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A stable isotope approach to the eastern Weddell Sea trophic web: focus on benthic amphipods

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Abstract Stable isotope ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) analyses were performed on 90 species belonging to different benthic communities sampled in the eastern Weddell Sea. The study focused on eight amphipod species whose isotopic composition was compared to their previously described respective gut contents. Amphipod stable isotope ratios correspond fairly accurately to the trophic classification based on gut contents and attest to their wide spectrum of feeding types. Since the fundamental difference between the isotope and the gut content approaches to diet studies is the time scale each method addresses, this coincidence indicates that there would be no significant changes in feeding strategies over time. Three levels of the food web are covered by the eight species and, instead of belonging strictly to one trophic category, amphipods display a continuum of values from the suspension-feeder to scavengers.

Introduction

With more than 1,000 strictly Antarctic species, the peracarid Crustacea are the most speciose animal group in the Southern Ocean. Among them, the amphipods, with 531 Antarctic species and 821 species in the whole Southern Ocean, are clearly the most diverse. (Klages 1991; De Broyer and Jazdzewski 1996; De Broyer et al. 1999; Gutt et al. 2000). Trophic diversity and species diversity are obviously related. In Antarctic waters, and

on Antarctic bottoms, suitable microhabitats for amphipods are numerous and diversified, which allows them to adopt various life-styles: epontic dwellers, (benthic-) pelagic swimmers, walkers, crawlers, burrowers, borers and inquilines in or on different invertebrates. This diversity in microhabitats, associated with the variety of potential food, is likely to be a factor that has favoured the adaptive radiation of the Amphipoda and the diversification of trophic types in Antarctic waters (Jazdzewski et al. 1996; Dauby et al. 2001a, b; De Broyer et al. 2001). Furthermore, peracarid crustaceans are important food sources for many Southern Ocean benthic invertebrates (e.g. Dearborn 1977; Dearborn et al. 1991; McClintock 1994), demersal and benthic fishes (e.g. Kock 1992; Olaso et al. 2000), many birds (e.g. Ainley et al. 1992; Cherel and Kooyman 1998; Jazdzewski and Konopacka 1999) and marine mammals (e.g. Dearborn 1965; Green and Burton 1987). Regarding total energy flow in the eastern Weddell Sea shelf ecosystem, they are among the key taxa in the benthic sub-system (Jarre-Teichmann et al. 1997). The discrepancy between the ecological significance of amphipods and our poor knowledge of their ecofunctional role calls for a more detailed investigation of their role in Antarctic trophodynamics.

Compared to observational techniques in studies of animal diet (i.e. gut content examination), stable isotope ratio analyses provide signatures based on actual food assimilation, and are integrated over a period corresponding to the turnover time of the analysed tissues (Tieszen et al. 1983; Hobson et al. 1996, 1997). The technique relies upon the direct relationship between the carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios of animals and those of their diets (DeNiro and Epstein 1978, 1981; Peterson and Fry 1987). Changes in ratios (i.e. fractionation) occur through metabolic processes which cause the lighter isotope to be preferentially lost and the heavier one to be retained. As a result, the stable isotope composition of a consumer is indicative of, and heavier than, that of its prey. Within a food chain, $\delta^{15}\text{N}$ displays a stepwise increment of about 3‰ at each suc-

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cessive trophic level (Minagawa and Wada 1984; Hobson and Welch 1992; Michener and Schell 1994) and is generally used to predict an organism's trophic level. Likewise, animal carbon isotope values, closer to that of the diet, allow the determination of the original source of organic matter to the food web. Isotopes have been successfully applied to the Antarctic Ocean (Wada et al. 1987; Burns et al. 1998) and particularly to the pelagic fauna and the top predators of the Weddell Sea (Rau et al. 1991a, b, 1992). However, there is a lack of such studies for Antarctic benthic ecosystems, except for some sub-Antarctic Islands (Kaehler et al. 2000).

The previously presumed simplicity of Antarctic food webs is questionable. Until about 20 years ago, the main flow of energy in the Antarctic marine environment was considered to be a food chain directly from phytoplankton (diatoms) to herbivores (krill) and higher trophic levels (see, for example, Heywood and Whitaker 1984) but those simple food chain descriptions are no longer useful (Marchant and Murphy 1994). Indeed, diatoms are recognized as major components of Antarctic marine phytoplankton but, as the microbial loop – in the Weddell-Scotia Sea bacterial production ranged from 11% of primary production in spring (Sullivan et al. 1990) to 76% of primary production in autumn (Cota et al. 1990) – other production pathways have to be considered. The sea-ice community, for example, is suspected to be an important food source for some Southern Ocean invertebrates (Marschall 1988; Daly 1990). The complexity of the Antarctic marine food web is now considered to be as high as that of many others in lower-latitude ecosystems (Garrison et al. 1991). Hence we have to deal with the complicated multiple and isotopically contrasting food bases often present in marine environments (Fry 1988; Marguillier et al. 1997; Lepoint et al. 2000).

Using carbon and nitrogen stable isotope analyses, our aim was to determine the trophic position of selected amphipod species in the eastern Weddell Sea food web and to combine our results with gut content analyses carried out by Dauby et al. (2001b).

Materials and methods

Sampling and storage

During the expedition ANT XIII/3 (EASIZ I) of R.V. *Polarstern* to the eastern Weddell Sea in 1996, more than 500 samples referring to 110 benthic invertebrate species (from sponges to finfish) were collected with either Agassiz, bottom, benthopelagic trawls or traps. Among these organisms, the following amphipod species were determined: *Ampelisca richardsoni* Karaman, 1975; *Waldeckia obesa* (Chevreux, 1905); *Parschisturella carinata* (Schellenberg, 1926); *Orchomenella* cf. *pinguides* (Walker, 1903); *Iphimediella cyclogena* K. H. Barnard, 1930; *Tryphosella murrayi* (Walker, 1903); *Eusirus perdentatus* Chevreux, 1912 and *Epimeria similis* Chevreux, 1912. Additional suspended particulate organic matter (SPOM), composed mainly of diatoms (*Corethron* sp. and *Chaetoceros* sp.), and zooplankton samples were collected from the onboard seawater. All samples were immediately freeze-dried and stored until their preparation for analyses.

Isotopic analysis

When possible, muscle tissues or soft body parts from five individuals of every sampled species (except from the amphipod *Epimeria similis*, $n = 1$) were sampled and ground with mortar and pestle into a homogenous powder. From 110 species initially analysed, 90 species provided valuable results. In amphipods, isotope ratios were determined individually in each specimen, whereas in other invertebrate species, five individuals were pooled prior to analysis.

The lipids were not extracted from the tissues. Stable carbon and nitrogen isotope ratios were analysed with an Optima (Micromass, UK) continuous flow isotope ratio mass spectrometer (CF-IRMS) directly coupled to an N-C elemental analyser (Fisons, UK) for combustion and automated analysis. Isotopic ratios are expressed in δ notation as the proportional deviation of the sample isotope ratio from that of an international standard according to the formula: $\delta X(\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where X is ^{13}C or ^{15}N , R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, and the appropriate standards were Vienna Pee Dee Belemnite (V-PDB) and atmospheric nitrogen for carbon and nitrogen, respectively. Intercomparison materials were IAEA-N1 ($\delta^{15}\text{N} = +0.4 \pm 0.2\text{‰}$) and IAEA CH-6 (sucrose) ($\delta^{13}\text{C} = -10.4 \pm 0.2\text{‰}$). As recommended by Pinnegar and Polunin (1999), when samples were acidified to eliminate carbonates, $^{15}\text{N}/^{14}\text{N}$ ratios were measured before acidification due to significant modifications of nitrogen ratios after HCl addition (Bunn et al. 1995). Experimental precision (based on the standard deviation of replicates of an atropina standard) was 0.5 and 0.4‰ for carbon and nitrogen, respectively.

Based on findings of several authors (e.g. Minagawa and Wada 1984; Wada et al. 1987; Hobson and Welch 1992; Michener and Schell 1994; Hobson et al. 1995), a “per-trophic-level” ^{15}N enrichment factor of about 3.0‰ was applied to obtain trophic level estimates according to the relationship:

$$TL = (D - 3.1)/3.0 + 1$$

where D is the $\delta^{15}\text{N}$ value of the organism, 3.1 refers to the mean value of SPOM, and TL is the organism's trophic level (see Table 1).

Parametric tests were used to compare isotope ratios between different taxa. Normality of the data was checked by the Kolmogorov-Smirnov test followed by ANOVA and post-hoc comparisons of means. Correlations between data were explored by the Spearman rank coefficient. A significance level of $P < 0.01$ was used in all tests (Scherrer 1984).

The calculation of the gut content percentages displayed in Table 1 are described in Dauby et al. (2001b).

Results

The ranges of isotope ratios of each taxon – grouped by phylum, class or order following the number of samples – as well as those of suspended matter are presented in Figs. 1 and 2. The first plan of gathering the taxa by order had to be abandoned because of the lack of significance of statistical tests. Our isotopic analyses revealed a considerable range in both ^{13}C and ^{15}N values for benthic components. Stable carbon isotope ratios ranged from -32‰ for the SPOM to -16.1‰ for the anthozoan *Thouarella* sp. Considerable overlap in ^{13}C values appears throughout the food web and the trophic enrichment between trophic levels is not really obvious. ^{15}N values were generally less variable than ^{13}C values and a step-wise increase with trophic level ranged from 2.6‰ for SPOM to 16.1‰ for the fish *Pogonophryne*

Table 1 Trophic types based on gut content analyses (modified from Dauby et al. 2001b), $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C:N ratios (mean \pm SE) and estimated trophic level (TL) (from Hobson and Welch 1992) (n number of samples)

Species	Trophic types	C/N	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	TL
<i>Ampelisca richardsoni</i> ($n=5$)	SUSPENSION-FEEDER [Diatoms (54%), undetermined organic matter (36%), Porifera (7%), Crustacea (3%)]	5.4 ± 0.4	-27.1 ± 0.9	6.6 ± 0.6	2.1
<i>Eusirus perdentatus</i> ($n=5$)	PREDATOR [Crustacea (44%), mineral particles (27%), unidentified organic matter (25%), Polychaeta (4%)]	5.1 ± 1.2	-23.7 ± 1.9	9.3 ± 1.5	3.0
<i>Epimeria similis</i> ($n=1$)	PREDATOR [Cnidaria (63%), Porifera (14%), Polychaeta (9%), diatoms (9%), others (5%)]	5.6	-25.1	10.1	3.3
<i>Orchomenella cf pinguides</i> ($n=5$)	DEPOSIT-FEEDER [Crustacea (36%), Porifera (24%), diatoms (24%), unidentified organic matter (16%)]	7.0 ± 0.4	-22.3 ± 1.8	10.9 ± 0.3	3.6
<i>Iphimediella cyclogena</i> ($n=5$)	PREDATOR [Holothurioida (70%), Polychaeta (20%), unidentified organic matter (10%)]	4.0 ± 0.3	-25.9 ± 1.1	11.2 ± 0.5	3.7
<i>Tryphosella murrayi</i> ($n=5$)	SCAVENGER [Carrion (47%), Crustacea (43%), Polychaeta (51%), others (5%)]	5.5 ± 0.2	-22.5 ± 0.8	11.4 ± 0.8	3.8
<i>Waldeckia obesa</i> ($n=5$)	SCAVENGER [Carrion (85%), diatoms (5%), mineral particles (5%), Porifera (5%)]	6.7 ± 0.5	-22.8 ± 0.7	11.6 ± 0.3	3.8
<i>Parschisturella carinata</i> ($n=5$)	No gut content data but considered as SCAVENGER	6.9 ± 1.1	-21.1 ± 2.1	11.8 ± 0.7	3.9

barsukovi (Artedidraconidae), suggesting a food web composed of about five trophic levels (see Minagawa and Wada 1984; Wada et al. 1987; Hobson and Welch 1992; Michener and Schell 1994; Hobson et al. 1995).

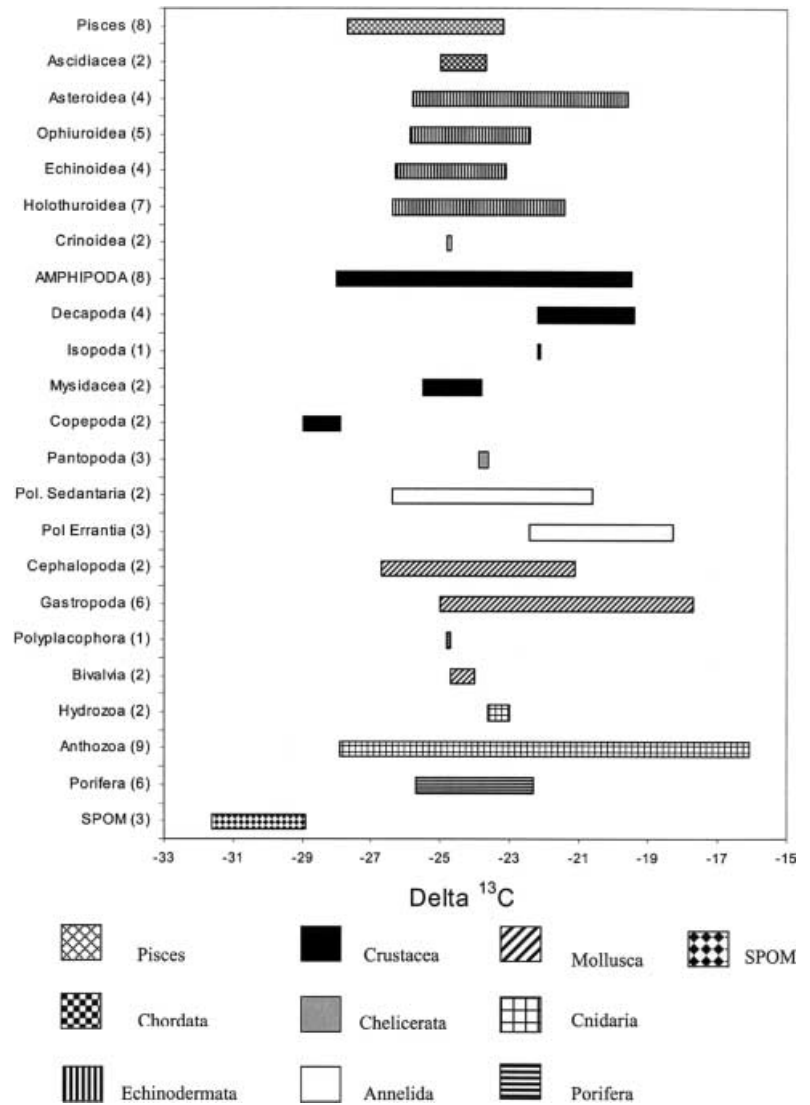
As expected, SPOM isotopic ratios ($n=3$) are the lowest, ranging from -32 to -28.7 ‰ in $\delta^{13}\text{C}$ and from 2.6 to 3.9 ‰ in $\delta^{15}\text{N}$. For both isotopes, amphipod ranges are among the widest (from -27.8 to -19.6 ‰ in $\delta^{13}\text{C}$ and from 5.8 to 12.9 ‰ in $\delta^{15}\text{N}$), together with those of anthozoans and echinoderms. Unfortunately, in this study, the isotopic ratios of some groups cannot be discussed because of their poor sampling (for example, isopods are represented by a single species). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in amphipods are presented in Fig. 3. Displaying the lowest δ ($\delta^{13}\text{C} = -27.1 \pm 0.9$ ‰; $\delta^{15}\text{N} = 6.6 \pm 0.6$ ‰), *A. richardsoni* values are closest to those of SPOM and are significantly different from values of all the other species (ANOVA $P < 0.01$), except for *Epimeria similis* and *I. cyclogena* $\delta^{13}\text{C}$. The two last species present similar $\delta^{13}\text{C}$ but their nitrogen ratios are significantly different from each other (ANOVA $P < 0.001$). *Eusirus perdentatus* $\delta^{15}\text{N}$ values differ significantly from all other species nitrogen ratios except from the single *Epimeria similis* value. Unlike its $\delta^{13}\text{C}$, *I. cyclogena* $\delta^{15}\text{N}$ values are among the highest, together with those of *O. cf. pinguides*, *W. obesa*, *T. murrayi* and *Parschisturella carinata*. Furthermore, these four last species' stable isotope ratios are not significantly different from each other, either for the carbon or the nitrogen.

When amphipods' ^{13}C are compared to their respective C/N ratio, no correlation appears except with one species: *Parschisturella carinata*, which displays a significant decrease of $\delta^{13}\text{C}$ with C/N ratio increase (Fig. 4).

Discussion

The SPOM isotope data are typical of high-latitude northern and southern hemisphere food webs with ^{13}C and ^{15}N -depleted food bases (Wada et al. 1987; Schell and Ziemann 1988; Saupe et al. 1989). More enriched isotopic ratios have been recorded in Antarctic POM but only in fraction samples in or closely associated with sea ice (Rau et al. 1991a; Hobson et al. 1995). Even though there is no sea ice POM available for this study, the high values displayed by some sponge species (-22.3 and 12.5 ‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) compared to SPOM ratios could reflect an assimilation of sea ice POM by these benthic suspension-feeders. Indeed, by a process of coagulation primarily determined by the stickiness of the cells, many of the dominant ice algae form aggregates, which are subject to rapid sedimentation (Riebesell et al. 1991). Another hypothesis to explain the great enrichment between POM and POM grazers is that the assimilation by suspension-feeders of benthic resuspended organic matter originates from a strong microbial loop – the period of sampling (post-bloom, late-summer period) corresponding to its maxi-

Fig. 1 Range of $\delta^{13}\text{C}$ values (‰) for SPOM, benthic invertebrates and vertebrates from the eastern Weddell Sea shelf (*Pol. Sedentaria* = Polychaeta Sedentaria; *Pol. Errantia* = Polychaeta Errantia). Numeral in parentheses indicates the amount of analysed species



mal activity (Karl 1993) – through which fixed carbon is first cycled through flagellates and microzooplankton before being consumed. A greater enrichment of benthic organisms due to the assimilation of resuspended and microbially reworked organic matter has already been suggested by Hobson et al. (1995) in an Arctic polynia food web.

Within amphipod species, and particularly for *O. cf. pinguides*, *Eusirus perdentatus* and *Parschisturella carinata*, $\delta^{13}\text{C}$ values were generally more variable than ^{15}N values, as observed in most taxa (see Fig. 3, Table 1). As lipids – both N- and ^{13}C -poor – were not extracted prior to analysis, the intraspecific variation of amphipod $\delta^{13}\text{C}$ could be attributed to the individual differences in concentration of isotopically lighter lipids (DeNiro and Epstein 1977; Tieszen et al. 1983; Wada et al. 1987; Pinnegar and Polunin 1999). There is, however, no significant correlation between amphipods' biomass ^{13}C and their biomass C/N, except in one species, *Parschisturella carinata* (Fig. 4). For this species only, the intraspecific variation of the $\delta^{13}\text{C}$ could be attributed to

a difference of lipid content between individuals (Rau et al. 1991a, b, 1992).

Few other benthic groups seem to cover a similarly wide trophic spectrum as amphipods (Figs. 1, 2). Quite wide ranges of $\delta^{15}\text{N}$ have already been recorded for pelagic amphipod species from the same sampling area and this has been interpreted as a sign of "diverse feeding strategies and trophic roles within this group" (Rau et al. 1991a). In the present study, the widest ranges of isotopic ratios are displayed by anthozoans, poriferans (for nitrogen) and amphipods, although the first two groups represent higher taxonomic entities. Indeed, our data indicate that benthic amphipods live at many levels of the food web, from the base (*A. richardsoni*) to the top (*Parschisturella carinata*) (see Fig. 3). The step-wise increase of $\delta^{15}\text{N}$ with trophic level displayed by the eight amphipod species (see Table 1) suggests a coverage of approximately three of the five levels of the food web. Except for *A. richardsoni*, which is clearly isolated from the other species at the second trophic level, instead of belonging to a definitive trophic

Fig. 2 Range of $\delta^{15}\text{N}$ values (‰) for SPOM, benthic invertebrates and vertebrates from the eastern Weddell Sea shelf (*Pol. Sedentaria* = Polychaeta Sedentaria; *Pol. Errantia* = Polychaeta Errantia). *Numerals in parentheses* indicates the amount of analysed species

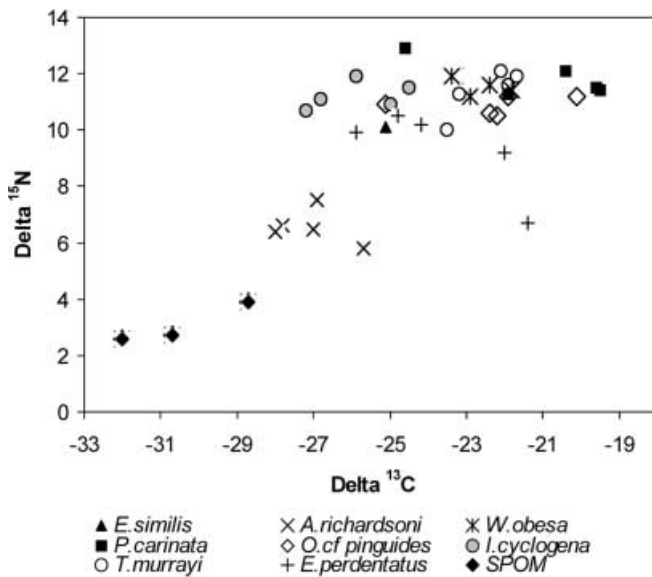
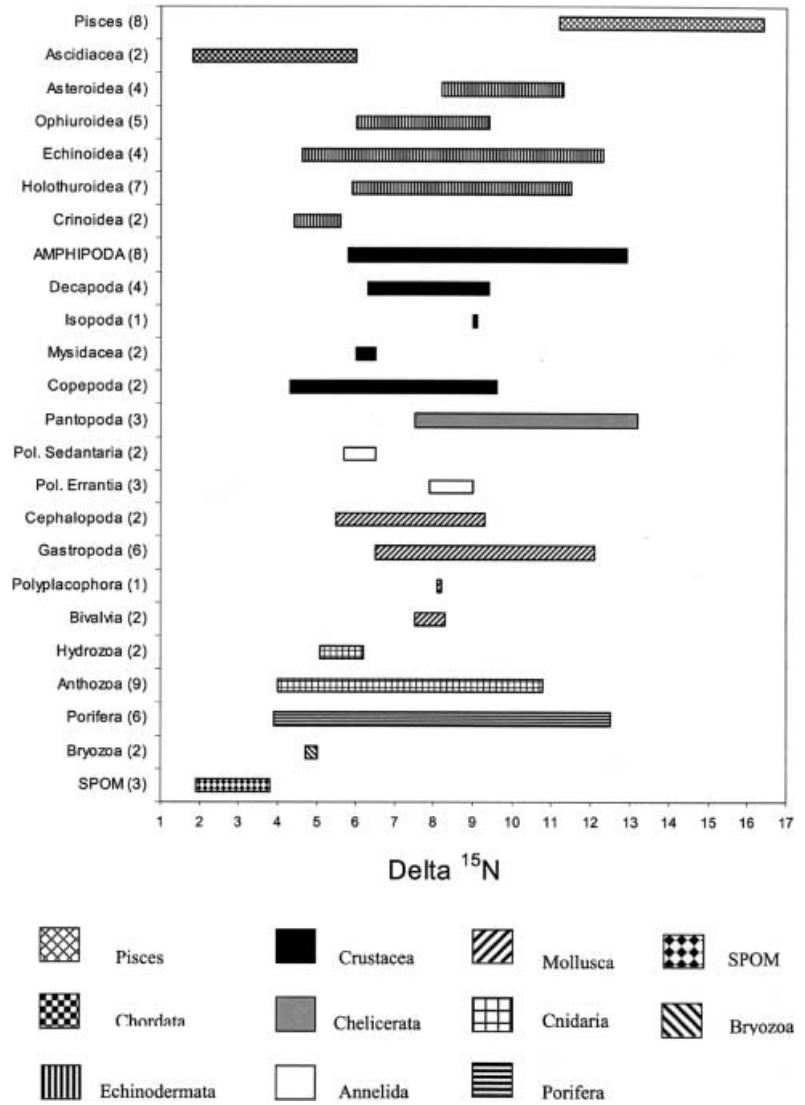


Fig. 3 The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values (‰) in SPOM and in amphipods from the eastern Weddell Sea shelf

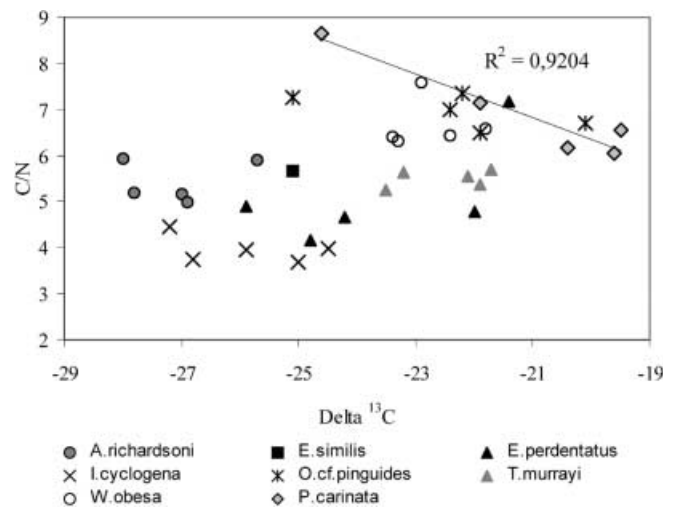


Fig. 4 Relationship between the $\delta^{13}\text{C}$ (‰) and the C/N ratio for amphipods from the eastern Weddell Sea shelf. The displayed regression involves only data from the species *Parschisturella carinata*

type, amphipods occupy a continuum between the third and the fourth level. This may indicate opportunistic amphipod feeding behaviour (at least for the sampled species).

Our trophic characterization of amphipods based on isotopic values coincides quite well with the trophic classification based on gut contents analyses of Dauby et al. (2001b); see Table 1. Since the fundamental difference between the isotope and the stomach content approaches to diet studies is the time scale each method addresses, this coincidence indicates that there are no distinct changes in feeding strategies over time. The low $\delta^{13}\text{C}$ ($-27.1 \pm 0.9\text{‰}$) and $\delta^{15}\text{N}$ ($6.6 \pm 0.6\text{‰}$) values of *A. richardsoni*, which are close to SPOM isotopic ratios ($\delta^{13}\text{C} = -30.5 \pm 1.7\text{‰}$; $\delta^{15}\text{N} = 3.1 \pm 0.7\text{‰}$), confirm that *A. richardsoni* is suspension-feeding on predominantly planktonic items. Further evidence is given by *Ampelisca* lipids, which consist mainly of marked fatty acids of planktonic origin (Graeve et al. 2001). Klages and Gutt (1990) consider *Eusirus perdentatus* a passive predator, which preys on various organisms from different trophic levels such as polychaetes, amphipods or other smaller crustaceans. Their conclusions coincided with results of gut content analyses (Dauby et al. 2001b), but *Eusirus perdentatus* opportunistic trophic behaviour is also confirmed by its scattered isotopic ratios. Furthermore, according to Graeve et al. (2001), the lack of specialization both in the lipid accumulation and in fatty acid biosynthesis observed for *Eusirus perdentatus* supports this feeding opportunism hypothesis.

The quite high nitrogen ratios of *I. cyclogena* is surprising as its diet seems to be mainly composed of holothurian tissues considered for the most part as suspension- or deposit-feeders (Table 1). Antarctic sea cucumbers' isotopic values, however, are also higher than expected (Figs. 1, 2). This may indicate significant microbial or meiofaunal pathways in the organic matter cycle.

Species displaying the highest isotopic values – *W. obesa*, *T. murrayi*, *O. cf. pinguides* and *Parschisturella carinata* – appear to share the same necrophagous trophic behaviour. The carbon and nitrogen isotopic compositions of *W. obesa* and *T. murrayi* are the closest and these data are supported by the high similarity of their diet where carrion-derived organic matter is a major item (e.g. Presler 1986; Dauby et al. 2001b). As noticed by Graeve et al. (2001), the fatty acid composition of *W. obesa* is unique since it is dominated by oleic acid (nearly 50% of total fatty acids). Lipid-rich fishes as potential food items are known to contain high amounts of this fatty acid (Hagen et al. 2000) but not as high as found for *W. obesa*. *O. cf. pinguides* gut content analyses suggest that this species (at least in this sampling period) is a deposit-feeder. Its rather high isotopic ratios could be explained by the crustacean remains, which form almost 40% of its diet. For *Parschisturella carinata*, no gut content data are available, but its common occurrence in baited traps, the feeding experiments performed with living specimens in aquaria (Y. Scailteur and C. De

Broyer, unpublished work), and the high isotopic ratios would suggest a scavenging trophic behaviour.

In conclusion, the combination of both techniques – and eventually a third as introduced with fatty acid analysis – allows us to characterize amphipod trophic status with more accuracy. Some species are rather specific in their diet selection, such as the suspension-feeder *A. richardsoni*, but the continuum of values displayed by the other species suggests some trophic opportunism and, in many amphipods, the potential to adapt their diet to food availability. Our results are preliminary and have to be validated by additional analyses with larger samples of species representative of the Weddell Sea benthic amphipod community. Furthermore, controlled feeding experiments with living Antarctic amphipods could provide more insight into fractionation factors (Gannes et al. 1997).

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