

CHAPTER 7: GENERAL DISCUSSION AND CONCLUSIONS

The main objective of this work was to assess the ecological role of amphipod crustaceans in the Southern Ocean and more particularly their significance in the benthic trophic webs of the eastern Weddell Sea and the Antarctic Peninsula.

This final chapter is intended to provide:

- (1) an integrated overview of the results detailed in previous chapters, in order to present an overall image of amphipod crustaceans trophic significance and diversity in Antarctic shelf benthic communities. This section will include data obtained for other groups representative of the Antarctic benthos in order to get a global picture of the benthic food webs where amphipods are involved as well as some considerations on benthic-pelagic coupling in the study area,
- (2) an evaluation of the usefulness of stable isotope ratios (in particular, of carbon and nitrogen) and fatty acids as natural trophic biomarkers,
- (3) and finally, the major conclusions drawn from this study.

7.1. TROPHIC SIGNIFICANCE OF AMPHIPOD CRUSTACEANS IN ANTARCTIC BENTHIC COMMUNITIES AND SOME CONSIDERATIONS ABOUT BENTHIC-PELAGIC COUPLING

Until about 20 years ago the main flow of energy in Antarctic marine environment was considered to be a direct food chain from phytoplankton (diatoms) to herbivores (krill) and higher trophic levels (see e.g. Heywood and Whitaker 1984). Those simple food chain descriptions, however, fall quite short of reality (Marchant and Murphy 1994). Indeed, diatoms are major components of Antarctic marine phytoplankton but other production pathways have to be considered as, notably, the microbial loop (e.g. Cota et al. 1990, Sullivan et al. 1990). The sea-ice community also is suspected to be an important food source for some Southern Ocean invertebrates (Marschall 1988, Daly 1990). Considering all those aspects, the Antarctic marine food web is now considered to be as complex as many others in lower-latitude ecosystems (Garrison 1991).

As they may explain part of the apparent discrepancies between seasonally limited food resources and the richness of benthic life, the study of the feeding habits have received considerable attention in the last decades (Arntz et al. 1994). However, because of the large number of benthic and benthopelagic species and the wide and variable food spectra of many of these, there subsist many trophic interactions to clarify. Furthermore, due to the remoteness of the region, research in Antarctica is never an easy task to achieve. Many factors have to be taken into account: the financial costs of all logistics implied by an expedition to the Antarctic as well as the strong seasonality of the Southern Ocean system are some of the parameters that have to be considered.

The reason for focusing this work on amphipod crustaceans can be briefly summarized as follow:

- (i) With more than 830 different species, among which about 75% endemics, the amphipod crustaceans form one of the most speciose animal group of the Southern Ocean (De Broyer & Jazdzewski 1996).
- (ii) These peracarids have colonized a wide variety of ecological niches, in benthic habitats as well as in the water column (De Broyer *et al.* 2001), and have developed a large range of feeding strategies, from suspension-feeding to scavenging on big carrion and specialized modes like micro-predatory browsing on invertebrate colonies (Dauby *et al.* 2001; Nyssen *et al.* 2002).
- (iii) Furthermore, peracarid crustaceans are important food sources for many Southern Ocean benthic invertebrates (see review in chapter VI). Indeed, the discrepancy between the suspected ecological significance of amphipods and our poor knowledge of their eco-functional role calls for a more detailed investigation of their role in Antarctic trophodynamics.

We approached the trophic ecology of amphipods in a multidisciplinary way, but nevertheless methods lead to the same conclusion: amphipod trophic ecology is diverse, rich and complex.

Even, in their morphology, and we have investigated the mandible in particular because of its central role in the nutrition, they appear to have developed a multitude of morphological patterns (see Chapter IV). However, the link between amphipods mandible morphology and feeding habits is often not sufficiently distinct to be considered as a reliable method of trophic classification. The evolution of amphipod mandible morphology has not only been guided by its alimentary functionality, but other factors did interfere also in the process. However, the global analysis of all mouthparts

morphological features (maxillipeds, maxille 1 and maxille 2) would probably provide better insights to infer trophic type.

As demonstrated also by the other approaches considered in this work (stable isotopic ratios and fatty acid composition analyses, see chapters II and III), few other benthic groups seem to cover a similarly wide trophic spectrum as amphipods do. Considerably wide ranges have already been recorded for pelagic amphipod species from the same sampling area (Rau et al. 1991). Therefore, as trophic diversity is generally associated to functional role diversity, both benthic and pelagic amphipods appear as key components in Antarctic systems.

Our data indicate that benthic amphipods live at many trophic levels of the Weddell Sea food web (see chapters II & III). And, besides some highly specialized species as for example, micro-grazers feeding on a single food item (species of the genus *Echiniphimedia* feed exclusively on sponges, as revealed by their guts full of hexactinellid spicules) there are numerous signs of opportunism in amphipod feeding behavior.

The trophic characterization of amphipod based on isotopic values coincides quite well with the trophic classification based on gut contents analyses. So, as the fundamental difference between both approaches to diet studies is the time scale each method addresses – diet integration over weeks for the first and snapshot of last meals for the latter - this similarity indicates that overall there are only small changes in diet over lifetime.

The presence of amphipods at all levels of Weddell Sea benthic food web can be generalized to the other ecosystem considered in this study: the Antarctic Peninsula.

Based on our own unpublished stable isotope data of zoobenthos in Antarctic Peninsula, we can exemplify an Antarctic food web including amphipods to figure out which position they occupy and how important they are among the

other zoobenthic groups. All analyzed organisms are listed in Table 7.1. As chapter III has been conducted in the same area, we can refer to it for the sampling map. Among amphipods, sixteen species have been considered. This collection gathers several feeding types, notably, suspension-feeder (*A. richardsoni*), deposit-feeders (*Byblis* sp., *P. gibber*), micrograzers (*E. echinata*, *E. hodgsoni*, *E. similis*), predator (*Iphimediella* sp.), scavengers (e.g. *A. plebs*, *P. coatsi*, *W. obesa*). We have classified amphipods into hyperids and gammarids because of their different habitats, the hyperid amphipods being exclusively planktonic.

Table 7.1. Carbon and nitrogen isotopic ratios (mean \pm SD, ‰) of all animals sampled on the shelf of the Antarctic Peninsula; TL corresponds to estimated trophic level

PHYLUM	Class / Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	TL
CNIDARIA	Hydrozoa	-26.9 ± 0.0 (1)	4.9 ± 0.0 (1)	2,9
	Anthozoa	-25.1 ± 1.3 (6)	7.8 ± 0.7 (6)	4,1
	Scyphozoa	-24.1 ± 0.3 (2)	7.7 ± 0.6 (2)	4,0
ANNELIDA	Polynoid	-24.4 ± 0.4 (2)	9.3 ± 0.9 (2)	4,7
	<i>Laetmonice producta</i>	-23.7 ± 0.5 (2)	8.9 ± 1.0 (2)	4,5
MOLLUSCA	Cephalopoda			
	<i>Paraledone turqueti</i>	-24.2 ± 0.4 (7)	9.6 ± 0.7 (7)	4,8
	<i>Paraledone charcoti</i>	-25 ± 0.0 (1)	8.6 ± 1.0 (1)	4,4
	<i>Paraledone</i> sp.	-24.7 ± 0.0 (1)	8.5 ± 0.0 (1)	4,4
	<i>Megaledone setosus</i>	-21.5 ± 0.0 (1)	9.5 ± 0.0 (1)	4,8
	Bivalvia			
	<i>Limopsis marionensis</i>	-24.3 ± 1.6 (5)	7.7 ± 0.8 (5)	4,0
ARTHROPODA	Isopoda			
	<i>Glyptonotus antarcticus</i>	-22.9 ± 0.0 (1)	6.3 ± 0.0 (1)	3,5
	<i>Seratoserolis trilobitoides</i>	-22.9 ± 1.2 (2)	7.5 ± 0.2 (5)	4,0
	<i>Natatolana</i> sp.	-21.6 ± 0.8 (6)	6.8 ± 0.4 (6)	3,7
	Antarcturidae gen. sp	-21.4 ± 1.5 (4)	6.3 ± 0.8 (6)	3,5
	Mysidacea	-26.3 ± 0.0 (1)	4.5 ± 0.0 (1)	2,7
	Amphipoda			
	Hyperid			
	<i>Themisto</i> sp	-25.1 ± 0.7 (2)	2.9 ± 0.7 (2)	2,0
	Gammarid			
	<i>Ampelisca richardsoni</i>	-29.3 ± 0.2 (3)	4.1 ± 0.1 (3)	2,5
	<i>Byblis</i> sp	-24.8 ± 1.2 (3)	6.1 ± 0.3 (3)	3,4
	<i>Eusirus perdentatus</i>	-23.4 ± 0.7 (19)	7.3 ± 1.0 (19)	3,9
	<i>Djerboa furcipes</i>	-27.8 ± 0.6 (5)	4.9 ± 0.3 (5)	2,9
	<i>Echiniphimedia echinata</i>	-21.5 ± 2.1 (3)	6.2 ± 1.0 (3)	3,4
	<i>Echiniphimedia hodgsoni</i>	-24.3 ± 1.3 (2)	10.6 ± 1.8 (2)	5,3
	<i>Iphimediella</i> sp	-21.7 ± 1.0 (6)	11.8 ± 1.0 (6)	5,8
	<i>Pseudorchomene coatsi</i>	-22.7 ± 0.3 (3)	9.3 ± 0.3 (3)	4,7

PHYLUM	Class / Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	TL
	<i>Waldeckia obesa</i>	-22.8 ± 0.9 (4)	7.3 ± 0.7 (4)	3,9
	<i>Eurythenes gryllus</i>	-27.3 ± 1.1 (9)	8.5 ± 0.5 (9)	4,4
	<i>Abyssorhynchomene plebs</i>	-26.5 ± 0.4 (6)	9.5 ± 0.8 (6)	4,8
	<i>Epimeria georgiana</i>	-22.9 ± 1.9 (9)	7.9 ± 0.4 (9)	4,1
	<i>Epimeria similis</i>	-25 ± 1.4 (15)	7.6 ± 0.5 (15)	4,0
	<i>Leucothoe spinicarpa</i>	-22.7 ± 0.6 (6)	8.3 ± 0.8 (6)	4,3
	<i>Paraceradocus gibber</i>	-23.5 ± 0.7 (12)	5.0 ± 0.5 (12)	2,9
	Euphausiacea			
	<i>Euphausia superba</i>	-28.6 ± 1.1 (6)	2.8 ± 0.4 (6)	2,0
	Decapoda			
	<i>Notocrangon antarcticus</i>	-23.6 ± 0.3 (4)	9.3 ± 0.2 (4)	4,7
	<i>Chorismus antarcticus</i>	-24.0 ± 1.8 (2)	7.4 ± 1.3 (2)	3,9
BRYOZOA	<i>Reteporella</i> sp.	-26.9 ± 0.0 (1)	6.5 ± 0.0 (1)	3,5
ECHINODERMATA	Crinoidea	-26.1 ± 0.0 (1)	7.9 ± 0.0 (1)	4,1
	Holothuroidea			
	<i>Psolus</i> sp.	-26.6 ± 1.4 (3)	8.0 ± 0.8 (3)	4,2
	<i>Bathyploetes fusciculum</i>	-24.8 ± 0.3 (2)	8.8 ± 0.7 (2)	4,5
	<i>Echinocucumis</i> sp.	-29 ± 0.3 (2)	7.5 ± 0.2 (2)	4,0
	Ophiuroidea			
	<i>Astrotoma agassizii</i>	-23.9 ± 2.1 (3)	7.5 ± 0.9 (3)	4,0
	<i>Ophioparte gigas</i>	-27.3 ± 1.6 (3)	5.5 ± 0.4 (3)	3,1
	<i>Ophionotus</i> sp.	-24.5 ± 1.5 (2)	6.7 ± 0.2 (2)	3,6
	Asteroidea	-24.0 ± 1.6 (4)	11.2 ± 1.3 (5)	5,5
CHORDATA	Osteichthyes			
	Channichthyidae			
	<i>Champscephalus gunnari</i>	-25.1 ± 0.3 (5)	8.5 ± 0.3 (5)	4,4
	Nototheniidae			
	<i>Gobionotothen gibberifrons</i>	-24.3 ± 0.1 (5)	9.8 ± 0.4 (5)	4,9
	<i>Notothenia coriiceps</i>	-23.6 ± 0.8 (6)	9.9 ± 0.6 (6)	5,0
	<i>Notothenia rossii</i>	-24.4 ± 0.5 (6)	9.2 ± 0.3 (6)	4,7
	<i>Trematomus bernacchii</i>	-19.7 ± 2.0 (2)	12.6 ± 0.2 (2)	6,1
	<i>Trematomus pennellii</i>	-20.2 ± 0.6 (3)	11.0 ± 0.8 (3)	5,4
	<i>Trematomus nicolaii</i>	-20.5 ± 0.0 (1)	11.0 ± 0.0 (1)	5,4
	<i>Trematomus hansonii</i>	-21.9 ± 0.0 (1)	10.2 ± 0.0 (1)	5,1
	<i>Trematomus eulepidotus</i>	-24.5 ± 0.4 (5)	9.0 ± 0.6 (5)	4,6

As observed in the figure 7.1., the most striking features are, on the one hand, a general impoverishment in ^{13}C compared to other systems (e.g. tropical), probably originating from a depleted food source but transferred throughout the food web. This pronounced depletion in ^{13}C at the base of Antarctic food web is not new. The SPOM isotopic ratios are considerably lower than values previously recorded for other regions but within the range of Antarctic as well as Arctic values (Wada et al. 1987, Hobson et al. 1995, Dunton 2001, Corbisier et al. 2004). Polar SPOM is in general depleted in ^{13}C as compared with predominantly

temperate SPOM ($-22 \pm 3\text{‰}$) (reviews in Rau et al. 1982, Fischer 1991, France 1995). Low temperature (below 2°C), low light intensity and high water $[\text{CO}_2(\text{aq})]$ values lead to very low ^{13}C content in the phytoplankton (Rau et al. 1989, 1991a). Thompson and Calvert (1994) also suggest a substantial role of irradiance in process of ^{13}C incorporation in marine diatoms.

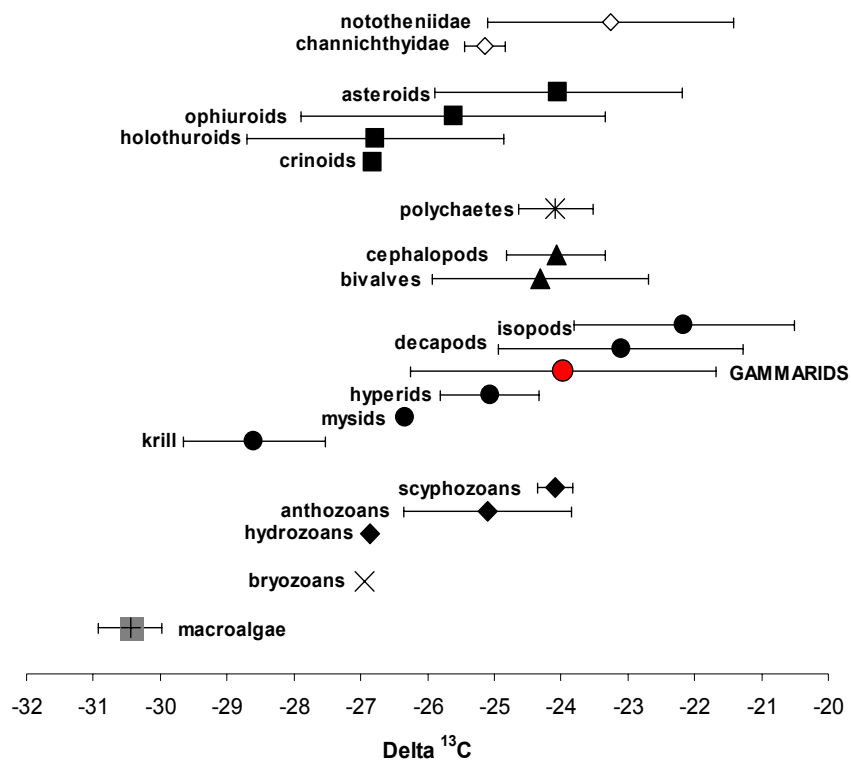
On the other hand, a considerable overlap of the $\delta^{13}\text{C}$ values is observed between groups.

The carbon isotopic signature of euphausiids (-28.6‰) corresponds to the range of particulate organic matter that is derived from phytoplankton (-30.4 to -28.0‰ ; Fisher 1991, Rau et al. 1991, Fisher & Wiencke 1992). Other invertebrates that demonstrated a clear dependence on phytoplankton (based on $\delta^{13}\text{C}$ values) included bryozoans, hydrozoans, holothurians, crinoids, mysids and some amphipods.

Studies of high latitude marine food webs suggest that stable carbon isotope analysis may be useful in elucidating the degree to which benthic consumers are coupled to pelagic primary production (McConnaughey & McRoy 1979, Dunton et al. 1989, Hobson et al. 1995). Close coupling of consumers with pelagic primary production results in less ^{13}C enrichment in consumer tissues compared with these links in deposit feeders and detrital-based food webs.

Our isotopic investigations support the hypothesis that a major part of the benthic community is supported primarily by phytoplanktonic POM reaching the benthos. Carbon evidence for this is the similarity in $\delta^{13}\text{C}$ values between pelagic POM-based feeders (e.g. *Euphausia superba*, *Themisto* sp.) and benthic filter feeders (e.g. *Echinocucumis* sp., *Ampelisca richardsoni*); (Table 7.1., Fig. 7.1.). Similar results have been found in isotopic investigations of Arctic marine food webs (Dunton et al. 1989, Hobson et al. 1995). Benthic organisms in systems exhibiting weaker benthic-pelagic coupling would be expected to be substantially enriched in ^{13}C relative to both POM and POM grazers.

Fig. 7.1. Distribution of stable-carbon isotope ratios (mean \pm SD) among benthic food web components in Antarctic Peninsula



In our study, the possible sources of significant primary production were POM, macroalgae and ice algae. The coastal waters along the west side of the Antarctic Peninsula and nearby islands are characterized by a rich and dense macroalgal flora composed of annual and perennial species (Zielinski 1990, Chung et al. 1994, Klöser et al. 1994, Amsler et al. 1998). Large amounts of algae are degraded, so they become a suitable food resource for benthic organisms (Richardson 1979, Brouwer 1996, Iken et al. 1997, 1998). Detached algae can be decomposed by biological and hydrodynamical processes (Reichardt & Dieckmann 1985, Rakusa-Suszczewski 1993) and

some may drift into deeper waters to provide food for benthic deposit and suspension feeders (Fischer & Wiencke 1992). The macroalgae $\delta^{13}\text{C}$ values we have recorded range from -31 to -30‰. Owing to the strong similarity with POM isotopic ratios (see Chapter II, Nyssen et al. 2002), it was impossible to distinguish between these two primary producers on a carbon isotopic base. On the contrary, the difference in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between SPOM and ice algae, generally more enriched (e.g. $\delta^{13}\text{C} = -18.5\text{‰}$, $\delta^{15}\text{N} = 8.3\text{‰}$, Hobson et al. 1995) (Fischer et al. 1991, Rau et al. 1991, Kennedy et al. 2002) permit further insight into the relative input of these sources to the food web. While the enrichment in ^{13}C from POM to some POM grazers may point towards some contribution of ice algae, $\delta^{15}\text{N}$ values clearly indicate direct feeding on POM and not on the isotopically heavier ice algae. Low $\delta^{13}\text{C}$ values were generally maintained through the food web, including fishes and benthic invertebrates, again confirming the importance of POM as a major food source for the entire food web. It has to be mentioned that those conclusions are based on isotopic ratios only and then, the contribution of macroalgae as a primary carbon source in the food web can not be totally excluded (see section 7.2.).

From the nitrogen stable isotopic ratios of euphausiids (2.8‰) and the mean value of 0.4‰ used by Dunton (2001) for Antarctic phytoplankton, a "per-trophic-level" ^{15}N enrichment factor of about 2.4‰ was applied to obtain trophic level estimates according to the relationship:

$$TL = (D - 0.4)/2.4 + 1$$

Where D is the $\delta^{15}\text{N}$ value of the organism, 0.4 refers to the mean value of SPOM, and TL is the organism's trophic level.

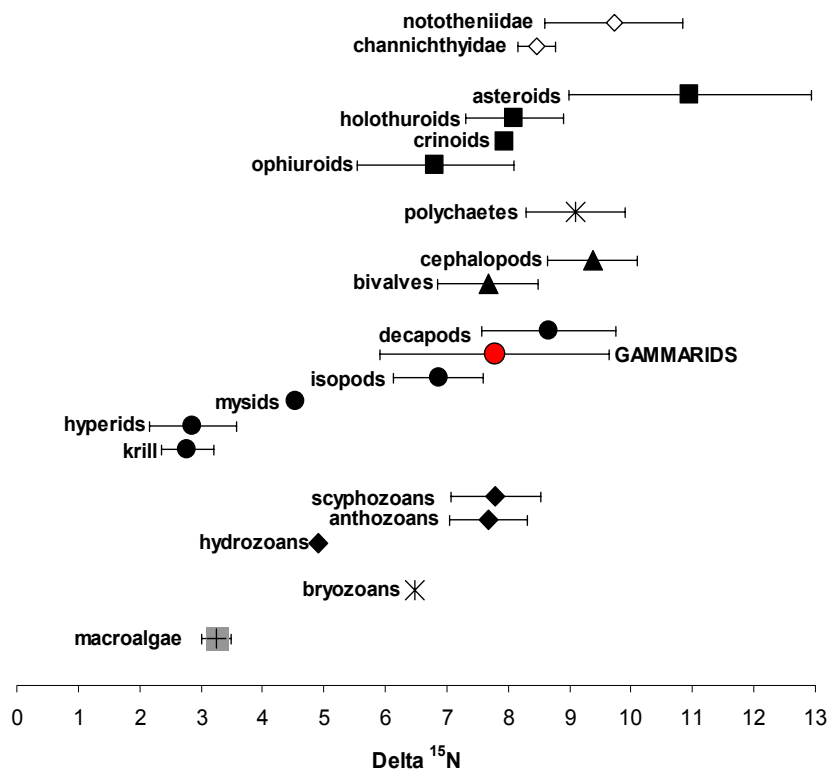
Based on the assumption that POM is the first trophic level, the range of $\delta^{15}\text{N}$ values in Antarctic Peninsula fauna reflects a food web characterized by 6 trophic levels, the highest level being occupied only by the demersal emerald

rockcod *Trematomus bernachii*. Other Fish range over two trophic levels from planktivorous species such *Champsocephalus gunnari* and *Trematomus eulepidotus* (TL 4.4 to 4.6) through *Trematomus pennellii* and *T. nicolai* (TL 5.4), which are predatory on larger benthic invertebrates and fishes (Gon and Heemstra 1990, Barrera-Oro 2002). They share these levels of the food web (4th and 5th ones) with asteroids, cephalopods, polychaetes and some amphipod and decapod crustaceans (see Fig. 7.2.). The sixteen species of amphipods considered in this study range over 3 trophic levels from herbivorous species (*A. richardsoni*, *D. furcipes*, TL 2.5 and 2.9, respectively) to scavengers (*E. gryllus*, *A. plebs*, TL 4.4 to 4.8) and predator (*Iphimediella* sp, TL 5.8). One can be surprised by the trophic levels estimation which put species between two consecutive trophic levels. Those calculations have to be considered with caution. Indeed, as they are based on assumptions (SPOM isotopic ratio, exclusive trophic link between SPOM and krill ...), one can suppose that are probably biased. Those trophic level estimations then provide only a rough idea of each group relative position in the food web.

Among amphipods in general, the trophic relationships predicted by $\delta^{15}\text{N}$ are in good agreement with information in the literature and with results we obtained previously (see Chapter II and III; Nyssen et al. 2002, Nyssen et al. 2005). For example, the well established trophic link between the species *Epimeria similis* and hydrozoans is confirmed by their carbon and nitrogen isotopic ratios (see Table 7.1.). However, for species such as the iphimediids *Echiniphimedia echinata* and *E. hodgsoni*, some clarifications are needed. Although gut contents indicate an exclusive reliance on sponges for both species, their carbon and nitrogen isotopic ratios differ respectively by 3‰ and 4‰, resulting in a difference of 2 trophic levels between them. This can be due to the consumption of different sponge species, as wide range of isotopic ratios have been recorded for these sessile organisms during this study ($\delta^{13}\text{C}=-26.5$ to -23.2 ‰ and $\delta^{15}\text{N}=3.9$ to 9.9 ‰ (Nyssen, unpublished

data). These isotopic values are also coherent with the classification of another amphipod species, *Leucothoe spinicarpa* ($\delta^{13}\text{C} = -22.7 \pm 0.6\text{‰}$ and $\delta^{15}\text{N} = 8.3 \pm 0.8\text{‰}$) as sponges consumers. This species is known to live in sponge atrial cavities as well as in ascidians (Thiel, 1999, personal observations).

Fig. 7.2. Distribution of stable-nitrogen isotope ratios (mean \pm SD) among benthic food web components in Antarctic Peninsula



The results of this analysis confirmed known trophic relationships among Peninsula organisms and revealed their position in the food web (Table 7.1).

The analysis also demonstrated that many consumers occupy similar trophic levels, but derive their carbon from different sources. For example, as first level consumers, both amphipods species *A. richardsoni*, *P. gibber* have similar $\delta^{15}\text{N}$ values (4.1‰ – 5.0‰), but their $\delta^{13}\text{C}$ values differ by 6‰ suggesting different carbon sources. Revealed as deposit-feeder from gut content analyses, *P. gibber* derives probably its carbon from microbially reworked organic matter that forms a thin layer on the sediment, whereas *A. richardsoni* feeds exclusively on phytoplankton (Dauby et al. 2001, Nyssen et al. 2002, Nyssen et al. 2005).

7.2. AN EVALUATION OF THE EFFICIENCY OF STABLE ISOTOPES AND FATTY ACIDS AS NATURAL TROPHIC BIOMARKERS

Stable carbon isotopes can be powerful tracers of the sources of organic carbon sustaining consumer communities, provided that the primary carbon sources are adequately characterized and differ in their $\delta^{13}\text{C}$ signatures (reviewed by Lajtha & Michener 1994). The latter conditions are essential; however, unfortunately, they are not always met. Furthermore, phytoplankton is a difficult component to characterize isotopically, as it is practically infeasible to separate it from the detrital suspended matter pool. Its carbon isotope composition is thus often masked and the available value corresponds to a mixing of the different components.

Stable isotopes of nitrogen usually have little value as an indicator of the primary nitrogen sources of a consumer's diet, but have proven to be an indicator of the trophic level of organisms, due to the more pronounced fractionation that occurs between trophic levels. However, drawbacks in its application remain that (i) the degree of fractionation shows a rather large variability and may be dependent on the N content of the food source (as an indicator of the food quality) (Adams & Sterner 2000), and (ii) that the mechanisms underlying the fractionation of ^{15}N are still poorly understood (see Chapter I for a more thorough discussion). Therefore when detailed information on the trophic position of an organism is required, it may be necessary to determine the actual degree of fractionation under controlled conditions first (Hobson et al. 1996, Gannes et al. 1997, Webb et al. 1998, Gorokhova & Hansson 1999). Fortunately, in many cases, such detailed information is not required, and (average) $\delta^{15}\text{N}$ data of consumers can still provide very useful information.

During our study, we experienced directly one of the weak points inherent to stable isotope analysis. In the Antarctic Peninsula, we had the opportunity to

sample the brown macroalgae *Desmarestia menziesii*. Usually, isotopic distinction between phytoplankton and macroalgae is quite obvious, but our brown macroalgae samples were highly depleted in carbon compared to the data referred by other authors for Antarctic Peninsula (Dunton 2001, $\delta^{13}\text{C}$ values of five common species of large brown algae ranged from -14 to -25‰, Corbisier et al. 2004). In this case, the estimation of each primary producer contribution to consumers' diet was very difficult. To counteract inconveniences inherent to a technique, one solution is to combine it with another one, so that the new dimension brought by the second method can make up for the lacks of the initial method.

The combined use of stable isotopes and fatty acids as trophic biomarkers has effectively facilitated the understanding of the trophic relationships between the different organisms in Antarctic ecosystems. Indeed, we were not able to separate different primary producers (phytoplankton and macroalgae) based on their carbon isotopic signatures, but based on their distinct fatty acid composition. Thus, the presence or absence in consumers of fatty acid biomarkers of phytoplankton or of macroalgae has allowed assessing the contribution of each primary producer to higher trophic levels. For example, from their similar isotopic values, the amphipod species *A. richardsoni* and *D. furcipes* were both classified as primary consumers. Their respective fatty acid profiles reveal that, even if they were at the same trophic level, they did not rely on the same primary producers: the former being a suspension-feeder and the latter a macroalgae consumer. On the other hand, isotopic data did assist in the correct interpretation of fatty acid compositions, too. As illustrated in Chapter III, significant proportions of monounsaturated fatty acids typical of dominant Antarctic copepods (Hagen et al. 1993, Kattner et al. 1994, Hagen et al. 2000) in the amphipod *Iphimediella* sp. would have classified this species as a zooplankton feeder. However, its $\delta^{15}\text{N}$ value (highest value for amphipod

ever recorded so far in Antarctic, to our knowledge) as well as its known predatory behaviour strongly indicates that there exists an additional trophic level between copepods and *Iphimediella* sp.

So, the combination of fatty acid trophic markers and stable isotope analyses may provide additional information for resolving trophic interactions in marine ecosystems.

7.3. CONCLUSIONS

Recent reviews on the knowledge about marine biodiversity in the Southern Ocean (e.g. Arntz et al. 1997) have stressed for instance the relative importance of some zoological groups, like mollusks and polychaetes, and the predominance of crustaceans. Among the latter, amphipods form the most diversified group within the Antarctic macrozoobenthos, both from the taxonomic point of view (more than 830 species have been recorded in the Southern Ocean (De Broyer and Jazdzewski 1996) as by niche occupation (De Broyer et al. 2001, Dauby et al. 2001) and at the community level.

The discrepancy between the ecological significance of amphipods and our poor knowledge of their ecofunctional role calls for a more detailed investigation of their share in Antarctic trophodynamics as well as a more systematic and efficient approach towards this aspect of their ecology.

Our multidisciplinary approach has allowed tackling the complex problem of amphipod trophic role in the Southern Ocean from different angles, each adding a particular aspect to overall food web picture.

All along this study, we have completed the gut content data base and have widened the impressive trophic spectrum suspected for the Antarctic amphipods. Although the numerous biases brought by gut content analyses, they are still essential to obtain a rough pre-classification of species in different trophic types. The revealed trophic categories are numerous and diversified, from the typical suspension feeders to the obligate scavengers. If a lot of species are opportunist, some amphipods have been revealed as very specialized in food foraging, sometimes pushing the selection to mono-specific level. In general, these first categorizations achieved with gut contents were globally confirmed afterwards by the analytical methods.

Part of this work has revealed that the degree of specialization reached sometimes in the food selection is unfortunately not reflected by the morphology, at least not enough to lead to an indisputable conclusion. We have to remind that we did only consider morphology of mandible because of its crucial role in the feeding. But the examination of the other mouthparts to get a more global idea of the functioning would probably enhance the accuracy of the conclusions.

We have also demonstrated that both fatty acid composition and stable isotope ratios are suitable tools for trophic ecosystem analysis in their own right. Fatty acids point towards food web links and stable isotopes identify trophic positions. However, the use of only one of the two tools can sometimes lead to misinterpretations with serious implications. The combination of both the approaches creates a 2-dimensional biomarker assay with higher accuracy and better trophic resolution. In the same line, another interesting approach that could be used in the future to characterize carbon fluxes between prey and predators as well as to validate the applicability of both methods, involves feeding experiments with ^{13}C -enriched experimental diets. Such studies would provide informations on carbon accumulation, transfer and turnover rates as well as biosynthesis of lipids and individual FA (e.g. Albers 1999).

Another aspect of amphipod trophic ecology that could be worth to consider in future researches is the contribution of bacteria to their diet. Bacteria influence undoubtedly Antarctic invertebrates feeding and more particularly the species such as the deposit-feeders which feed on the thin layer covering sea bottoms.

During this study, we have often been confronted to the scavenger trophic guild, essentially constituted by species of the Lysianassoidea super family. The trophic link between the pelagic and benthic scavenger assemblages formed by large food falls has been understudied in marine ecological and

carbon/energy cycling research, despite its potentially great significance in marine systems, especially at greater depths.

A potential research could investigate this question in a systematic and synoptic manner by:

- analyzing scavenger food sources with state-of-the-art methods (stable isotopes and fatty acids),
- estimating scavenger energy budgets and food demand,
- using the Antarctic shelf system as a proxy for other marine and especially deep sea systems, which are much more difficult to access.

By evaluating the trophic level of benthic deep-sea communities, but also by determining trophic links they have built with other organisms within this ecosystem, it could be possible to predict how the different compartments of the food web will react to any changes in food supply, natural and/or human-induced.

If the food falls – scavenger link proves to be as important as existing evidence indicates, then the proposed study would alter significantly our view of vertical organic matter/energy transfer in the sea. Furthermore, the results obtained within this work together with information from the literature could be integrated in a balanced model of scavenger assemblage trophic links and energy flows. By outlining the share of scavengers in overall benthic energy flow, this model would show how sensitive the system may be to changes in food supply, i.e. would allow us to estimate how sensible the amount, the frequency and the quality of food falls are to eventual changes (climatic, human-induced) in pelagic ecosystems.

LITERATURE CITED

- Albers C (1999) Lipidstoffwechsel polarer Copepoden: laborexperimente und Felduntersuchungen. PhD Thesis, University of Bremen
- Amsler CD, Rowley RJ, Laur DR, Quetin LB, Ross RM (1995) Vertical distribution of Antarctic peninsular macroalgae: cover, biomass, and species composition. *Phycology* 34: 424–30
- Amsler CD, McClintock JB, Baker BJ (1998) Chemical defense against herbivory in the Antarctic marine macroalgae *Iridea cordata* and *Phyllophora antarctica* (Rhodophyceae). *J Phycol* 34: 53–59
- Arntz WE, Brey T, Gallardo VA (1994) Antarctic zoobenthos. *Oceanogr Mar Biol Annu Rev* 32: 241–304
- Arntz W, Gutt J, Klages M (1997) Antarctic marine biodiversity: an overview. In: Battaglia B, Valentia J, Walton DWH (eds), *Antarctic Communities: Species, Structure and Survival* pp. 3–14 Cambridge University Press
- Barrera-Oro (2002) Review. The role of fish in the Antarctic food web: differences between inshore and offshore waters in the southern Scotia Arc and west of Antarctic Peninsula. *Antarct Sci* 14 (4): 293–309
- Brouwer PEM, Geilen EFM, Gremmen NJM, van Lent F (1995) Biomass, cover and zonation pattern of sublittoral macroalgae at Signy Island, South Orkney Islands, Antarctica. *Bot. Mar.* 38:259–70.
- Chung HYS, Lee OIK, Kim DY (1994) Macroalgal vegetation of Maxwell Bay in King George Island, Antarctica. *Korean J Phycol* 9: 47–58
- Corbisier TN, Petti MAV, Skowronski RSP, Brito TAS (2004) Trophic relationships in the nearshore zone of Martel Inlet (King Georges Island, Antarctica): $\delta^{13}\text{C}$ stable-isotope analysis. *Polar Biol* 27: 75–82
- 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, De Broyer C (2001) Trophic diversity within the eastern Weddell Sea amphipod community. *Hydrobiologia* 443:69-86
- De Broyer C, Jazdzewski K (1996) Biodiversity of the Southern Ocean: towards a new synthesis for the Amphipoda (Crustacea). *Boll Mus Civ Sta nat Verona* 20:547-568
- 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
- Dunton KH (2001) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ measurements of Antarctic Peninsula fauna: trophic relationships and assimilation of benthic seaweeds. *Am Zool* 41: 99-112
- Dunton KH, Saupe SM, Golikov AN, Schell DM, Schonberg SV (1989) Trophic relationships and isotopic gradients among Arctic and subarctic marine fauna. *Mar Ecol Prog Ser* 56: 89-97
- Fischer G (1991) Stable carbon isotope ratios of plankton carbon and sinking organic matter from the Atlantic sector of the Southern Ocean. *Mar Chem* 35:581-596
- Fischer G, Wiencke C (1992) Stable carbon isotope composition, depth distribution and fate of macroalgae from the Antarctic Peninsula region. *Polar Biol* 12: 341-348
- France RL (1995) Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Mar Ecol Prog Ser* 124:307-312
- 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
- Gon O, Heemstra PC (eds) 1990. *Fishes of the Southern Ocean*. Grahamstown, South Africa: JLB Smith Institute of Ichthyology, 462 pp
- Gorokhova E, Hansson S (1999) An experimental study on variations in stable carbon and nitrogen isotope fractionation during growth of *Mysis mixta* and *Neomysis integer*. *Can J Fish Aquat Sci* 56: 2203-2210
- Heywood RB, Whitaker TM (1984) The Antarctic flora. In: Laws RM (ed) *Antarctic ecology*, 2 London: Academic Press, 373-419
- 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, Ambrose WG, 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
- Iken K, Barrera-Oro ER, Quartino ML, Casaux RJ, Brey T (1997). Grazing by the Antarctic fish *Notothenia coriiceps* evidence for selective feeding on macroalgae. *Antarct sci* 9: 386–391.
- Iken K, Quartino ML, Barrera-Oro E, Palermo J, Wiencke C, Brey T (1998). Trophic relations between macroalgae and herbivores, *Ber Polarforsch* 299, 258–262.
- Kennedy H, Thomas DN, Kattner G, Haas C, Dieckmann GS (2002) Particulate organic matter in Antarctic summer sea ice: concentration and stable isotopic composition. *Mar Ecol Prog Ser* 238:1–13
- Klöser H, Mercuri G, Laternus F, Quartino ML, Wiencke C (1994) On the competitive balance of macroalgae at Potter Cove (King George Island, South Shetlands). *Polar Biol* 14: 11–16
- Lajtha K, Michener RH (1994) *Stable Isotopes in Ecology and Environmental Sciences*. Blackwell Science Ltd, pp
- McConnaughey T, McRoy CP (1979) Food-web structure and the fractionation of carbon isotopes in the Bering Sea. *Mar Biol* 53: 257–262
- Marschall HP (1988) The overwintering strategy of antarctic krill under the pack ice of the Weddell Sea. *Polar Biol* 9:129–135
- 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, p 267–285
- Nyssen F, Brey T, Lepoint G, Bouqueneau JM, De Broyer C, Dauby P (2002) A stable isotope approach to the eastern Weddell Sea trophic web: focus on benthic amphipods. *Polar Biol* 25: 280–287
- Nyssen F, Brey T, Dauby P, Graeve M (2005) Trophic position of Antarctic amphipods - enhanced analysis by a 2-dimensional biomarker assay. *Mar Ecol Prog Ser* (in press)
- Rakusa-Suszczewski S (1993) *The maritime Antarctic coastal ecosystem of Admiralty Bay*. Warsaw: Polish Academy of Sciences, 216 p.
- Rau GH, Sweeney RE, Kaplan IR (1982) Plankton $^{13}\text{C}:^{12}\text{C}$ ratio changes with latitude: differences between northern and southern oceans. *Deep-Sea Res* 29: 1035–1039

- Rau GH, Takahashi T, DesMarais DJ (1989) Latitudinal variations in plankton $\delta^{13}\text{C}$: implications for CO_2 and productivity in past oceans. *Nature* 341:516–518
- Rau GH, Takahashi T, DesMarais DJ, Sullivan CW (1991a) Particulate organic matter $\delta^{13}\text{C}$ variations across the Drake passage. *J Geophys Res* 96:15131–15135
- 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 LI (1991b) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variations in Weddell Sea particulate organic matter. *Mar Chem* 35:355–369
- Reichardt W, Dieckmann G (1985) Kinetics and trophic role of bacterial degradation of macro-algae in Antarctic coastal waters. In Siegfried WR, Condy PR, Laws RM (eds) *Antarctic Nutrient Cycles and Food Webs*. Springer-Verlag, Berlin, pp. 115–122
- Richardson MG (1979) The distribution of Antarctic marine macro-algae related to depth and substrate. *Brit Antarctic Sur Bull* 49:1–13.
- 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
- Thiel M (1999) Host-use and population demographics of the ascidian-dwelling amphipod *Leucothoe spinicarpa*: indication for extended parental care and advanced social behaviour. *J Nat Hist* 33: 193–206
- Thompson PA, Calvert SE (1994) Carbon-isotope fractionation by a marine diatom: the influence of irradiance, daylength, pH, and nitrogen source. *Limnol Oceanogr* 39: 1835–1844
- 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
- Webb SC, Hedges REM, Simpson SJ (1998) Diet quality influences the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of locusts and their biochemical components. *J Exp Biol* 201: 2903–2911
- Zielinski K (1990) Bottom macroalgae of the Admiralty Bay (King George Island, South Shetlands, Antarctica). *Pol Polar Res* 11: 95–13