranged from 2 to almost 7‰ (T. N. Corbisier et al. unpubl. data; Fig. 4). This seems to indicate a common food process of primary productivity in shallow and continental platform habitats, with phytoplankton being the main driver of energy flux processes even in coastal areas. Hence, the results obtained in the present study and the available literature support the hypothesis that the diet of

Antarctic gorgonians relies mostly on sinking or resuspended microphytoplanktonic material, but also partially on microzooplankton (e.g. ciliates, foraminiferans, heterotrophic flagellates). Previous studies on Antarctic gorgonian species have found a very low proportion of zooplanktonic prey in their gastrovascular cavities (Alvà et al. 1997, Orejas et al. 2001, 2003). Aposymbiotic Mediterranean gorgonians feed on zooplankton and detrital POM in similar proportions, with smaller plankton ($<10\ \mu\text{m}$) accounting only for <5 to 10% of the energy demand (Ribes et al. 1999, 2003), and the trophic signature of the $\delta^{15}\text{N}$ in Gori et al. (2012) is similar to the one found in

Table 4. One-way ANOVA for protein, carbohydrate and lipid values comparing *Primnoisis sp.*, *Fannyella nodosa*, *Ainigmaptilon antarcticum*, *Notisis sp.*, *Primnoella sp.*, *Dasystenella sp.* and *Thouarella sp.* between stations. Station codes as in Table 1

| Species | df | Protein | | | Carbohydrate | | | Lipid | | |
|-------------------------|----|---------|-------|----------------|--------------|--------|---------------------------|-------|-------|-------------|
| | | F | p | Difference | F | p | Difference | F | p | Difference |
| <i>Primnoisis sp.</i> | 31 | 3.46 | 0.029 | 102 ≠ 119 | 7.29 | 0.001 | 109 ≠ 102, 119; 119 ≠ 124 | 0.36 | 0.779 | |
| <i>F. nodosa</i> | 25 | 9.03 | 0.006 | 155 ≠ 158 | 1.05 | 0.316 | | 0.00 | 0.980 | |
| <i>A. antarcticum</i> | 36 | 4.21 | 0.012 | 136 ≠ 119, 135 | 7.09 | 0.001 | 124 ≠ 119, 135, 136 | 0.59 | 0.630 | |
| <i>Notisis sp.</i> | 7 | 2.07 | 0.192 | | 2.81 | 0.143 | | 1.98 | 0.207 | |
| <i>Primnoella sp.</i> | 9 | 11.33 | 0.010 | 111 ≠ 111-5 | 171.74 | <0.001 | 111 ≠ 111-5 | 10.20 | 0.013 | 111 ≠ 111-5 |
| <i>Dasystenella sp.</i> | 18 | 3.02 | 0.076 | | 6.21 | 0.010 | 85 ≠ 109 | 1.57 | 0.238 | |
| <i>Thouarella sp.</i> | 50 | 1.12 | 0.355 | | 0.75 | 0.561 | | 2.74 | 0.039 | 109 ≠ 119 |

Table 5. One-way ANOVA for protein, carbohydrate and lipid values comparing the factor Species (*Primnoisis sp.*, *Ainigmaptilon antarcticum*, *Notisis sp.*, *Dasystenella sp.* and *Thouarella sp.*). Station codes as in Table 1

| Stn no. | df | Protein | | | Carbohydrate | | | Lipid | | |
|---------|----|---------|--------|---|--------------|--------|---|-------|--------|---|
| | | F | p | Difference | F | p | Difference | F | p | Difference |
| 85 | 11 | 34.85 | <0.001 | <i>Dasystenella sp.</i> ≠ <i>Thouarella sp.</i> | 2.43 | 0.147 | | 40.21 | <0.001 | <i>Dasystenella sp.</i> ≠ <i>Thouarella sp.</i> |
| 102 | 33 | 3.70 | 0.022 | | 13.34 | <0.001 | <i>Dasystenella sp.</i> ≠ <i>Notisis sp.</i> , <i>Primnoisis sp.</i> , <i>Thouarella sp.</i> | 0.92 | 0.551 | |
| 109 | 21 | 2.30 | 0.110 | | 19.41 | <0.001 | <i>Primnoisis sp.</i> ≠ <i>Dasystenella sp.</i> , <i>Notisis sp.</i> , <i>Thouarella sp.</i> | 1.88 | 0.170 | |
| 119 | 23 | 30.75 | <0.001 | <i>A. antarcticum</i> ≠ <i>Primnoisis sp.</i> , <i>Thouarella sp.</i> and <i>Primnoisis sp.</i> ≠ <i>Thouarella sp.</i> | 4.54 | 0.023 | <i>Primnoisis sp.</i> ≠ <i>Thouarella sp.</i> | 2.22 | 0.140 | |
| 124 | 38 | 9.46 | <0.001 | <i>A. antarcticum</i> ≠ <i>Primnoisis sp.</i> , <i>Thouarella sp.</i> | 37.88 | <0.001 | <i>A. antarcticum</i> ≠ <i>Primnoisis sp.</i> , <i>Thouarella sp.</i> and <i>Primnoisis sp.</i> ≠ <i>Thouarella sp.</i> | 2.32 | 0.111 | |

the present study. While the primary productivity processes and the available food are clearly different in both areas (warm temperate mediterranean versus polar sea), the morphological constraints of the octocorals are crucial to understand these differences in the diet and prey capture rates (Gili et al. 2001a).

One hypothesis to explain the $\delta^{15}\text{N}$ enrichment between POM and benthic suspension feeders (in this case octocorals) is that the assimilation of resuspended or sinking OM takes place during a period of strong microbial activity (Antarctic autumn is characterized by a post-bloom situation, Isla et al. 2006b) corresponding with maximal bacterial activity (Karl 1993). Part of the OM carbon would probably be assimilated by flagellates, ciliates and other microzooplankton, which will then be consumed by the

gorgonians. This greater isotopic enrichment of benthic organisms due to the assimilation of resuspended and microbial-derived OM has already been suggested by Hobson et al. (1995) for an Arctic polynia food web (Nyssen et al. 2002) and highlighted by Mincks et al. (2008). These authors found significant differences for $\delta^{15}\text{N}$ of sinking POM between the winter samples and the rest of the seasons. Higher $\delta^{15}\text{N}$ values during winter months suggest sedimentation of refractory OM such as the one contained in krill faecal strings and exuviae following the end of the summer blooms (Smith et al. 2006).

These findings suggest that the studied gorgonians (and probably other passive suspension feeders) could survive for long periods (e.g. Antarctic autumn and winter) fuelled by the so-called 'foodbanks'

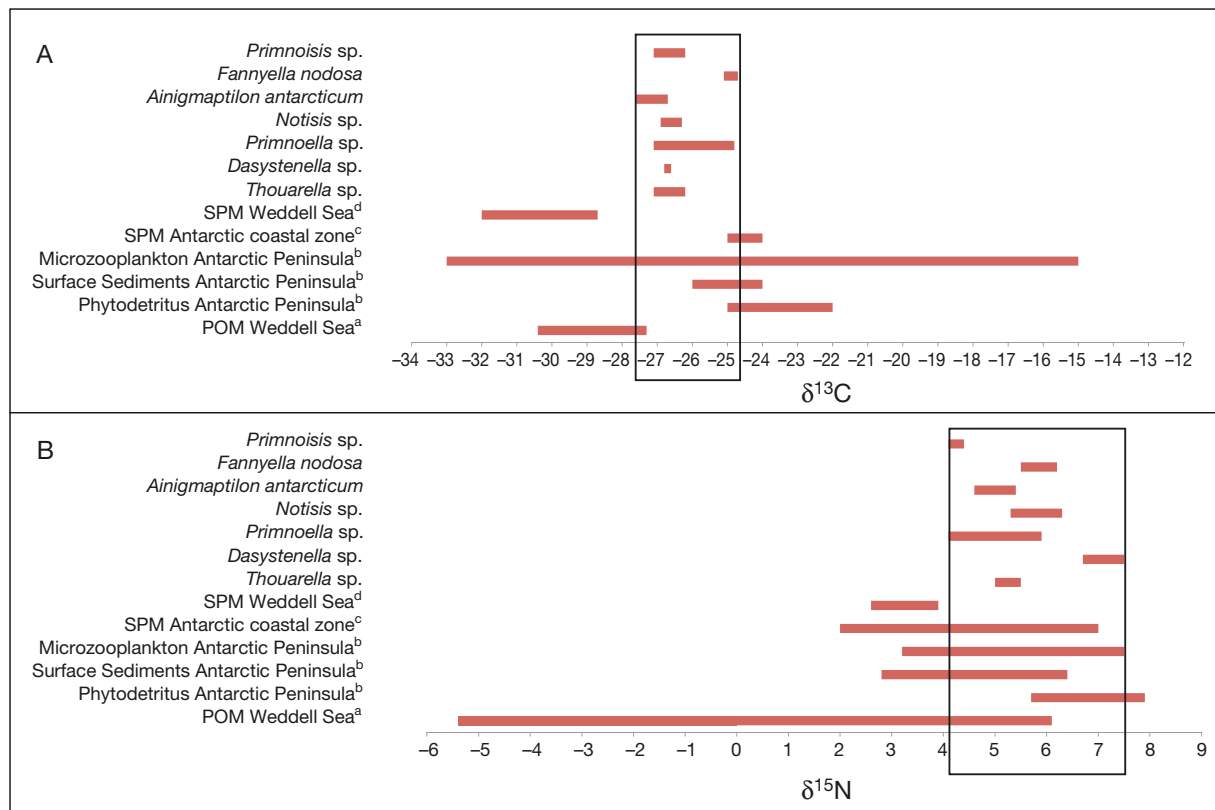


Fig. 4. Comparison between stable isotope values for the 7 gorgonian species *Primnoisis* sp., *Fannyella nodosa*, *Ainigmaptilon antarcticum*, *Notisis* sp., *Primnoella* sp., *Dasysystenella* sp. and *Thouarella* sp. from Eastern Weddell Sea and Bransfield Strait in autumn 2000 (ANTXVII/3 cruise), and data from ^aRau et al. (1991), ^bMincks et al. (2008), ^cT. N. Corbisier et al. (unpubl. data) and ^dNyssen et al. (2002). (A) $\delta^{13}\text{C}$ values (‰) and (B) $\delta^{15}\text{N}$ values (‰). SPM: suspended particulate matter; POM: particulate organic matter

(Smith & DeMaster 1999, Mincks et al. 2005, Smith et al. 2006). Mintenbeck et al. (2007) suggested that large diatoms are not the main food source for benthic suspension feeders in Antarctic waters, but we show that the values obtained for the 7 gorgonian species agree with values obtained from POM originating from algal blooms or faecal pellets. It is important to stress that Mintenbeck et al. (2007) did not consider gorgonians in their study, but mainly analysed carnivorous anemones. So this could be the reason why their results do not agree with ours. The large blooms, dominant in late spring to early summer (Michels et al. 2012), disappear in early autumn (Dower et al. 1996). Even if the picoplankton and bacterioplankton remain active throughout the year in very low concentrations, the green carpets are almost the only food source for suspension feeders. The carpets may fuel the system with resuspended and horizontally transported material through the tidal currents (Isla et al. 2006b) during autumn and winter. Indeed, Barnes & Clarke (1995) demonstrated that most benthic suspension feeders did not experi-

ence a dormant period during autumn and winter in Antarctic shallow waters. For example, some bryozoan species were active during winter and hydrozoans only had a short dormant period in August. The OM deposited in the sediment has a high nutritive value due to the slow decomposition rates in Antarctica (Cripps & Clarke 1998), and reaches the sea floor in fairly fresh condition (Isla et al. 2006a, Mincks et al. 2008). It is possible that this OM, once captured or ingested, is rapidly processed by the benthic suspension feeding and depositivore organisms (McMahon et al. 2006, Sun et al. 2009). An increment in food input in the Arctic sediments results in a subsequent fast increase in benthic (meiofaunal) activity (oxygen demand) (Morata et al. 2011). Carroll & Carroll (2003) suggest a mismatch scenario in polar seas, resulting in strong vertical fluxes of fresh POM to the seafloor which can be directly used by benthic organisms (Hobson et al. 1995, McMahon et al. 2006). The sediment is only OM depleted at the end of the winter and the beginning of the spring (Isla et al. 2011), which may

explain the lower activity of these suspension feeding organisms (Barnes & Clarke 1995).

It is important to stress that the results obtained for stable isotopes showed few significant differences between species and stations regarding the main trophic source (only *Primnoella* sp. showed large differences, but this species also showed differences in the biochemical balance, see next section). The differences do not seem to be ecologically relevant, because isotopic signatures in consumer tissues are related to the isotopic composition of the diet, with an enrichment of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) in the consumer compared with its food of ~1‰ and 3 to 4‰, respectively (Minagawa & Wada 1984, Fry 2006). This enrichment is too small to represent any important ecological difference, because in long-lived benthic invertebrates, turnover rates for $\delta^{13}\text{C}$ in muscle tissue can last a year or more (Fry 2006). The food source seems to be the same for these 7 gorgonian species, in line with previous results found in Antarctica (Orejas et al. 2001, 2003), even comparing a large geographical area. We concluded that the main source of food for gorgonians in the austral autumn is the green carpet material, but the energy storage strategy revealed by the biochemical balance seems to be quite different between species and locations.

Strategies to cope with food constraints

Although the stable isotope analyses indicated similar feeding strategies for the 7 gorgonian species, the biochemical analyses indicated different energy storage capabilities. Some differences in energy storage capability were also observed within the same species among different stations. This was especially evident in *Primnoella* sp., the only species from the 7 that was sampled at the shallow Four Seasons Bank (Weddell Sea; 80 to 100 m depth), a seamount with a fauna clearly different from its much deeper surroundings (Raguá-Gil et al. 2004). This seamount displays higher chlorophyll *a* concentrations at its surface during autumn in comparison to surrounding areas ($0.12 \pm 0.02 \mu\text{g chl } a \text{ l}^{-1}$ versus $0.05 \pm 0.01 \mu\text{g chl } a \text{ l}^{-1}$ at Austasen, S. Rossi pers. obs.). The lipid and carbohydrate concentrations for *Primnoella* sp. (and different $\delta^{15}\text{N}$ signatures) indicated different energy storage capabilities or strategies, probably due to different food availability even when the depth range is similar. In this type of megapibenthic community, local environmental constraints are the main contributors to species distribu-

tion and abundance, which are especially marked in this case for a singular topography (Raguá-Gil et al. 2004). The sediments in Four Seasons bank are coarse (>90 % are >200 μm) and sediment lipid concentration in autumn is low compared to adjacent areas (Isla et al. 2006a), so the main food source for this gorgonian will be more irregular and probably also based on microzooplankton (which seems to be in line with the isotopic signature of the $\delta^{15}\text{N}$). This could be the cause of the significant difference between Stns 111 and 111-5. Rossi et al. (2006a) argue that lipids reflect the capability of a species to integrate environmental differences, even over very short distances (Rossi & Tsounis 2007, Gori et al. 2012). Studies conducted on warm temperate sea gorgonians have shown that small differences in spatial location can be reflected in different biochemical patterns (Rossi 2002, Gori et al. 2007, 2012). The other 6 gorgonian species (not sampled on the Four Seasons Bank) showed fairly similar protein, lipid and carbohydrate concentrations, probably because the flatter substrate (Gutt & Starman 1998) promotes a more homogeneous distribution of food due to tidal currents (Isla et al. 2006b).

Lipid content in sediments may vary among different areas of the eastern Weddell Sea, but in general is high (0.3 to 4.4 $\mu\text{g lipid mg}^{-1}$ DW, Isla et al. 2006a). In the Bransfield area, lipid content is even higher (0.7 to 7.9 $\mu\text{g lipid mg}^{-1}$ DW, S. Rossi & E. Isla pers. obs.) due to the rapid sinking of OM in the submarine canyon (Isla et al. 2004). The amount of labile metabolites (lipids) seems to contradict this, because *Fannyella nodosa* has lower carbohydrate and lipid values with respect to the other studied gorgonian species. The overall balance is far from 100% (protein-lipid-carbohydrate) (e.g. *F. nodosa* 462.6 $\mu\text{g C-P-L mg}^{-1}$ OM and *Primnoella* sp. 756.3 $\mu\text{g C-P-L mg}^{-1}$ OM), due to the high amount of structural proteins (gorgonin-like) undetectable by the Lowry et al. (1951) methodology (Rossi et al. 2006a). The relatively low lipid and carbohydrate levels of *F. nodosa* could be related to the sampling location (Bransfield Strait), which is environmentally different from the eastern Weddell Sea.

The low lipid values, however, could also be related to recent spawning events, which highly influence the lipid content of several Mediterranean gorgonians (Rossi et al. 2006a,b, 2012, Rossi & Tsounis 2007, Gori et al. 2012). Is possible that spawning had already occurred in *Fannyella nodosa* and part of the lipids had been spent on gonadal output, as has been observed for *F. rossi* and *F. spinosa* (Orejas et al. 2007). Individual biochemical reactions examined in

previous studies on polar species are typically exposed to narrower temperature ranges than those in other latitudes (Clarke 2003), and this could highly influence the investment of organisms in storage, metabolism and biological processes. However, reproductive traits also have to be taken into account in understanding this large energy storage in late summer to early autumn (40 up to 80% of the OM). Lipid stores could provide the energy and materials needed for reproduction in the studied octocorals before winter, because POM quantity and quality decrease over time (Lee et al. 2006, Isla et al. 2011).

The long Antarctic winter with its low food availability seems to be one of the main causes for the observed lipid storage in Antarctic benthos (Gili et al. 2009). Considering that the spawning of some Antarctic gorgonians can take place in the austral spring and summer (Orejas et al. 2002, 2007), the high level of lipids observed in most of the studied gorgonians may be a response to the autumn and winter period, but also a strategy to store energy which will be needed for the sexual products (larvae or eggs).

Orejas et al. (2002) show that in some Antarctic and deep-sea species, oocytes are large (>600 µm). In autumn, oocytes of *Ainigmaptilon antarcticum* can reach diameters of up to 900 µm (which is large compared to oocytes from gorgonians sampled at different latitudes and also Antarctica; e.g. Coma et al. 1995, Kapela & Lasker 1999, Excoffon et al. 2004, Tsounis et al. 2006, Orejas et al. 2007, Ribes et al. 2007). The possible brooding reproductive strategy of *A. antarcticum* (Orejas et al. 2002) could be the reason for the high lipid content detected in this species. This energy storage strategy may also be related to the reproductive traits observed in some of the other studied species; nevertheless, none of these species showed such a high lipid content as *A. antarcticum*, *Thouarella* sp., *Fannyella nodosa*, *Dasystenella* sp. and *Primnoella* sp. showed a lower energy storage capability than *Primnoisis* sp., *Notisis* sp. and *A. antarcticum*. Spawning of *T. variabilis* presumably occurs during the summer and the swimming planulae settle soon after release (Brito et al. 1997, Arntz & Gili 2001). Larvae have been found in the gastrovascular cavities of the polyps of *F. rossi*, *F. spinosa* and *Thouarella* sp. (Orejas et al. 2007) in samples collected in the late summer. The relatively small oocyte size for these species suggest small larvae, which could be the reason for a lower level of lipid storage in comparison to *A. antarcticum*. Hence, reproductive strategies can help to increase understanding of differences in lipid concentration and storage capa-

bility. *Dasystenella* sp. also exhibits small oocytes in late summer to early autumn (Orejas et al. 2007), but gametes may not have been present during sampling (April 2000), which could also explain the low lipid amounts detected in this study.

The accumulation of persistent sediment food banks may constitute an important energy source for the Antarctic benthic ecosystem, which will act as a buffer to the strong seasonal variability of the surface waters (Smith et al. 2006, Gili et al. 2009). The 7 gorgonian species studied seem to store energy in different ways. There is a potential relationship with different reproductive strategies, and we do need to understand how these organisms invest their energy in other biological processes (i.e. growth, respiration, production of secondary metabolites) in autumn and winter. Measurements of seasonal and latitudinal changes in stable isotope composition and biochemical balance would help to better understand the ecology of benthic organisms and their role in benthic–pelagic coupling.

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