

Fabienne Nyssen · Thomas Brey · Gilles Lepoint
Jean-Marie Bouqueneau · Claude De Broyer
Patrick Dauby

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

Accepted: 22 October 2001 / Published online: 12 December 2001
© Springer-Verlag 2001

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-

F. Nyssen (✉) · C. De Broyer · P. Dauby
Institut Royal des Sciences Naturelles de Belgique (IRScNB),
rue Vautier 29, 1000 Brussels, Belgium
E-mail: fabienne.nyssen@naturalsciences.be

F. Nyssen · G. Lepoint · J.-M. Bouqueneau · P. Dauby
Laboratoire d'océanologie, Université de Liège,
Sart Tilman B6, 4000 Liège, Belgium

T. Brey
Alfred-Wegener-Institut für Polar- und Meeresforschung,
Columbusstrasse, 27568, Bremerhaven, Germany

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).

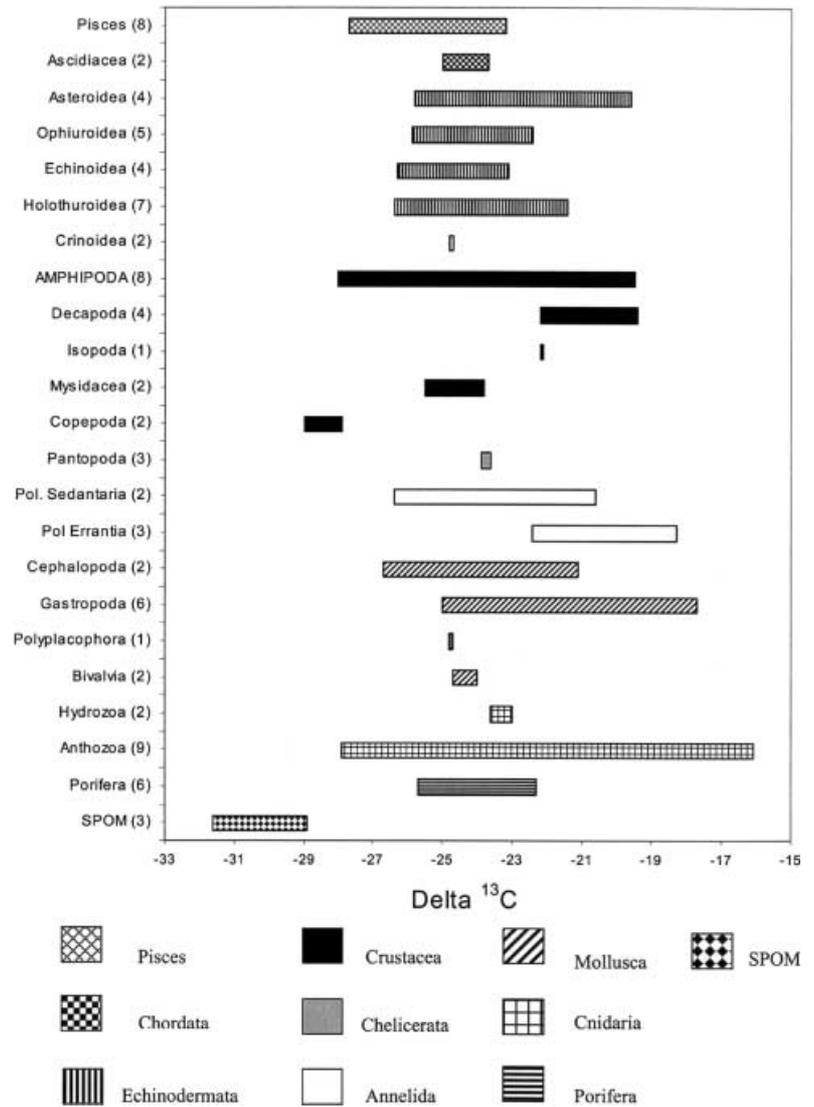
As expected, SPOM isotopic ratios ($n=3$) are the lowest, ranging from -32 to -28.7 ‰ in $\delta^{13}\text{C}$ and from 2.6 to 3.9 ‰ in $\delta^{15}\text{N}$. For both isotopes, amphipod ranges are among the widest (from -27.8 to -19.6 ‰ in $\delta^{13}\text{C}$ and from 5.8 to 12.9 ‰ in $\delta^{15}\text{N}$), 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). Numeral in parentheses indicates the amount of analysed species

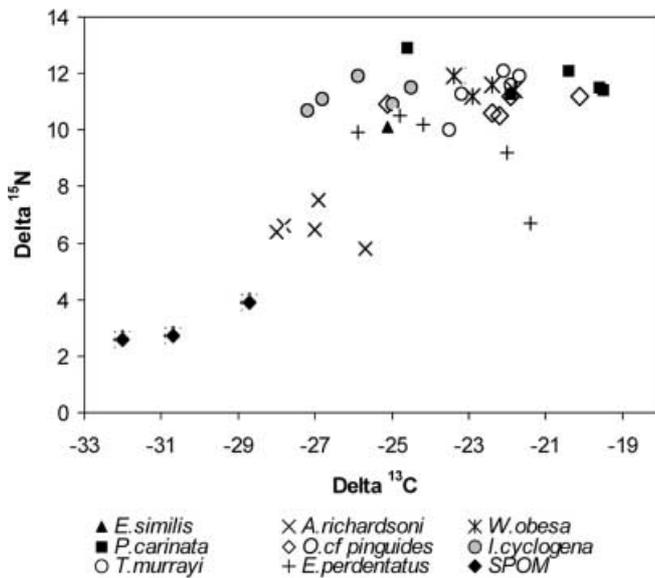
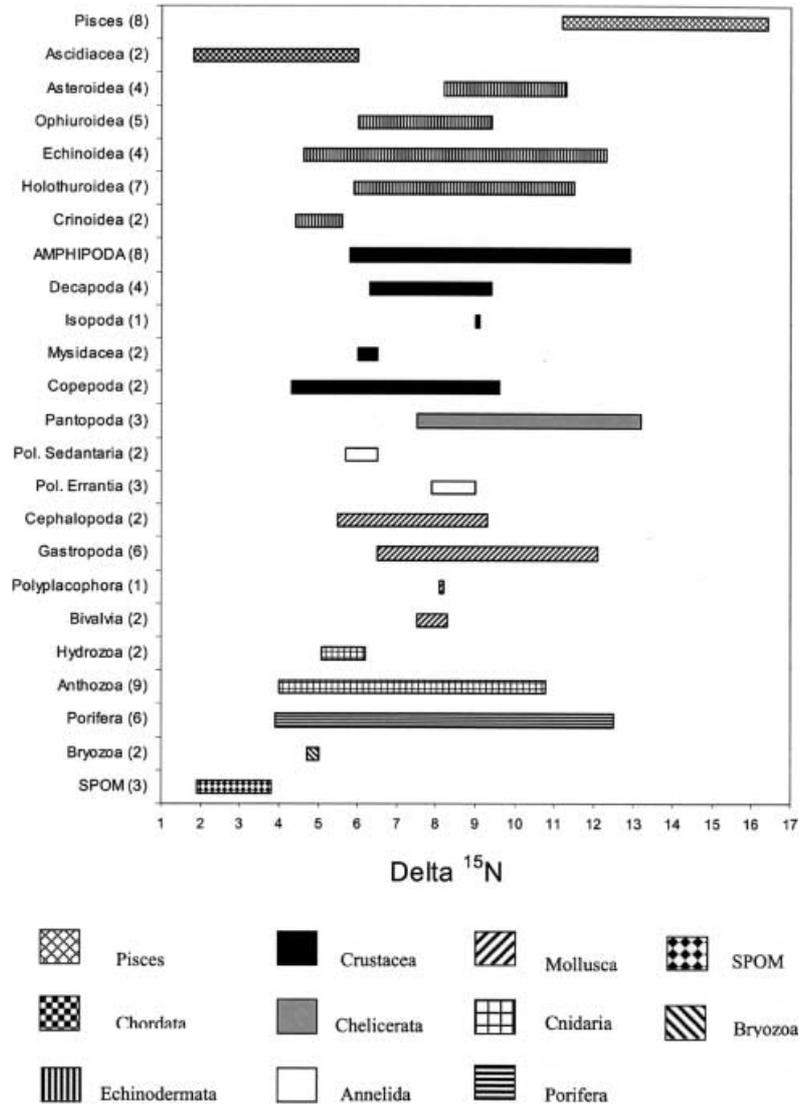


Fig. 3 The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values (‰) in SPOM and in amphipods from the eastern Weddell Sea shelf

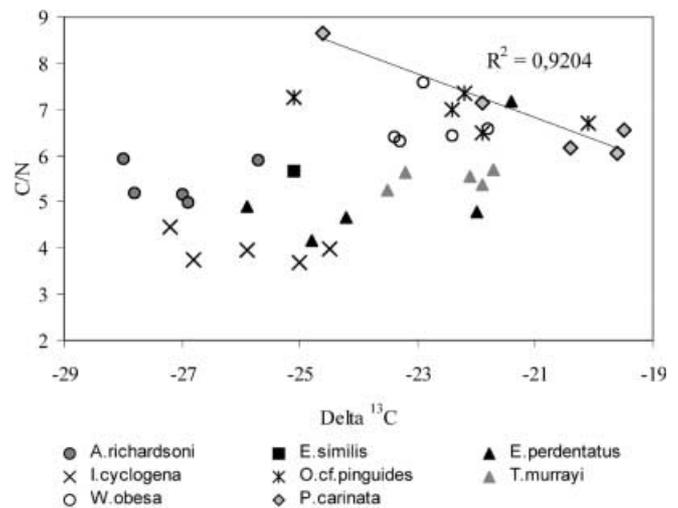


Fig. 4 Relationship between the $\delta^{13}\text{C}$ (‰) and the C/N ratio for amphipods from the eastern Weddell Sea shelf. The displayed regression involves only data from the species *Parschisturella carinata*

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).

Acknowledgements We would like to thank Professor W. Arntz (AWI, Bremerhaven) for his invitation to participate in the EASIZ cruises, to officers and crew of the R.V. *Polarstern*, and colleagues at the AWI (Bremerhaven, Germany), who helped in collecting and sorting samples. Dr. Y. Scailteur (IRScNB) is acknowledged for his work on gut content analyses. The first author received a grant from the Belgian “Fonds de la Recherche pour l’Industrie et l’Agriculture” (FRIA). The present research was performed under the auspices of the Scientific Research Programme on Antarctic (Phase IV) from the Belgian Federal Office for Scientific, Technical and Cultural Affairs (OSTC contract no. A4/36/BO2).

References

- Ainley DG, Ribic CA, Fraser WR (1992) Does prey preference affect habitat choice in Antarctic seabirds? *Mar Ecol Prog Ser* 90:207–221
- Bunn SE, Loneragan NR, Kempster MA (1995) Effects of acid washing on stable isotope ratios of C and N in penaeid shrimp and seagrass: implication for food-web studies using multiple stable isotopes. *Limnol Oceanogr* 40:622–625
- Burns JM, Trumble SJ, Castellini MA, Testa JW (1998) The diet of the Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. *Polar Biol* 19:272–282
- Cherel Y, Kooyman GL (1998) Food of emperor penguins (*Aptenodytes forsteri*) in the western Ross Sea, Antarctica. *Mar Biol* 130:335–344
- Cota GF, Kottmeier ST, Robinson DH, Smith WO Jr, Sullivan CW (1990) Bacterioplankton in the marginal sea ice zone of the Weddell Sea: biomass, production and metabolic activities during austral autumn. *Deep Sea Res* 37:1145–1167
- Daly KL (1990) Overwintering development, growth and feeding of larval *Euphausia superba* in the Antarctic marginal ice zone. *Limnol Oceanogr* 35:1564–1576
- Dauby P, Scailteur Y, Chapelle G, De Broyer C (2001a) Impact of the main benthic amphipod species populations on the eastern Weddell Sea shelf ecosystem. *Polar Biol* 24:657–662
- Dauby P, Scailteur Y, De Broyer C (2001b) Trophic diversity within the eastern Weddell Sea amphipod community. *Hydrobiologia* 443:69–86
- Dearborn JH (1965) Food of Weddell seals at McMurdo sound, Antarctica. *J Mammal* 46:37–43
- Dearborn JH (1977) Foods and feeding characteristics of Antarctic asteroids and ophiuroids. In Llano GA (ed) Adaptations within Antarctic ecosystems. Proceedings of the Third SCAR Symposium on Antarctic Biology. Smithsonian Institution, Washington DC, pp 327–334

- Dearborn JH, Edwards KC, Fratt DB (1991) Diet, feeding behavior, and surface morphology of the multi-armed Antarctic sea star *Labidiaster annulatus* (Echinodermata: Asteroidea). *Mar Ecol Prog Ser* 77:65–84
- De Broyer C, Jazdzewski K (1996) Biodiversity of the Southern Ocean: towards a new synthesis for the Amphipoda (Crustacea). *Boll Mus Civ Stor Nat Verona* 20:547–568
- De Broyer C, Rauschert M, Scailteur Y (1999) Structural and ecofunctional biodiversity of the benthic amphipod taxocoenoses. In: Arntz W, Gutt J (eds) The expedition ANTARKTIS XV/3 (EASIZ II) of “Polarstern” in 1998. *Ber Polarforsch* 301:163–174
- De Broyer C, Scailteur Y, Chapelle G, Rauschert M (2001) Diversity of epibenthic habitats of gammaridean amphipods in the eastern Weddell Sea. *Polar Biol* 24:744–753
- DeNiro MJ, Epstein S (1977) Mechanism of carbon isotope fractionation associated with lipid synthesis. *Science* 197:261–263
- DeNiro MJ, Epstein S (1978) Influence of the diet on the distribution of the carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495–506
- DeNiro MJ, Epstein S (1981) Influence of the diet on the distribution of the nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341–351
- Fry B (1988) Food web structure on George Bank from stable C, N and S isotopic compositions. *Limnol Oceanogr* 33:1182–1190
- Gannes LZ, O’Brien DM, Del Rio CM (1997) Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. *Ecology* 78:1271–1276
- Garrison DL, Buck KR, Gowing MM (1991) Plankton assemblages in the ice-edge zone of the Weddell Sea during austral winter. *J Mar Syst* 2:132–130
- Graeve M, Dauby P, Scailteur Y (2001) Lipid, fatty acids and digestive tract analyses: a powerful combination for estimating feeding modes of Antarctic amphipods. *Polar Biol* 24:853–862
- Green K, Burton HR (1987) Seasonal and geographical variation in the food of the Weddell seals, *Leptonychotes weddellii*, in Antarctica. *Aust Wildl Res* 14:475–489
- Gutt J, Sirenko BI, Arntz W, Smirnov I, De Broyer C (2000) Biodiversity of the Weddell Sea: macrozoobenthic species (demersal fish included) sampled during the expedition ANT XIII/3 (EASIZ I) with RV “Polarstern”. *Ber Polarforsch* 372:1–103
- Hagen W, Kattner G, Friedrich C (2000) The lipid compositions of five Antarctic fish species with different life strategies. *Polar Biol* 23:785–791
- Heywood RB, Whitaker TM (1984) The marine flora. In: Laws RM (ed) Antarctic ecology (2). Academic Press, London, pp 373–419
- Hobson KA, Welch HE (1992) Determination of trophic relationships within a high Arctic food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar Ecol Prog Ser* 84:9–18
- Hobson KA, Ambrose WG Jr, Renaud PE (1995) Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar Ecol Prog Ser* 128:1–10
- Hobson KA, Schell D, Renouf D, Noseworthy E (1996) Stable-carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. *Can J Fish Aquat Sci* 53:528–533
- Hobson KA, Sease JL, Merrick RL, Piatt JF (1997) Investigating trophic relationships of pinnipeds in Alaska and Washington using stable isotope ratios of nitrogen and carbon. *Mar Mammal Sci* 13:114–132
- Jarre-Teichmann A, Brey T, Bathmann UV, Dahm C, Dieckmann GS, Gorny M, Klages M, Pages F, Plötz J, Schnack-Schiel SB, Stiller M, Arntz WE (1997) Trophic flows in the benthic communities of the eastern Weddell Sea, Antarctica. In: Battaglia B, Valencia J, Walton DWH (eds) Antarctic communities: species, structure and survival. Cambridge University Press, Cambridge, pp 118–134
- Jazdzewski K, Konopacka A (1999) Necrophagous lysianassoid Amphipoda in the diet of Antarctic tern at King George island, Antarctica. *Antarct Sci* 11:316–321
- Jazdzewski K, Weslawski JM, De Broyer C (1996) A comparison of the amphipod faunal diversity in two polar fjords: Admiralty Bay, King George Island (Antarctic) and Hornsund, Spitsbergen (Arctic). *Pol Arch Hydrobiol* 42:367–384
- Kaehler S, Pakhomov EA, MacQuaid CD (2000) Trophic structure of the marine food web at the Prince Edward Islands (Southern Ocean) determined by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar Ecol Prog Ser* 208:13–20
- Karl DM (1993) Microbial processes in the Southern Oceans. In: Friedmann EI (ed) Antarctic microbiology. Wiley, Chichester, pp 1–63
- Klages M (1991) Biologische und populationsdynamische Untersuchungen an ausgewählten Gammariden (Crustacea: Amphipoda) des Südöstlichen Weddellmeeres, Antarktis. Thesis, University of Bremen
- Klages M, Gutt J (1990) Observations on the feeding behaviour of the Antarctic gammarid *Eusirus perdentatus* Chevreux, 1912 (Crustacea: Amphipoda) in aquaria. *Polar Biol* 10:359–364
- Kock KH (1992) Antarctic fish and fisheries. University Press, Cambridge
- Lepoint G, Nyssen F, Gobert S, Dauby P, Bouquegneau JM (2000) Relative impact of a seagrass bed and its adjacent epilithic algal community in consumer diets. *Mar Biol* 136:513–518
- Marchant HJ, Murphy EJ (1994) Interactions at the base of the Antarctic food web. In: El-Sayed SZ (ed) Southern Ocean ecology: the BIOMASS perspective. Cambridge University Press, Cambridge, pp 267–285
- Marguillier S, Van der Velde G, Dehairs F, Hemminga MA, Rajagopal S (1997) Trophic relationships in an inter-linked mangrove-seagrass ecosystem as traced by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. *Mar Ecol Prog Ser* 151:115–121
- Marschall HP (1988) The overwintering strategy of antarctic krill under the pack ice of the Weddell Sea. *Polar Biol* 9:129–135
- McClintock JB (1994) Trophic biology of Antarctic shallow-water echinoderms. *Mar Ecol Prog Ser* 111:191–202
- Michener RH, Schell DM (1994) Stable isotopes ratios as tracers in marine aquatic foodwebs. In: Lajtha K, Michener RH (eds) Stable isotopes in ecology and environmental sciences. Blackwell, Oxford, pp 138–157
- Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim Cosmochim Acta* 48:1135–1140
- Olaso I, Rauschert M, De Broyer C (2000) Trophic ecology of the family Artedidraconidae (Pisces: Osteichthyes) and its impact on the eastern Weddell Sea benthic system. *Mar Ecol Prog Ser* 194:143–158
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystems studies. *Annu Rev Ecol Syst* 18:293–320
- Pinnegar JK, Polunin NVC (1999) Differential fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among fishes tissues: implications for the study of trophic relationships. *Funct Ecol* 13:225–231
- Presler P (1986) Necrophagous invertebrates of the Admiralty Bay of King George Island (South Shetland Islands, Antarctica). *Pol Polar Res* 7:25–61
- Rau GH, Hopkins TL, Torres JJ (1991a) $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ in Weddell Sea invertebrates: implications for feeding diversity. *Mar Ecol Prog Ser* 77:1–6
- Rau GH, Sullivan CW, Gordon LJ (1991b) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variations in Weddell Sea particulate organic matter. *Mar Chem* 35:355–369
- Rau GH, Ainley DG, Bengston JL, Torres JJ, Hopkins TL (1992) $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ in Weddell Sea birds, seals and fish: implications for diet and trophic structure. *Mar Ecol Prog Ser* 84:1–8
- Riebesell U, Schloss I, Smetacek V (1991) Aggregation of algae released from melting sea ice: implications for seeding and sedimentation. *Polar Biol* 11:239–248

- Saupe SM, Schell DM, Griffiths WB (1989) Carbon isotope ratio gradients in western Arctic zooplankton. *Mar Biol* 103:427–432
- Schell DM, Ziemann PJ (1988) Natural carbon isotope tracers in Arctic aquatic food webs. In: Rundel P, Ehleringer J, Nagy K (eds) *Stable isotopes in ecological research*. Springer, Berlin Heidelberg New York, pp 228–251
- Scherrer B (1984) *Biostatistiques*. Gaëtan Morin, Québec
- Sullivan CW, Cota GF, Krempin DW, Smith WO (1990) Distribution and abundance of bacterioplankton in the marginal ice edge zone of the Weddell-Scotia Sea during austral spring. *Mar Ecol Prog Ser* 69:239–252
- Tieszen LL, Boutton TW, Tesdahl KG, Slade NH (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implications for ^{13}C analysis of diet. *Oecologia* 57:32–37
- Wada E, Terazaki M, Kabaya Y, Nemoto T (1987) ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. *Deep Sea Res* 34: 829–841