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# ROLE OF BENTHIC AMPHIPODS IN ANTARCTIC TROPHODYNAMICS: A MULTIDISCIPLINARY STUDY

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Cette recherche a été réalisée dans le laboratoire d'océanologie de l'Université de Liège ainsi qu'au sein du laboratoire de carcinologie de l'Institut Royal des Sciences naturelles de Belgique à Bruxelles. Cette double appartenance, bien que peu évidente à gérer au début sans pour autant me rendre schizo (à Bruxelles: tiens vlà la Liégeoise! A Liège: tiens vlà la Bruxelloise!...) n'a rendu ce travail que plus riche en expériences de vie et professionnelles, en rencontres intéressantes et surprenantes, bref, en tout!
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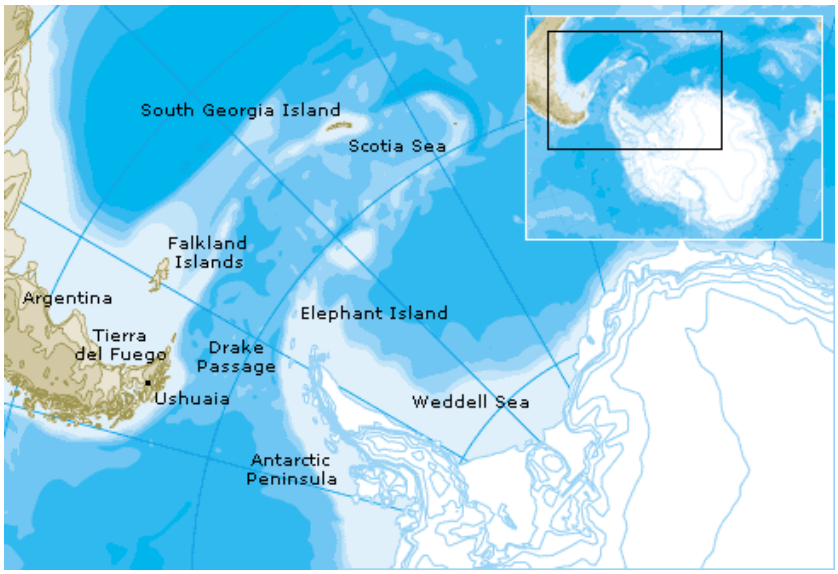
# OBJECTIVES

The purpose of this work is to assess the ecological roles of amphipod crustaceans in the Southern Ocean and, more particularly, on the continental shelf of the Weddell Sea and the Antarctic Peninsula.




Within this ecological study, focus has been made on the significance of amphipods in Antarctic trophodynamics through:

- A systematic determination of gut content composition. The amphipods have been chosen because they cover an extremely wide trophic spectrum; from sampling gathering suspension-feeders such as *Ampelisca richardsoni* to micropredators such as *Epimeria similis*, as well as scavengers such as *Waldeckia obesa*. The species considered in this work are representative of the Antarctic continental shelf amphipod community.

- An scan examination of the morphology of the mouthparts and especially of the mandibles in several species, representative of different trophic types.
- A systematic analysis of stable isotope ratios -$\delta^{13}C$ and $\delta^{15}N$ - in all the sampled species in order to estimate and compare their respective trophic position. The isotopic ratios have also been measured in specimens of other benthic groups to investigate the trophic relationships built by amphipods in the Antarctic benthic food web.
- The determination of the fatty acid composition in several species of amphipods to delineate the trophic links between amphipods and the rest of benthos.

This multidisciplinary approach allows 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.

The general introduction and results are presented according to the following framework:

**Chapter 1:** A general introduction puts the scientific question in its global context by summarizing information about the studied ecosystem: the Southern Ocean and the significance of amphipods in Antarctic benthic communities. The second part of this introduction is devoted to the description of the different techniques that have been used to assess benthic amphipod ecological role in Antarctic trophodynamics.

Some of the following chapters have already been published in peer-review journals or submitted.

**Chapter 2:** "*A stable isotope approach to the Eastern Weddell Sea trophic web: focus on benthic amphipods"*, Polar Biology (2002) 25: 280-287.

**Chapter 3:** "*Trophic position of Antarctic amphipods - enhanced analysis by a 2-dimensional biomarker assay"*, Marine Ecology Progress Series, (2005) in press.

**Chapter 4:** "*Antarctic amphipod feeding habits inferred from gut contents and mandible morphology"*, to be submitted.

**Chapter 5:** "*The crustacean scavenger guild in Antarctic shelf, bathyal and abyssal communities"* Deep-Sea Research, part II (2004) 51: 1733-1752.

**Chapter 6:** "*Amphipods as food sources for higher trophic levels in the Southern Ocean: a synthesis"*, In: Huiskes AHL, Gieskes WWC, Rozema J, Schorno RML, van der Vies SM, Wolff WJ (eds) Antarctic Biology in a Global Context. Backhuys Publ, Leiden, (2003) p 129-134.

**Chapter 7:** *General Discussion and Conclusions.*

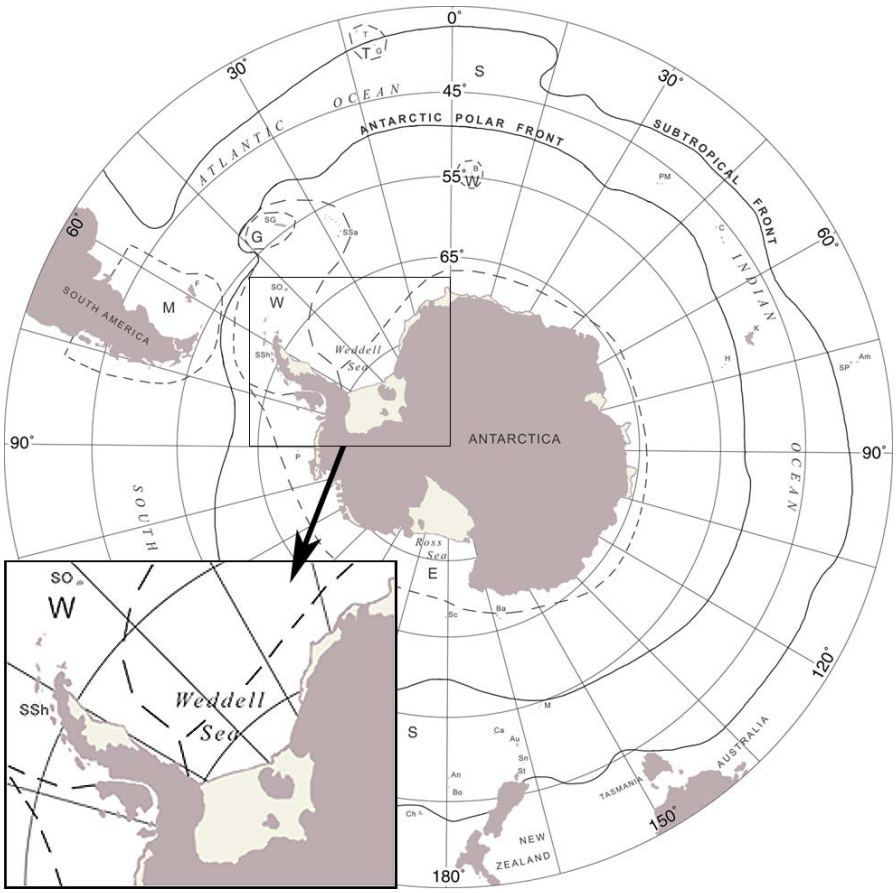
# CHAPTER 1: GENERAL INTRODUCTION

# 1.1. THE SOUTHERN OCEAN

## 1.1.1. OCEANOGRAPHIC FEATURES

The Southern Ocean consists of the southern parts of the Atlantic, Indian and Pacific oceans (Fig 1.1.). Used in its wide sense, according to Deacon (1984), the Southern Ocean includes all waters south of the Subtropical Front zone (at about 42°S). In its restricted sense, it comprises only the waters extended south of the Polar Front (50°S in the Atlantic and Indian sectors and 60°S in the Pacific sector) (e.g. Dell 1972, Clarke 1996a). We will privilege the restricted sense of the definition. The northern boundary of the Southern Ocean, the Antarctic Polar Front, is characterized by a steep surface temperature gradient of 3–4°C, as well as by changes in other oceanographic parameters like salinity. At the frontal boundary, northward-flowing Antarctic Surface Water sinks beneath warmer Subantarctic Surface Water, generating a transition zone between surface water masses of different temperatures. From an oceanographic perspective, the surface circulation around Antarctica consists of two main currents. Close to the Antarctic Continent, easterly winds generate a counterclockwise water circulation, i.e. the Antarctic Coastal Current or East Wind Drift. North of 60°S, westerly winds produce a clockwise and northward water flow, known as Antarctic Circumpolar Current or West Wind Drift, representing the major current in the Southern Ocean. In large embayments of the Antarctic Continent, particularly the Weddell and Ross Seas, the Antarctic Coastal Current forms clockwise gyres, which probably concentrate nutrients like silicate, phosphate and nitrate. Unlike other areas of Antarctica, the continental shelves of the Weddell and Ross Seas are wide and 500–600 m deep, with inner shelf depressions reaching depths of over 1,200 m (Anderson 1999). Furthermore, much of the Antarctic coastline is covered by ice shelves, which are exceptionally large in the Weddell and Ross Seas. During much of the year, the adjacent shelf waters are covered by pack ice.

**Figure 1.1. Map of Southern Ocean and detail displaying sampling zones: the Weddell Sea and the Antarctic Penisula. SO: South Orkney Islands, SSh: South Shetland Islands, F: Falklands, E: East Antarctic sub-region, W: West Antarctic sub-region (including South Georgia district), S: Subantarctic sub-region, M: Magellanic sub-region, T: Tristan da Cunha district**



The most obvious physico-chemical characteristic of the Antarctic coastal and shelf ecosystem (ACSE) is the year round low water temperature. For example, temperature close to the sea bed varies annually between 0 and 3°C in South Georgia (54° S), -1.8 and 2°C in the South Orkney Islands (West Antarctic, 61° S), and -1.9 and -1.8°C at McMurdo Sound (East Antarctic, 78° S) (Clarke 1983). This low and – compared to boreal waters - very stable temperature has important biological consequences. For instance, the inverse relationship between gas solubility and temperature leads to extraordinary high levels of oxygen in Antarctic waters. Another major characteristic of the ACSE is the highly seasonal character of the primary production (Clarke 1988). This primary production relies mainly on phytoplankton, not only in the shelf waters, but also in the intertidal and shallow subtidal areas, due to the paucity of macroalgae resulting from the negative impact of ice bergs, brash ice and solid ice on the macroalgae (Clarke 1996a). Compared to warmer latitudes, this primary bloom is also more decoupled from the grazing bloom of the zooplankton, ensuring an important phytoplankton input to the sea floor (Gray 2001).

The seasonally ice-covered regions of the Southern Ocean feature distinct ecological systems due to sea ice microalgae . Although sea ice microalgal production is exceeded by phytoplankton production on an annual basis in most offshore regions of the Southern Ocean, blooms of sea ice algae differ considerably from the phytoplankton in terms of timing and distribution. Thus sea ice algae provide food resources for higher trophic level organisms in seasons and regions where water column biological production is low or negligible. A flux of biogenic material from sea ice to the water column and benthos follows ice melt, and some of the algal species are known to occur in ensuing phytoplankton blooms. A review of algal species in pack ice and offshore plankton showed that three species are commonly dominant: *Phaeocystis antarctica, Fragilariopsis cylindrus* and *Fragilariopsis curta* (Lizotte 2001). As pointed out by Grassle (1989), spatial patchiness of

organic matter sedimentation is highest in Polar Regions, and this could in part account for the high diversity of the Antarctic benthos, together with the - still controversially discussed - link between energy input and diversity (Gage & Tyler, 1991; Roy et al., 1998; Gray, 2001).

Also important is the physical disturbance caused by icebergs. This adds to the heterogeneity of the environment and increases niche diversity (Arntz et al. 1997). According to a recent assessment, iceberg scouring is one of the 5 most significant physical impacts on any ecosystem on Earth (Garwood et al. 1979, Gutt & Starmans 2001). It has most likely been a major driving force in structuring Antarctic benthos since the continent began to cool and glaciers extended up to the coast approx 25 to 30 million yr ago (Hambrey et al. 1991). Mainly quantitative effects of scouring on meio- and macrobenthos have been described and reviewed by Gutt et al. (1996), Conlan et al. (1998), Peck et al. (1999), Gutt (2001) and Lee et al. (2001a, b). Type and strength of physical iceberg impact on the benthos vary (e.g. Kauffmann 1974), but it is estimated that 5% of the Antarctic shelf shows detectable scours (Gutt et al. 1999). Iceberg impact causes various degree of damage to the benthos up to local extinction of the fauna (Dayton et al. 1974, Brey & Clarke 1993, Arntz et al. 1994, Peck et al. 1999) and disturbed bottoms are subsequently recolonized. Temporal distribution of iceberg scouring and time-scale of recolonization are still poorly understood, but seem to be an intrinsic feature of Antarctic shallow-water and shelf benthic community dynamics leading to a spatial and temporal patchwork of benthic recovery (Gutt et al. 1999, Brenner et al. 2001, Texeido et al. 2004).

Another factor responsible for this higher diversity compared to the Arctic is the long evolutionary history of the Southern Ocean (Clarke, 1996b). When the first has only been isolated 2-3 million years ago, separation of the Antarctic occurred at least 25 million years ago (Dunton, 1992; Dayton et al., 1994; Clarke & Crame, 1997).

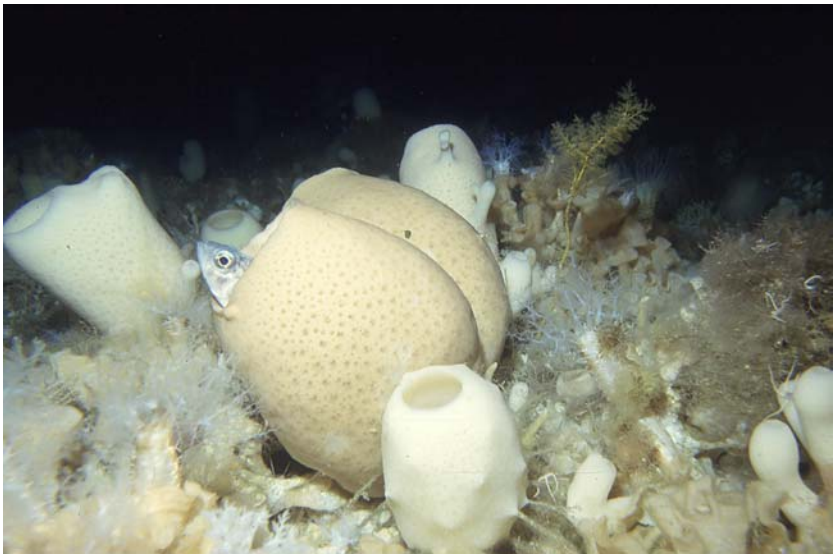
## 1.1.2. BENTHOS BIODIVERSITY IN THE SOUTHERN OCEAN

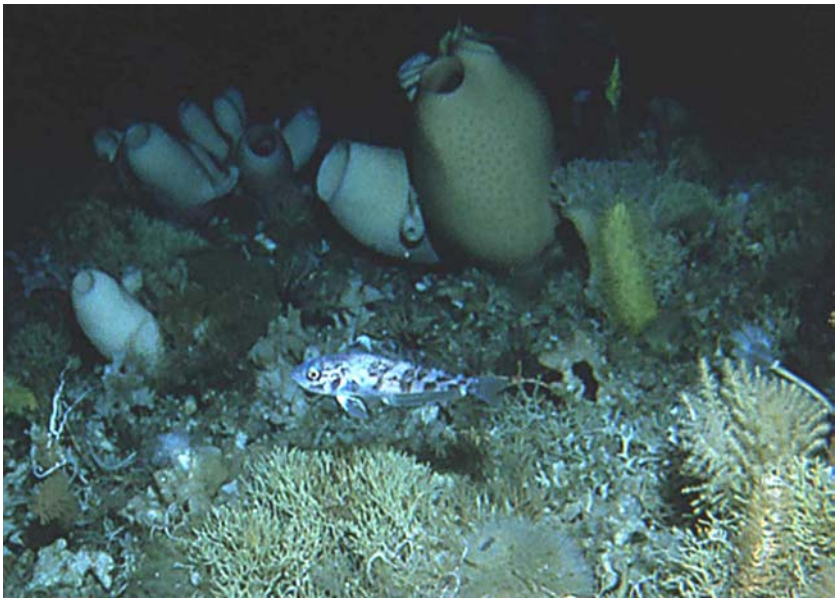
### 1.1.2.1. The Antarctic benthos

Antarctic marine biodiversity is strongly influenced by the geological and glaciological history of the Antarctic continent. The origin of distinct benthic marine invertebrate faunas in both Antarctic and Subantarctic waters can be traced back as far as the Early Cretaceous, about 130 million years ago, when the break-up of the Gondwana continent first became evident, and eastern Gondwana became isolated in the high southern latitudes (Lawver et al. 1992; Crame 1999). Antarctic cooling may have started as late as 35 million years ago as a result of ongoing continental drift and the establishment of the Antarctic Circum-polar Current (Barker et al. 1991), leading to an isolation of the Antarctic marine realm from surrounding seas (Clarke 1990).

Recent observations, notably by video underwater cameras coupled with analyses of benthos samples, have described a variety of benthic assemblages from the eastern Weddell Sea shelf (i.e. Galéron et al. 1992, Gutt & Schickan 1998). As our study had focused particularly on this part of Southern Ocean and because of the numerous studies already conducted on Weddell Sea benthic communities, we will take it as our reference in terms for Antarctic benthos. The unusually deep continental shelf of the Weddell Sea locally exhibits a complex 3-dimensional community with patchy distribution of organisms (Gutt & Starmans 1998, Gili et al. 2001, Teixidó et al. 2002, Gerdes et al. 2003). The fauna in this area is dominated by a large proportion of benthic suspension feeders such as sponges, gorgonians, bryozoans and ascidians, which locally cover most of the sediment (Gutt & Starmans 1998, Starmans et al. 1999, Teixidó et al. 2002). Those diverse and multistratified sessile benthic assemblages offer a high diversity of potential microhabitats to small vagile invertebrates (see Fig. 1.2 & 1.3).

**Figures 1.2 & 1.3. Illustrations of typical Antarctic sessile benthic assemblages composed of sponges, bryozoans, cnidarians… (Photos from Julian Gutt, AWI)**





In a recent overview of Antarctic marine biodiversity, Arntz et al. (1997) compiled the species numbers per taxon for most groups of marine animals and plants occurring south of the Polar Front. This compilation, albeit yet being far from representing the complete Antarctic species inventory, clearly shows the relative importance of polychaetes and mollusks and the predominance of crustaceans. In terms of composition, more particularly, the Antarctic crustacean fauna includes some extreme groups, from a total absence for some taxa to particular richness for others:

**- Stomatopoda.** They are totally lacking in Polar seas.

**- Cirripedia.** They are characterized by the extremely high proportion of lepadiform versus balaniform. This seems to be correlated with the lack of suitable littoral habitats and with the geological history of Antarctica (Dell 1972).

- **Decapoda.** The impoverished Antarctic decapod fauna, compared with the high diversity of decapod crustaceans recorded in the Subantarctic (Gorny 1999), constitutes one of the most enigmatic phenomena in present-day marine biodiversity research. The decapod fauna composition was reviewed by Gorny (1999). Twenty-four decapods (12 pelagic and 12 benthic species) occur south of the Antarctic Convergence. They represent only 0.25% of the world decapod fauna. Different hypotheses were proposed to explain the poor decapod fauna and the absence of the whole group of brachyurans. Low temperatures in general have been hypothesised to reduce decapod activity, especially in combination with high [$Mg^{2+}$] levels in the haemolymph, as [$Mg^{2+}$] has a relaxant effect (Frederich 1999; Frederich et al. 2001). Since Reptantia regulate $[Mg^{2+}]_{HL}$ only slightly below the [$Mg^{2+}$] of seawater, their activity should be hampered. In contrast, Natantia are known to regulate $[Mg^{2+}]_{HL}$ to very low levels (Tentori and Lockwood 1990; Frederich et al. 2001). The combined effect of low temperatures and high $[Mg^{2+}]_{HL}$ might explain the limits of cold tolerance in decapods and might be the principal

reason for the absence of reptant decapods from the high polar regions (Frederich et al. 2001). At present only lithodids may tolerate environmental and physiological constraints imposed by the low temperatures and short periods of food availability at high- Antarctic latitudes (Clarke 1983, Thatje 2003a, Thatje and Fuentes 2003b, Thatje et al. 2003c, Thatje et al. 2004). On the other hand, among the Antarctic crustacean fauna, amphipods and isopods form obviously highly species-rich groups. This will be described in details in the section 1.2. The issue of the Antarctic benthos species richness in a worldwide latitudinal context has been recently discussed in details (Clarke 1992, Clarke & Crame 1997, Crame (1999) and Gray 2001a) but useable data are still too few and of limited comparability. The reasons for latitudinal variation in marine species richness are contentious but most likely related to variation in time available to species diversification and to variation in the area and productivity.

Another interesting aspect of the latitudinal gradient issue is the size distribution within marine organisms. Significant progress has been made recently in elucidating the trend towards gigantism in polar Crustacea, in particular among the highly species-rich and widely distributed Amphipoda. Indeed, from a large data set, Chapelle & Peck (1999) and Chapelle (2001) confirmed the existence of a clear trend towards larger amphipod species in polar regions and especially in the Antarctic. A crucial finding was that this trend toward larger size is explained best by oxygen content rather than by temperature, with the largest species to be found in waters with the highest oxygen concentration. Chapelle & Peck (1999) and Peck & Chapelle (1999) demonstrated that the maximal potential size in amphipod crustaceans was dictated by oxygen availability.

Circumpolarity in species distribution and extended range of eurybathy were considered as common features in Antarctic benthos (Brey et al 1996). However recent studies have revisited this concept and the most striking progress in this context has been accomplished by molecular methods. For

example, after analyzing the sequences from the mitochondrial 16S ribosomal RNA of the isopod *Ceratoserolis trilobitoides* (Eights, 1833), Held (2003) demonstrated that this species, known as a cosmopolitan and highly plastic species in the Southern Ocean, contains "at least one, possibly many more, previously overlooked species" with poorly overlapping distribution. Furthermore, from a phylogenetic analysis of the circumpolar giant isopod *Glyptonotus antarcticus* Eights, 1853 he concluded that there was good evidence that four different *Glyptonotus* species might exist where only one circumpolar species was recognized so far (DeBroyer et al. 2003).

Another feature of Antarctic zoobenthos is the high degree of species endemism that has been recorded in many taxa (White 1984). Regarding benthic amphipods, 85% of all species are endemic to the Antarctic (DeBroyer & Jazdzewski 1993, 1996).

# 1.2. AMPHIPODA

## 1.2.1. WHAT IS AN AMPHIPOD?

### 1.2.1.1. Systematics

Up to now, Peracarida are still treated as a superorder that contains nine orders in the crustacean classification. However, there have been suggestions made to abandon the Peracarida or at least significantly revise it (e.g. Dahl 1983a), and the relationships among the various peracarid groups (and of peracarids to other groups of crustaceans) are very controversial.

Following the updated classification of crustaceans from Martin & Davis (2001), Peracarida contain the orders Lophogastrida and Mysida, plus the Thermosbaenacea, in addition to the Spelaeogriphacea, Mictacea, Amphipoda, Isopoda, Tanaidacea, and Cumacea.

The most diversified orders are the isopods, with 4,000 species (Brusca & Brusca, 1990), and the **amphipods**, with around 8,000 described species, to which this work is devoted.

Classically, Amphipoda are divided in four suborders; the mainly benthic Gammaridea, the interstitial Ingolfiellidea, the rod-shaped and benthic Caprellidea and the exclusively marine and planktonic Hyperidea. However, Dahl (1977) and later Bowman & Abele (1982) considered that there were only three suborders, by including the Ingolfiellidae within the Gammaridea. This new classification did not last long, as in 1983, Barnard (in Barnard and Karaman, 1983) proposed that the Amphipoda should be divided into three suborders: Corophiidea, Hyperiidea, and Gammaridea. According to their phylogenetic hypothesis, the Ingolfiellidea are placed under Gammaridea, and the Caprellidea are reduced to a superfamily under the new suborder Corophiidea. In this study, we refer to Barnard classification.

With more than 6,000 species, the Gammaridea are by far the most species-rich of these groups. Our study will focus mainly on benthic gammarid species living on the continental shelf.

#### 1.2.1.2. Morphology

Much morphological variation exists within the order Amphipoda. Furthermore, within the suborder Gammaridea, which represents 80% of the species, the shape varies with family. However, all species, as much differentiated as they may be, correspond, at least by a certain amount of characters, to the typical "amphipod common type". A typical amphipod can be described as a small crustacean, of around 10 mm, with an arched and laterally compressed body divided in three parts (Fig. 1.4.): the head, the 7-segmented pereon and the 6-segmented pleon (Bellan-Santini, 1999).

- The head: the term, commonly used in amphipod taxonomy, is wrong as this part of the body corresponds to a cephalothorax (Bellan-Santini 1999). The head bears sessile eyes, two pairs of antennae and mouthparts.

Eyes are composed of a large amount of ommatidies. Their development is variable: absent in some cave species, the eyes reach a considerable size in some hyperiid species.

The peduncle of the first pair of antennae is smaller than the second, three articles instead of five, respectively. Both are terminated by pluri-articulated flagella.

Most of amphipods mouthparts correspond to a common scheme although a large panel of modifications to the basic pattern can be observed (Watling 1993). Consequently, mouthpart morphology is essential in amphipod taxonomy. The most frequent type bears above and beneath the mouth: an upper lip (*labrum*) and a lower lip (*labium*). Between the lips, around the mouth, the mandibles are found; constituted of an incisor process, generally provided with cusps and teeth; the *lacinia mobilis*, inserted close to the

incisor and generally in line with; the molar process, a plane surface provided with diverse triturative structures and a palp, generally tri-articulated (Watling 1993). Posterior of the lower lip the maxillae 1 followed by the maxillae 2 are found. The following appendages are the maxillipeds.

- The pereon: this part is composed of seven segments, generally well separated but which can be partially fusioned in some hyperiids. The seven pairs of pereopods beard by the pereion are oriented in two directions: three point towards the rear and four are directed towards the front. This feature is the origin of the name "Amphi - poda".

The pereopods are generally long and brittle, but most frequently the first two pairs are modified in kind of hooks and are so called, gnathopods. A typical pereopod is classically divided - from the proximal to the distal part - in the following parts: coxa, basis, ischium, merus, carpus, propodus and dactylus. The coxa is often flattened in a coxal plate. The Gammaridea present various forms of coxal plate. For example, in the Lysianassidae, the first four coxal plates are highly developed and form a kind of lateral shield and in some Iphimediidae, the coxal plates present characteristic incurvate teeth. The two pairs of gnathopods present different evolutive stages but the most common is the one modified in a claw constituted by a hook-shaped dactylus and a large propodus.

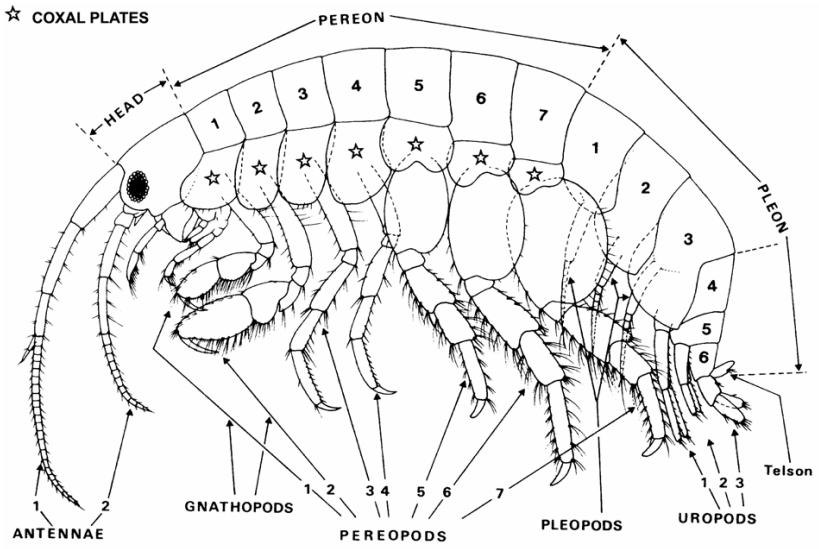
The pereopods bear generally a gill inserted at the junction with the body. Those gills are present from the second to the seventh pereopods but the number can vary.

The oostegites are generally large inner medially directed lamella provided with setae arising from coxa of pereipod in females participating in formation of mid-ventral brood pouch proper to peracarids, “the marsupium”.

- The pleon: this part is composed of six somites: the first three (metasome) bear swimming appendages, the pleopods, and the last three bear the uropods (urosome). The pleon is ended by the telson, a kind of blade situated on the last segment of the urosome. It can show various shape following the family

(complete or cut, armed with spines and setae) but can also be strongly reduced. Morphology of telson is a significant taxonomical character.

**Fig. 1.4. – Basic morphology of gammaridean amphipod. From Chapelle (2001)**




### 1.2.1.3. Ecology in brief

The Amphipoda inhabit nearly all aquatic habitats. They have been recorded in the hot vents of the deep sea or beneath the polar sea ice, in mountain streams or in caves, in the interstitial water of aquifers or on the bottom of the deepest abyssal trenches, on the skin of cetaceans or inside jellyfish, in the shell of hermit crabs or on the shell of sea turtles, under decaying algae on every beach or in the litter of some rain forests. This habitat diversity is coupled to an equally diverse trophic spectrum; amphipods comprise specialized predators, herbivores, scavengers, detritivores as well as many opportunistic omnivorous species.

### 1.2.2. AMPHIPODA IN ANTARCTIC BENTHOS

Within Antarctic benthic communities, crustaceans form by far the most species-rich animal group (Arntz et al 1997), and, among crustaceans, amphipods represent the richest groups, with more than 820 recorded species so far (DeBroyer & Jazdzewski 1993, 1996) about 320 of wich inhabit Weddell Sea waters. These peracarids have colonized a wide variety of ecological niches, from epontic to below-ground biotopes. They have achieved a successful eco-ethological diversification, occupying apparently all the micro-habitats (De Broyer et al. 2001) and developing various feeding strategies, from suspension-feeding to scavenging on big carrion, as well as specialized modes such as micro-predatory browsing on invertebrate colonies (Dauby et al. 2001a).

"This trophic diversity of amphipods is in a way unique if considering that Antarctic marine fauna is part of the same immense cold-water system (Arntz et al. 1997)".

Why are amphipod communities so diversified in Antarctic waters? The theme of the high biodiversity of Antarctic fauna and of cold deep-sea fauna in general has been widely debated (see section 1.1.2.1.). Antarctic species richness is attested for amphipods, especially the families Epimeriidae and Iphimediidae, with usually a high degree of endemism. The origin of the Antarctic amphipod fauna and of Iphimediidae in particular, has been discussed by Watling & Thurston (1989). They showed that the most primitive genera were distributed primarily outside Antarctica and were suspected to be relicts of a global distribution, which is in good agreement with the third evolutionary historical model of Crame (1992). Watling & Thurston (1989) suggested that once the Antarctic began to cool (at the Eocene-Oligocene boundary, 38 Ma BP), a radiation occurred in the Southern Ocean, followed by some adaptative morphological reorientations that eventually allowed species to spread outward from the Antarctic. They thus

consider the cooling Antarctic waters to act as an incubator for the Iphimediidae amphipod family.

As suggested for isopods (Clarke & Crame 1989), the expansion of amphipods in the Southern Ocean may represent the filling of an ecological vacuum left by the extinction of the decapods. The taxonomic affinities of the Southern Ocean amphipod fauna were discussed by Knox & Lowry (1977) who suggested this fauna to be a mixture of taxa with different biogeographic origins: (i) a relict of autochthonous fauna, (ii) a fauna which has spread southwards from South America along the Scotia arc (iii) a fauna which has spread northwards from Antarctica along the Scotia arc, and (iv) a fauna derived from adjacent deep-sea basins. The origin of the high amphipod species diversity could also be related to the high oxygen availability in Antarctic waters; indeed Levin & Gage (1998) have showed good correlations between oxygen concentrations and macrobenthos diversity for various bathyal areas. Oxygen availability was also proposed recently to be responsible for the phenomena of extended size spectrum and gigantism observed for the amphipods in the Southern Ocean (Chapelle & Peck 1999) (see Dauby et al. 2001).

The impressive diversity of amphipod taxocoenoses indicates that these crustaceans contribute significantly to biomass and trophodynamics of Antarctic ecosystems. Total biomass data, and *a fortiori* relative data on amphipods are more than scarce, only available for some restricted areas like the eastern Weddell Sea shelf where amphipods should count for about 5% of the benthic biomass (Gerdes et al 1992). Recently Dauby et al (2001b) showed, from an extensive study of gut contents of the most representative species, that their diet was highly complex. On the other hand, based on an exhaustive literature survey (more than 300 references); Dauby et al (2003) tried to delineate the importance of amphipods as potential food for higher trophic levels. About 200 different predators were recorded: 33 invertebrates, 101 fishes, 48 birds and 10 mammals. Using this vast dataset (up to 1500

citations) and published values about predator's standing stocks and feeding rates, an attempt was made to build up a small model, distinguishing between benthic and pelagic species of both amphipods and predators. The total amount of consumed amphipods was estimated to 60 millions of tons per year for the whole Southern Ocean, i.e. the second animal group in importance after euphausiids, the consumption of krill being estimated to about 250 $Mt.yr^{-1}$ (Everson 1977, Miller & Hampton 1989).

And just to please your eyes, here are pictures of some species that have been considered all along this study…

***Paraceradocus gibber*** **(Andres, 1984), from the family Hadziidae**

***Djerboa furcipes*** **(Chevreux, 1906), from the family Eusiridae**

***Waldeckia obesa*** **(Chevreux, 1905), from the superfamily Lysianassoidea**

***Epimeria similis*** **(Chevreux, 1912), from the family Epimeriidae**

***Echiniphimedia hodgsoni*** **(Walker, 1906), from the family Iphimediidae**

***Epimeria georgiana*** **(Schellenberg, 1931), from the family Epimeriidae**

# 1.3. TROPHIC ECOLOGY INFERRED FROM STABLE ISOTOPE RATIOS

The significance of naturally occurring stable isotopes in ecological research has increased tremendously in the last two decades. While initially restricted to the domain of earth sciences, stable isotope techniques are increasingly being used in physiology, ecology and atmospheric science to investigate questions ranging from the molecular to the ecosystem level (Lajtha & Michener 1994).

## 1.3.1. THEORY

Isotopes are atoms of the same element which nucleus contains the same number of protons (p), but a different number of neutrons (n), resulting in different atomic masses. There are two types of isotopes: the stable isotopes, which persist in nature, and the radioactive isotopes, which spontaneously degrade.

H, C, N, O and S isotopes are essential in the study of natural processes due to their abundance in Earth systems and their presence in a wide variety of solid, liquid, and gaseous compounds occurring in the biosphere, hydrosphere and lithosphere.

Our work did focus on the study and the analyses of carbon and nitrogen isotopic ratios.

The stable isotopes for carbon and nitrogen are $^{13}C$ and $^{12}C$, and $^{15}N$ and $^{14}N$, respectively. The average natural abundance of these isotopes is given in Table 1.1. In most cases, even for other elements, the light isotope is the more abundant one.

Typically, the value of interest is not the absolute abundance of an isotope in an organism or in a biogeochemical reservoir, but rather the relative

abundances or ratio of "light" to "heavy" isotopes. However those ratios, measured by mass spectrometry, are very small (e.g. the $^{13}C/^{12}C$ may vary between 0.010225 and 0.011574). To solve this inconvenient, ratios are measured and reported relative to standard reference materials as delta values:

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

where $R=^{13}C/^{12}C$ in the case of carbon and $^{15}N/^{14}N$ in the case of nitrogen, i.e. the absolute ratio of the atom occurrence of the "heavy" to "light" isotope, where X= $^{13}C$ or $^{15}N$, and where the delta values are expressed in parts per thousand or per mil (‰).

**Table 1.1.: Average natural abundance of the main stable isotopes of carbon and nitrogen, according to Ehleringer and Rundel, 1989**

| Element/Isotope | Abundance (atom %) |
|---|---|
| **CARBON** | |
| $^{12}C$ | 98.89 |
| $^{13}C$ | 1.11 |
| **NITROGEN** | |
| $^{14}N$ | 99.63 |
| $^{15}N$ | 0.37 |

The internationally accepted stable isotope standards for carbon and nitrogen are Vienna-PeeDee Belemnite (IAEA) and atmospheric nitrogen (Mariotti 1983) respectively.

As the chemical behaviour of atoms is a function of their electronic structure only, isotopes undergo the same reactions. On the other hand, the physical behaviour of atoms is a function of mass, which is determined by the nucleus (since electrons have virtually no mass); therefore isotopes react at different rates. This phenomenon is called "fractionation". Stable isotope fractionation

in the environment imparts unique isotopic ranges of signatures to various reservoirs (e.g. food sources), as well isotopic shifts that propagate through fluxes between reservoirs.

## 1.3.2. PATTERNS OF FRACTIONATION IN BIOGEOCHEMICAL PROCESSES

Stable isotopes fractionate during biogeochemical reactions; those small but significant natural variations do not occur randomly but are governed by different physico-chemical processes. Consequently, it is necessary to understand the degree of stable isotope fractionation that occurs during transfer of a chemical substance through an environmental reservoir (e.g. a food web) in order to use stable isotopes as tracers of material transfer.

### 1.3.2.1. Carbon

The main reaction responsible for the formation of sources with identifiable carbon-isotope signatures in the biosphere is the **photosynthesis**.

Differences in $\delta^{13}C$ among plants using the Calvin cycle ($C_3$), Hatch-Slack cycle ($C_4$) and Crassulacean acid metabolism (CAM) photosynthetic pathways are due to differences in fractionation at the diffusion, dissolution, and carboxylation steps, and are discussed in detail by e.g. O'Leary (1981, 1988a).

Carbon fixed by terrestrial $C_3$ plants ($\delta^{13}C$ range: -35 to -21‰) can be distinguished from that fixed by $C_4$ plants ($\delta^{13}C$ range: -14 to -10‰). This difference is due to the stronger discrimination against $^{13}C$ isotopes by the primary $CO_2$-fixing enzyme of the $C_3$ plants: the ribulose biphosphate carboxylase (Rubisco). In $C_4$ plants, the primary enzyme for $CO_2$ fixation, the phosphoenolpyruvate carboxylase (PEP) discriminates against $^{13}C$ in a lesser extent (O'Leary 1981, 1988, Farquhar et al 1989).

However, while marine phytoplankton uses the Calvin cycle as photosynthetic pathway, its isotopic ratio is significantly heavier (-22‰) than that of terrestrial $C_3$ plants. Such difference is likely to be caused by the use of bicarbonate as a carbon source in marine systems and by the slower diffusion of carbon dioxide in water, which might counteract the discrimination by the enzyme (O'Leary 1988, Boutton 1991, Kelly 1999).

Aquatic plants have been found to show widely varying stable isotope signatures (reviewed by Bouillon, 2002). The major factors influencing the carbon isotopic composition of aquatic plants are the following: the isotopic composition of the substrate, the substrate type ($CO_2$ or $HCO_3^-$) and the water velocity. It should be noted that a few additional factors such as the growth rate and the size and shape of the cells are particularly important for microalgae.

All these differences in $^{13}C/^{12}C$ ratios in primary consumers are sufficient enough to influence carbon isotopic composition of their respective consumers and assign them a specific isotopic signature.

#### 1.3.2.2. Nitrogen

In contrast to the numerous studies on the carbon fractionation during primary production, knowledge on fractionation processes during N-assimilation is quite limited. However, nitrogen isotopic composition of primary producers in aquatic as well as in terrestrial systems may give indications about nitrogen sources and transformations.

Kinetic isotope fractionation is associated with most biological reactions involving inorganic nitrogen. These reactions include the assimilation of dissolved inorganic nitrogen (either under the form of nitrates, nitrites or ammonium) by phytoplankton, or bacteria nitrification and denitrification, and $N_2$ fixation. Generally, the end product is depleted in $^{15}N$ relative to the substrate, resulting in an enrichment of the residual substrate pool.

Denitrification seems to be the reaction leading to the largest fractionation effects, probably due to the break of the particularly strong covalent bonds it implies.

As for carbon, a multitude of factors may influence nitrogen fractionation and the numerous studies devoted to this subject have revealed wide variations of nitrogen isotopic ratios with light intensity, species, nitrogen substrate, culture conditions resulting in various fractionation values for algae.

### 1.3.3. STABLE ISOTOPES IN FOOD WEBS

Standard approaches to food web analysis include gut content analysis, direct observation in the field as well as in the laboratory, and radiotracer techniques, each method having its own advantages and drawbacks (Auel & Werner 2003, Werner et al. 2002). For example, analysis of gut contents involves collecting and dissecting a broad range of organisms to determine food web structure and requires few tools and equipment (Dauby et al 2001). However, some preys are sometimes digested more quickly than others, making identification difficult and bringing biases in the determination of diet composition. Furthermore, gut content is only a snapshot of the diet revealing what the organisms fed on short time before the sampling and may include material which is not really assimilated.

An alternative technique for aquatic food web studies is the use of immunological methods (Theilacker et al. 1993). It involves the development of antisera for whole organisms extracts. It has been shown that the antisera are usually taxon-specific and can trace trophic relationships. For example, immunochemistry has been used successfully to examine predation by the euphausiid *Euphausia pacifica* on early life stages of anchovy (Theilacker et al. 1993). Also, while most immunochemistry studies have focused on identifying animal prey, Haberman et al. (2002) used immunochemical methods to analyze ingestion of the prymnesiophyte *Phaeocystis antarctica*

by Antarctic krill *Euphausia superba*. However, if this method sounds promising, to study ecosystems with a large number of species, it would be prohibitively expensive and time-consuming to check all possible antisera…

Stable isotopes analysis has more recently been used as an alternative, and is some cases, better tool for food web analysis.

Since food sources show considerable variations in their carbon-isotope signatures, the utility of these isotopes for trophic studies hinges on the relationships between the isotope composition of a consumer's diet and that of its tissues.

DeNiro and Epstein (1978a) were pioneers providing evidence that, first, the carbon-isotope composition of a consumer was a direct reflection of its diet and, secondly, that the whole bodies of consumers were enriched in $^{13}C$ only slightly over their diet (i.e. the fractionation was less than 2‰). Ensuing studies have confirmed Epstein and DeNiro's (1978) findings, for example, with birds (Mizutani et al. 1992, Hobson and Clark 1992a, 1992b, 1993) and mammals (Tieszen et al. 1983, Hobson et al. 1996, Hildebrand et al 1996). This minor stepwise trophic enrichment of the carbon isotope ratio that has been documented limits its use in discriminating trophic levels. However, this characteristic enhances the utility of carbon isotope ratios for tracking carbon sources through a food chain (Peterson & Fry 1987, Michener & Schell 1994). Specifically, since enrichment at each trophic level is small, the carbon isotope signature of secondary and tertiary consumers should reflect the source of carbon at the base of the food chain (reviewed by Kelly, 2000).

As with carbon, DeNiro and Epstein (1981a) found that $\delta^{15}N$ of a consumer reflects $\delta^{15}N$ of its diet, but in most cases the whole animal is enriched in $^{15}N$ relative to the diet. When enrichment occurs, it seems to be due to a preferential excretion of $^{15}N$-depleted nitrogen, usually in the form of urea and ammonia and this progressive enrichment increases along advancing

trophic levels (Minagawa and Wada 1984, Peterson and Fry 1987, Ehleringer and Rundel 1989).

Despite the multiple advantages and possibilities offered by the method, the researcher must be aware of its limits such as the isotopic variations in different tissues within an organism, as well as different rates of tissue turnover. Indeed, despite recent advances in stable isotope analysis, relatively few experimental studies have addressed the relationship between the isotopic composition of an animal and its food, and the response time of different tissue types to changes in the isotopic composition of the food source (Gannes et al. 1997). For example, in a feeding study of rodents, Tieszen at al. (1983) found that $^{13}C$ enrichment for individual tissues fell from hair > brain > muscle > liver > fat after switching the diet from a $C_4$ corn to a $C_3$ wheat. Obviously the speed at which isotopic composition changed over time to reflect the new diet depended on tissue type, with the more metabolically active tissues turning over more quickly. More recently, a study of the mysid crustaceans, *Mysis mixta* and *Neomysis integer* in Arctic waters demonstrated experimentally that the isotopic composition in muscle, exuviae, and feces may form a basis for diet reconstruction of mysids (Gorokhova & Hansson 1999).

Stable isotope based trophic studies have been applied successfully to the Antarctic marine communities (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). On the other hand, there is a lack of such studies for Antarctic benthic ecosystems except for some sub-Antarctic Islands (Kaehler et al. 2000) although there subsists many trophic interactions to clarify. Indeed, the previously presumed simplicity of Antarctic food webs (e.g. Heywood and Whitaker 1984) is questionable. Until about 20 years ago the main flow of energy in Antarctic marine environment was considered to

be a food chain directly from phytoplankton (diatoms) to herbivores (krill) and higher trophic levels (see e.g. Heywood and Whitaker 1984), but those simple food chain models do not reflect reality appropriately (Marchant and Murphy 1994). Diatoms constitute the major component of Antarctic marine phytoplankton indeed, but bacterial production - as part of the microbial loop – may attain from 11% (spring, Sullivan et al. 1990) to 76% of primary production (autumn, Cota et al. 1990) The sea-ice community is suspected to be yet another important food source (Marshall 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 1991). Hence we have to deal with the complicated multiple and isotopically contrasting food bases often present in marine environments (Fry 1988; Hobson 1993, Hobson et al. 1995, Marguillier et al. 1997; Lepoint et al. 2000, Nyssen et al. 2002).

# 1.4. TROPHIC ECOLOGY INFERRED FROM FATTY ACID COMPOSITION

## 1.4.1. FATTY ACID STRUCTURE

To describe precisely the structure of a fatty acid molecule, one must give the length of the carbon chain (number of carbon atoms), the number of double bonds and also the exact position of these double bonds. Fatty acids (FA) and their acyl radicals are named according to the IUPAC Rules or the Nomenclature of Organic Chemistry (IUPAC). This will define the biological reactivity of the fatty acid molecule and even of the lipid containing the fatty acids studied.

Marine fatty acids are straight-chain compounds with most frequently an even number of carbon atoms. Chain-length ranges commonly between 12 and 24 carbons.

Fatty acids can be subdivided into well-defined categories:

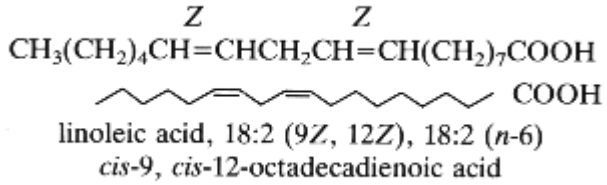
- **Saturated** fatty acids which have no unsaturated linkages

When double bonds are present, fatty acids are denominated unsaturated:

- **Monounsaturated** fatty acids (MUFA) if only one double bond is present.
- P**olyunsaturated fatty acids** (PUFA) if they have two or more double bonds generally separated by a single methylene group (methylene-interrupted unsaturation).

In some animals, but mainly in plants and bacteria, fatty acids may be more complex since they can have an odd number of carbon atoms, or may contain a variety of other functional groups, including **acetylenic** bonds, epoxy-, **hydroxy**- or keto groups and even **ring** structures (cyclopropane, cyclopropene, cyclopentene, furan, and cyclohexyl).

**Example:**




linoleic acid, 18:2 (9*Z*, 12*Z*), 18:2 (*n*-6)
*cis*-9, *cis*-12-octadecadienoic acid

*Nomenclature*: The double bonds are counted from the methyl group determining the metabolic family, noted by n-x (n being the total number of carbon, x the position of the first double bond). Thus linoleic acid or octadecadienoic acid is named in the shorthand nomenclature 18:2 (n-6). This compound has 18 carbon atoms, 2 double bonds and 6 carbon atoms from the first double bond. The International Commission on Biochemical Nomenclature agreed to the first form of this nomenclature because of its interest in describing the fatty acid metabolism.

### 1.4.2. FATTY ACID AS TROPHIC BIOMARKERS

Fatty acids are in many circumstances incorporated into consumers in a conservative manner, thereby providing information on predator-prey relations. Because of biochemical properties and limitations, many dietary fatty acids generally remain intact through digestion, absorption and transport in the bloodstream, and are incorporated into marine animal tissues with little or no modification of the original structure. Therefore these fatty acids are useful as indicators or markers of the dietary source. Combinations of these markers, or the whole suite of fatty acids present, are referred to as the fatty acid signature of an organism (Iverson 1993, Dalsgaard et al. 2003 for review).

Moreover, contrary to the more traditional gut content analyses, which provide information only on recent feeding, FA provide information on the

dietary intake and the food constituents integrated over a longer period of time (St. John and Lund 1996, Kirsch et al. 1998, Auel et al. 2002). This integrating effect helps to resolve the importance of specific prey items and can validate prey utilization strategies based on traditional stomach content analyses (Graeve et al. 1994b). If FA analysis has numerous advantages, it has also its drawbacks. For example, no single FA can be assigned uniquely to any one species and depending on the condition and metabolic strategies of the consumer, FA are not necessarily metabolically stable. In addition, turnover rate of individual FA, can be species-specific and are often linked to the metabolic condition of the organism, and have seldom been quantified (St. John and Lund 1996, Kirsch et al. 1998). Consequently; fatty acids have so far only been used as qualitative and "semi-quantitative" food web markers, the latter in concert with other tracers such as stable isotopes (Kiyashko et al. 1998, Kharlamenko et al. 2001).

Resolution of ecological niches is the strength of the fatty acid trophic markers (FATM) approach and a key to resolve complex trophic interactions. FATM are incorporated largely unaltered into lipid pool of primary consumers.

The concept of FA being transferred conservatively through aquatic food webs was first suggested by Lovern (1935) in a study about copepods. Almost 30 years later, Kayama et al. (1963) performed one of the first experiments demonstrating the transfer of FA through a linear, experimental food web consisting of diatoms, branchiopods and freshwater guppies. The FA profile of the branchiopods and the guppies clearly showed the transfer as well as endogenous modifications of dietary FA. Other studies recognized that the fatty acid composition of zooplankton lipids influenced the fatty acid composition of the blubber lipids of the baleen whales that fed on them (e.g. Ackman and Eaton 1966). However, Sargent et al. (1987) were among the first to suggest the use of marker fatty acids in the study of trophic relationships. Since that time, numerous studies have demonstrated that fatty

acid signatures can be passed from prey to predator, both at the bottom (e.g. Fraser et al. 1989, Graeve et al. 1994) and near the top of the food web (e.g. Iverson 1993, Kirsch et al. 1998, Kirsch et al. 2000, Iverson et al. 2002, Budge et al. 2002). Once fatty acids are characterized in the prey organism, they can be used to trace food webs and diets of predators. For example, fatty acids have been used to study the diets of fish and copepods (e.g. Sargent et al. 1989, Fraser et al. 1989, Graeve et al. 1994b, Graeve et al. 1997, St John and Lund 1996). Fatty acids have also been used to indicate the presence of fish and other preys in the diet of terrestrial and aquatic carnivores (e.g. Rouvinen et al. 1992, Colby et al. 1993), and spatial and temporal differences in diets both within and between marine mammals species (Iverson et al. 1997a,1997b, Smith et al. 1997).

In recent years, an increasing number of studies have applied this method to identify trophic relationships in various marine ecosystems. In polar areas, a variety of taxa and functional groups have been studied so far: copepods (e.g. Graeve et al. 1994a, Kattner and Hagen 1995, Scott et al. 1999), euphausiids (Hagen and Kattner 1998, Kattner and Hagen 1998, Phleger et al. 1998, Virtue et al. 2000, Stübing et al. 2003; see also Falk-Petersen et al. 2000 for review), amphipods (Graeve et al. 2001, Nyssen et al. in press), Arctic zooplankton (Scott et al. 1999, Falk-Petersen et al. 2002) and benthos in general (Graeve et al. 1997).

The most abundant fatty acids generally considered in lipid studies include:

- Saturated fatty acids: 14:0, 15:0, 16:0, 18:0;
- Monounsaturated fatty acids: 16:1(n-7), 18:1(n-9), 18:1(n-7), 20:1(n-9), 20:1(n-7), 22:1(n-11), 22:1(n-9);
- Polyunsaturated fatty acids: 16:2(n-4), 18:2(n-6), 16:3(n-4), 16:4(n-1), 18:3(n-6), 18:3(n-3), 18:4(n-3), 20:4(n-6), 20:4(n-3), 20:5(n-3), 22:5(n-3), 22:6(n-3).

Among the specific lipid components suggested for use as trophic biomarkers, the fatty acids 16:1(n-7), C16 PUFA and EPA and 18:1(n-7) are

considered indicators of a diatom-based diet (Graeve et al. 1994a, 1997). More specifically, sympagic diatoms constitute the bulk of ice algae, and produce high amounts of EPA (eicosapentanoic acid, 20:5(n-3)) (Falk-Petersen et al. 1998, Scott et al. 1999). In contrast, flagellates usually contain elevated concentrations of DHA (docosahexaenoic acid, 22:6(n-3)) as well as 18:4(n-3) (Graeve et al. 1994a).

Tracking trophodynamic relationships in omnivorous and carnivorous species in general, using FATM, is more complex than for herbivores. Secondary and higher order consumers may also incorporate dietary FA largely unaltered into their lipid reserves, but the signal of herbivory are obscured as the degree of carnivory increases and FA may derive from many different sources (Auel et al. 2002). Markers of herbivory may be replaced by markers of carnivory, reflecting changes in feeding behaviour such as during ontogeny. For example, the fatty acid 18:1(n-9) has been used as an indicator of carnivorous feeding in general (Sargent and Henderson 1986, Graeve et al 1994a, 1997). Another example are the long-chain monounsaturated fatty acids and alcohols 20:1(n-9) and 22:1(n-11) that are biosynthesized de novo by herbivorous calanoid copepods. So, these particular monounsaturates have been used to trace and resolve food web relationships at higher trophic levels, for example in hyperiid amphipods, euphausiids and zooplanktivorous fishes that typically consume large quantities of calanoid copepods (e.g. Sargent 1978, Falk-Petersen et al 1987, Hopkins et al. 1993, Kattner and Hagen 1998, Hagen et al. 2001, Auel et al 2002).

In order to obtain more decisive information on diet composition and trophic level using fatty acid composition, ratios of particular FA have also been used to assess the extent to which various species occupy different ecological niches. As diatoms contain high levels of 16:1(n-7) and EPA, whereas dinoflagellates and *Phaeocystis* are usually rich in DHA, the ratios 16:1(n-7)/ 16:0 and EPA/DHA could allow to differentiate between a diatom-versus a flagellate-based diet (Graeve et al. 1994a, Nelson et al. 2001). Moreover,

high EPA/DHA ratios may indicate an important influence of ice-algal primary production (Falk-Petersen et al. 1998, Scott et al. 1999).

The PUFA/SFA ratio has been used as an indicator of carnivory in Antarctic krill *Euphausia superba* (Cripps and Atkinson 2000). Similarly, the proportion of 18:1(n-7) to 18:1(n-9) (as a marker of primary or heterotrophic bacterial production vs. animal production) was, for example, found to decrease in Artic benthic organisms when considering a "succession" from suspension feeders via predatory decapods to scavenging amphipods (Graeve et al. 1997) as it has similarly been proposed as a relative measure of carnivory in various groups of marine invertebrates (Auel et al. 1999, 2002, Falk-Petersen et al. 2000).

At higher trophic levels, i.e. in fish and marine mammals, specific FATM are of less evident than in zooplankton and consequently more difficult to interpret. The advancement of multivariate statistical methods of pattern recognition has, however, proven particularly valuable for resolving trophic interactions in these organisms (Smith et al. 1997, Iverson et al. 1997b, 2002, Budge et al. 2002), and we urge that this becomes an integrated tool in future applications of FATM at all trophic levels.

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# CHAPTER 2: A STABLE ISOTOPE APPROACH TO THE EASTERN WEDDELL SEA TROPHIC WEB: FOCUS ON BENTHIC AMPHIPODS

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After Nyssen F, Brey T, Lepoint G, Dauby P, Bouquegneau JM, De Broyer C (2002) Polar Biology 25: 280-287

# ABSTRACT

Stable isotope ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) analyses were performed in ninety species belonging to different benthic communities sampled in the eastern Weddell Sea. The study focused on the eight amphipods species from which isotopic composition was compared to their respective gut contents previously described. Amphipod stable isotope ratios correspond rather accurately to the trophic classification based on gut contents and attest to their high 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.

# 2.1. INTRODUCTION

With more than one thousand 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 about 830 spp. 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 allowed them to adopt various life styles: epontic dwellers, (bentho-) pelagic swimmers, walkers, crawlers, burrowers, borers, inquilines in or on different invertebrates. This diversity in microhabitats, associated with the variety of potential food, is likely to be a factor which has favoured the adaptative radiation of the Amphipoda and the diversification of trophic types in Antarctic waters (Jazdzewski et al. 1996; Dauby et al. 2001; 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), for demersal and benthic fishes (e.g. Kock 1992; Olaso et al. 2000), for many of birds (e.g. Ainley et al. 1992; Cherel and Kooyman 1998; Jazdzewski and Konopacka 1999), and for marine mammals (e.g. Dearborn 1965; Green & 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 ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios of animals and those of their diets (De Niro 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, $\delta^{15}N$ displays a stepwise increment of about 3‰ at each successive trophic level (Minagawa and Wada 1984; Hobson and Welch 1992; Michener and Schell 1994) and is generally used to predict organism's trophic level. Likewise, animal carbon isotope values, closer to that of the diet, allow determining 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). On the other hand, 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 Antarctic marine environment was considered to be a food chain directly from phytoplankton (diatoms) to herbivores (krill) and higher trophic levels (see e.g. 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 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. (2001).

## 2.2. MATERIAL AND METHODS

### 2.2.1. 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 with 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.

### 2.2.2. ISOTOPIC ANALYSIS

When possible, muscle tissues or soft body parts from 5 individuals of every sampled species (except from the amphipod *E. similis,* n=1) were sampled and ground with mortar and pestle into a homogenous powder. From one hundred and ten species initially analysed, ninety 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 a 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 following formula:

$$\delta X\ (‰) = [(R_{sample}/R_{standard}) - 1] \times 1000$$

Where X is $^{13}C$ or $^{15}N$, R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$, and the appropriate standards were Vienna Peedee Belemnite (V-PDB) and atmospheric nitrogen for carbon and nitrogen, respectively. Intercomparison materials were IAEA-N1 ($\delta^{15}N$= +0.4 ± 0.2‰) and IAEA CH-6 (sucrose) ($\delta^{13}C$= -10.4 ± 0.2‰). As recommended by Pinnegar & Polunin (1999), when samples were acidified to eliminate carbonates, $^{15}N/^{14}N$ 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:

$$\boldsymbol{TL = (D - 3.1)/3.0 + 1}$$

Where D is the $\delta^{15}N$ 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 2.1 are described in Dauby *et al.* (2001).

**Table 2.1. Trophic types based on gut content analyses (modified from Dauby *et al.* 2001), $\delta^{13}C$, $\delta^{15}N$, C:N ratios (mean ± SE) and estimated trophic level (*TL)* (from Hobson and Welch 1992); n: number of samples.**

| Species | Trophic types | C/N | $\delta^{13}C$ (‰) | $\delta^{15}N$ (‰) | TL |
|---|---|---|---|---|---|
| *Ampelisca richardsoni* (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 |
| *Eusirus perdentatus* (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 |
| *Epimeria similis* (n = 1) | PREDATOR (Cnidaria (63%), Porifera (14%), Polychaeta (9%), diatoms (9%), others (5%)) | 5.6 | -25.1 | 10.1 | 3.3 |
| *Orchomenella cf pinguides* (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 |
| *Iphimediella cyclogena* (n = 5) | PREDATOR (Holothurioidea (70%), Polychaeta (20%), unidentified organic matter (10%)) | 4.0 ± 0.3 | -25.9 ± 1.1 | 11.2 ± 0.5 | 3.7 |
| *Tryphosella murrayi* (n = 5) | SCAVENGER (carrion (47%), Crustacea (43%), Polychaeta (5%), others (5%) | 5.5 ± 0.2 | -22.5 ± 0.8 | 11.4 ± 0.8 | 3.8 |
| *Waldeckia obesa* (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 |
| *Parschisturella carinata* (n = 5) | No gut content data but considered as SCAVENGER | 6.9 ± 1.1 | -21.1 ± 2.1 | 11.8 ± 0.7 | 3.9 |

## 2.3. Results

The ranges of isotope ratios of each taxon - grouped by phylum, class or order following the number of samples - as well as that of suspended matter are presented in Figs 2.1 and 2.2. 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 $^{13}C$ and a step-wise increase with trophic level ranged from 2.6 ‰ for SPOM to 16.1 ‰ for the fish *Pogonophryne barsukovi* (Artedidraconidae) suggesting a food web composed of about 5 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 $\delta^{13}C$ and from 2.6 to 3.9‰ in $\delta^{15}N$. For both isotopes, amphipod ranges are among the widest (from –27.8 to –19.6‰ in $\delta^{13}C$ and from 5.8 to 12.9‰ in $\delta^{15}N$) together with those of anthozoans and echinoderms.

Unfortunately, in this study, the isotopic ratios of some groups can not be discussed because of their poor sampling, for example, isopods are represented by one single species.

**Fig. 2.1. Range of $\delta^{13}C$ values (‰) for SPOM, benthic invertebrates and vertebrates from the eastern Weddell Sea shelf. Pol. Sedentaria = Polychaeta Sedentaria; Pol. Errantia = Polychaeta Errantia. Numeral between brackets indicates the amount of analysed species.**

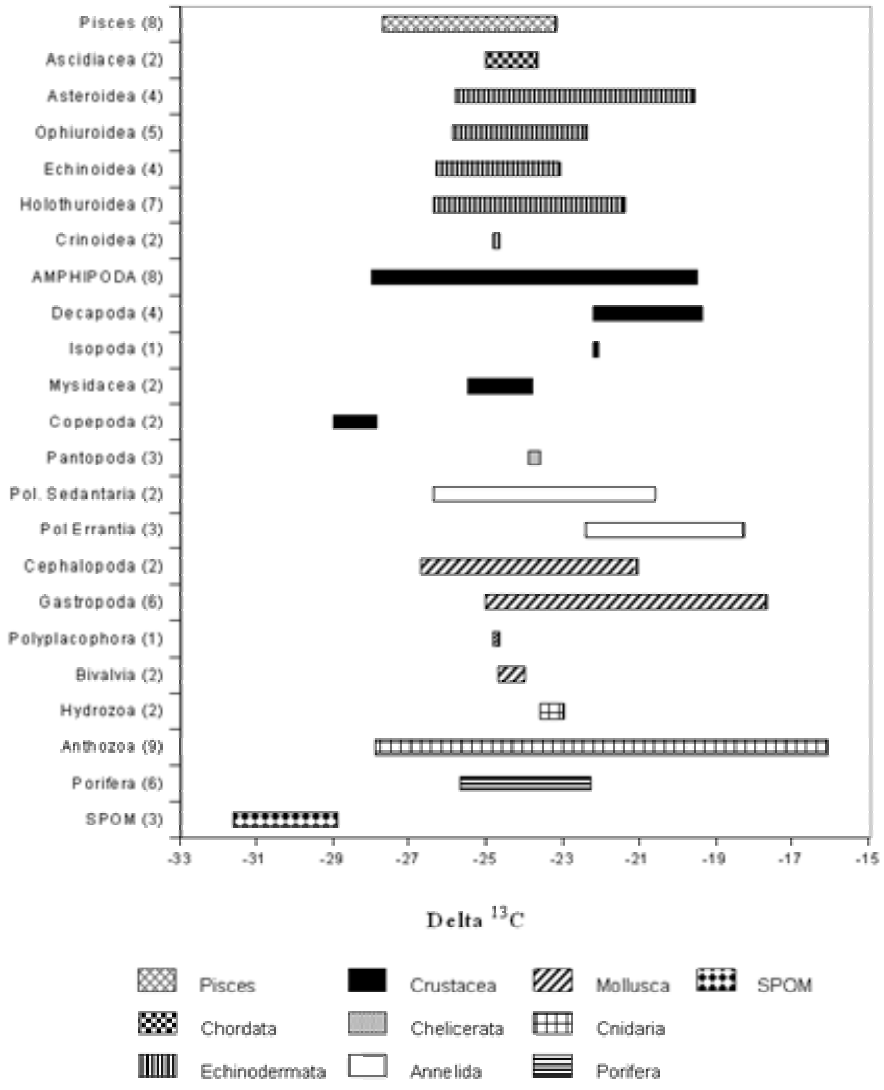
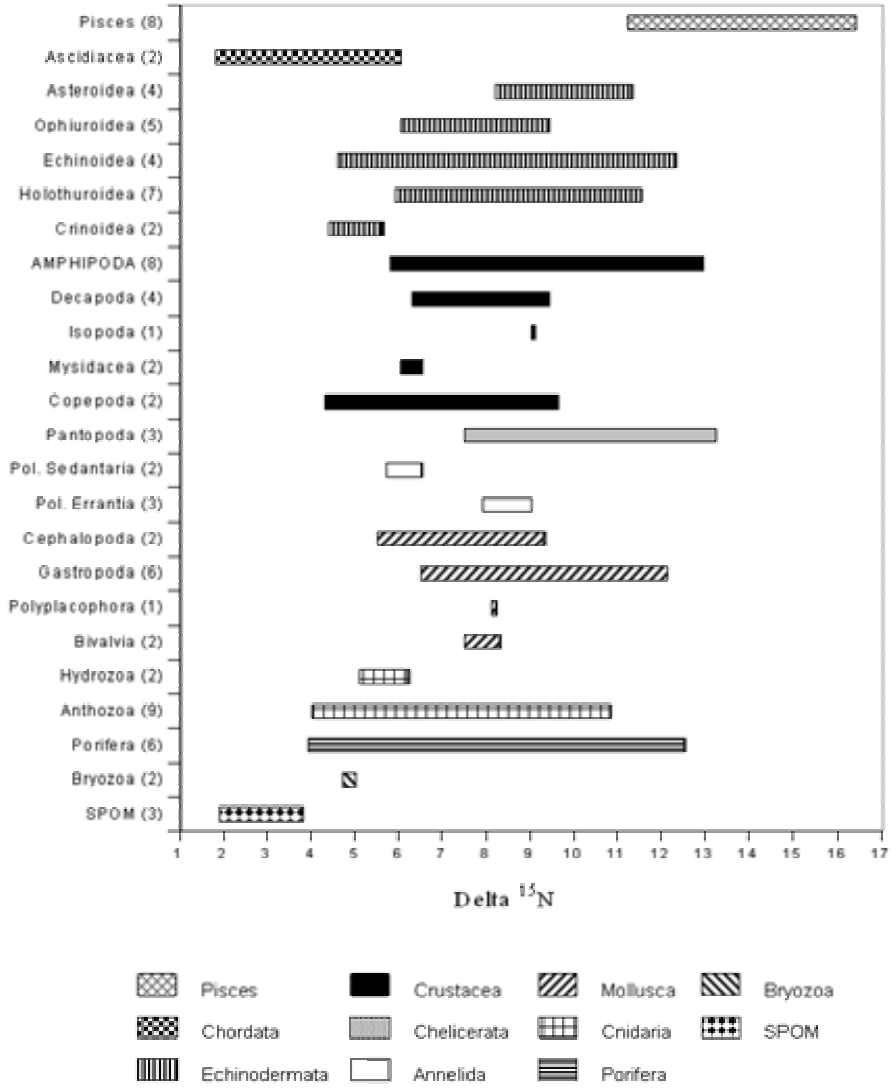
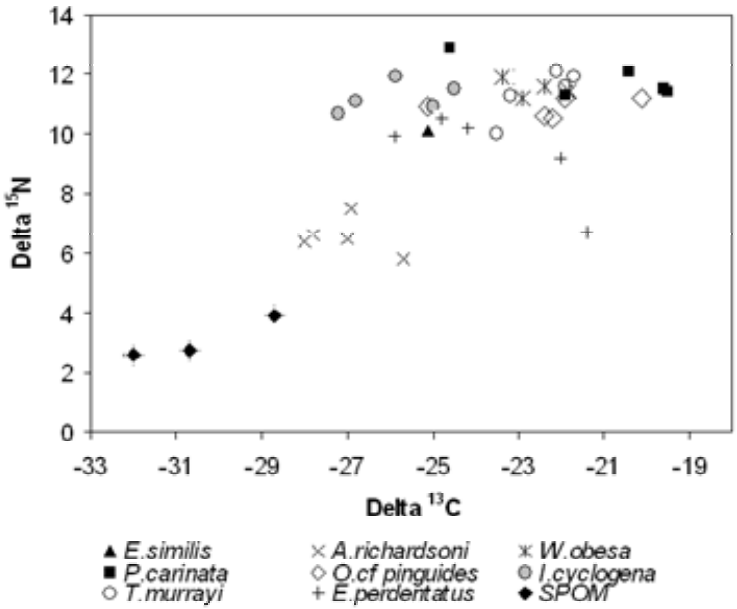


**Fig. 2.2. Range of $\delta^{15}N$ values (‰) for SPOM, benthic invertebrates and vertebrates from the eastern Weddell Sea shelf. Pol. Sedentaria = Polychaeta Sedentaria; Pol. Errantia = Polychaeta Errantia. Numeral between brackets indicates the amount of analysed species.**



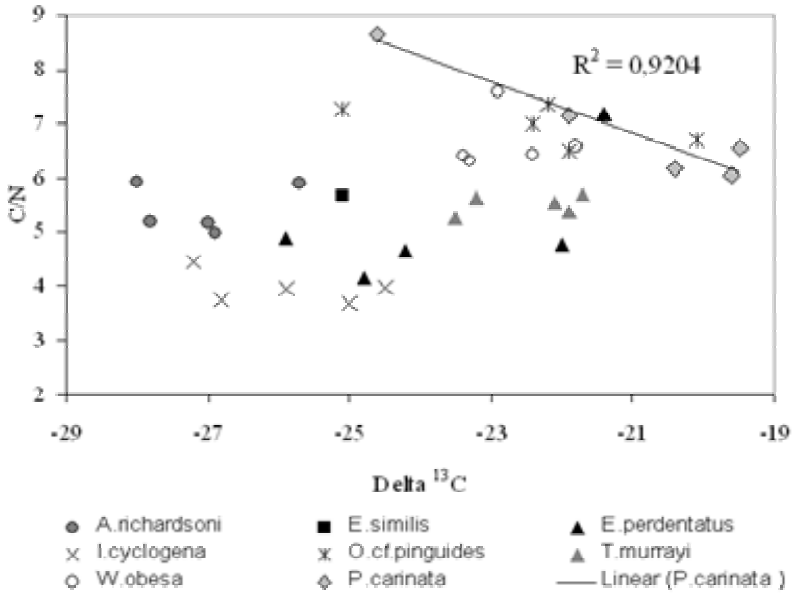
The $\delta^{13}C$ and $\delta^{15}N$ values in amphipods are presented in Fig 2.3. Displaying the lowest $\delta$ ($\delta^{13}C$ = -27.1 ± 0.9‰; $\delta^{15}N$ = 6.6 ± 0.6‰), *Ampelisca richardsoni* values are closest to those of SPOM and are significantly different from values of all the other species (ANOVA $p < 0.01$) except from *Epimeria similis* and *Iphimediella cyclogena* $\delta^{13}C$. Both latter species present similar $\delta^{13}C$ but their nitrogen ratios are significantly different from each other (ANOVA $p < 0.001$). *Eusirus perdentatus* $\delta^{15}N$ values differ significantly from all other species nitrogen ratios except from the single *E. similis* value. Unlike its $\delta^{13}C$, *I. cyclogena* $\delta^{15}N$ values belong to the highest with those of *Orchomenella* cf. *pinguides*, *Waldeckia obesa*, *Tryphosella murrayi* and *Parschisturella carinata*. Furthermore these four latter species stable isotope ratios are not significantly different from each other, neither for the carbon nor for the nitrogen.

**Fig. 2.3. The $\delta^{13}C$ and $\delta^{15}N$ stable isotope values (‰) in SPOM and in amphipods from the eastern Weddell Sea shelf.**



When amphipods $\delta^{13}C$ are compared to their respective C/N ratio, no correlation appears except with one species: *P. carinata*, which displays a significant decrease of $\delta^{13}C$ with C/N ratio increase (Fig. 2.4).

**Fig. 2.4. Relationship between the $\delta^{13}C$ (‰) and the C/N ratio for amphipod from the eastern Weddell Sea shelf. The displayed regression involves only data from the species *P. carinata*.**




## 2.4. 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 only in fraction samples in or closely associated with sea ice (Rau et al. 1991a; Hobson et al. 1995). Even if there isn't any sea ice POM available for this study, the high values displayed by some sponge species (–22.3 and 12.5 ‰ for $\delta^{13}C$ and $\delta^{15}N$

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 such great enrichment between POM and POM grazers would be the assimilation by suspension-feeders of benthic resuspended organic matter originate from a strong microbial loop - the period of sampling (post-bloom, late-summer period) corresponding to its maximal 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 *Orchomenella* cf *pinguides*, *Eusirus perdentatus* and *Parschisturella carinata*, $\delta^{13}C$ values were generally more variable than $^{15}N$ values as observed in most taxa $^{13}C$ values (see Fig 2.3, Table 2.1). As lipids - both N- and $^{13}C$-poor- were not extracted prior to analysis, the intraspecific variation of amphipod $\delta^{13}C$ 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, *P. carinata* (Fig.2.4). For this species only, the intraspecific variation of the $\delta^{13}C$ could be attributed to a difference of lipid content between individuals (Rau et al. 1991; 1992).

Few other benthic groups seem to cover a similarly wide trophic spectrum as amphipods do (Figs.2.1 and 2.2). Considerably wide ranges of $\delta^{15}N$ has already been recorded for pelagic amphipod species from the same sampling area and it 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 former 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 (*P. carinata*), see Fig.2.3. The step-wise increase of $\delta^{15}N$ with trophic level displayed by the eight amphipod species (see Table 2.1) suggests coverage of approximatively 3 of the 5 levels of the food web. Except *Ampelisca richardsoni* which is clearly isolated from the other species at the second trophic level, instead of belonging to a definitive trophic 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 amphipod based on isotopic values coincides quite well with the trophic classification based on gut contents analyses of Dauby et al. (2001), see Table 2.1. Since the fundamental difference between the isotope and the stomach content approach 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 $\delta^{13}C$ (-27.1 ± 0.9‰) and $\delta^{15}N$ (6.6 ± 0.6‰) values of *A. richardsoni* which are close to SPOM isotopic ratios ($\delta^{13}C$ = -30.5 ± 1.7‰; $\delta^{15}N$ = 3.1 ± 0.7‰) 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. in press). Klages and Gutt (1990) consider *E. perdentatus* as a passive predator which preys on various organisms from different trophic levels as polychaetes, amphipods or other smaller crustaceans. Their conclusions didn't only coincide with results of gut content analyses (Dauby et al. 2001) but *E. perdentatus* opportunistic trophic behaviour is also confirmed by its scattered isotopic ratios. Furthermore, according to Graeve et al. (in press) the lack of specialisation neither in the lipid accumulation nor in fatty acid biosynthesis observed for *E. perdentatus* supports this feeding opportunism hypothesis.

The quite high nitrogen ratios of *Iphimediella cyclogena* is amazing as its diet seems to be mainly composed of holothurian tissues considered for the most as suspension- or deposit-feeders (Table 2.1). Antarctic sea cucumbers isotopic values, however, are also higher than expected (Figs 2.1 & 2.2). This may indicate significant microbial or meiofaunal pathways in the organic matter cycle.

Species displaying the highest isotopic values: *Waldeckia obesa*, *Tryphosella murrayi*, *O.* cf. *pinguides* and *P. 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. 2001). As noticed by Graeve et al. (in press), the fatty acid composition of *W. obesa* is unique since it is by far 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 *P. carinata*, no gut content data are available, but its common occurrence in baited traps, the feeding experiments performed with living specimens in aquaria (Scailteur and De Broyer unpubl.) 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 characterizing amphipod trophic status with more accuracy. Some species are rather specific in their diet selection as the suspension-feeder *A. richardsoni*, but the continuum of values displayed by the other species suggests some trophic opportunism and the potential to adapt their diet to food availability in many amphipods. 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 in fractionation factors (Gannes et al. 1999).

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# CHAPTER 3: TROPHIC POSITION OF ANTARCTIC AMPHIPODS - ENHANCED ANALYSIS BY A 2-DIMENSIONAL BIOMARKER ASSAY

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After Nyssen F, Brey T, Dauby P, Graeve M (2005) Marine Ecology Progress Series, in press

# ABSTRACT

The discrepancy between the ecological significance of amphipods in the Antarctic and our poor knowledge of their ecofunctional role calls for a more detailed investigation of their trophic status in this ecosystem. Twelve amphipod species from suspension-feeder to scavenger have been considered in this study. Our objective was to investigate whether the combination of fatty acid and stable isotope signatures into a 2-dimensional trophic biomarker assay would increase accuracy in the identification of Antarctic benthic amphipod trophic position. Amphipod isotopic averages ranged from –29.3‰ ($\delta^{13}C$) and 4.1‰ ($\delta^{15}N$) for the suspension-feeder *Ampelisca richardsoni*, to –21.7‰ ($\delta^{13}C$) and 11.9‰ ($\delta^{15}N$) for the high predator *Iphimediella* sp. Cluster analysis of the fatty acid composition separated the amphipod species into 4 trophic groups; suspension feeders, macro-herbivores, omnivores and scavengers. The suspension feeder was isolated due to an important proportion of 18:4(n-3), fatty acid biomarker of phytoplankton. Macro-herbivores were found to rely heavily on macroalgal carbon, containing a high percentage of arachidonic acid 20:4(n-6). Scavenger amphipods revealed a unique fatty acid composition dominated by one single fatty acid, 18:1(n-9), probably the result of a very intensive de novo biosynthesis to cope with starvation periods. Our data emphasize the need to combine different types of information to be able to draw the right conclusions regarding trophic ecology. Indeed, in some cases, the exclusive use of one type of tracing method, fatty acids or stable isotopes, would have lead to misleading/false conclusions in the trophic classification of amphipods. Therefore a 2-dimensional biomarker assay is a useful tool to elucidate the trophic positions of benthic amphipods.

KEY WORDS: 2-dimensional biomarker, trophic relationships, stable isotopes, fatty acids, Amphipoda, Antarctic ecology

# 3.1. INTRODUCTION

In the Southern Ocean, amphipod crustaceans are among the most specious animal group in the zoobenthos. About 530 species have been recorded as strictly Antarctic species and more than 830 species have been described so far for the whole Southern Ocean (Klages 1991, De Broyer & Jazdzewski 1996, De Broyer et al. 1999, 2003a, b, Gutt et al. 2000). It is commonly assumed that species and trophic diversity are related (Ulanowicz 2000, Dauby et al. 2001b). Also, in Antarctic waters and on Antarctic bottoms, amphipods have developed a rich variety of life styles: epontic dwellers, (bentho-) pelagic swimmers, walkers, crawlers, and burrowers. They occupy many niches reserved for decapod crustaceans in other systems (Dauby et al. 2001a, b, De Broyer et al. 2001). This diversity in life style, associated with the variety of available food, is likely to be a factor which has favoured the adaptative radiation of the Amphipoda and the diversification of trophic types in Antarctic waters (Jazdzewski et al. 1996, De Broyer et al. 2001, Dauby et al. 2001b). Regarding total energy flow in the eastern Weddell Sea shelf ecosystem, Amphipods are among the key taxa in the benthic sub-system (Jarre-Teichmann et al. 1997, Dauby et al. 2003).

Biomarkers such as fatty acids and stable isotopes have been used successfully to identify trophic relationships in marine food webs (Hobson et al. 1995, Lepoint et al. 2000, Graeve et al. 2001, Auel et al. 2002, Nyssen et al. 2002). Fatty acids are the primary constituents of most lipids. They generally remain intact through digestion and can be deposited in the consumer's tissue with minimal modification from diet and in a predictable way (Lee et al. 1971). Certain fatty acids have specific known sources and can act as biomarkers. These features make fatty acids a potential food chain tracer in marine ecosystems, which has shown its suitability in various studies (Sargent 1976, Sargent & Henderson 1986, Graeve et al. 2001, Iverson et al. 2002, Dalsgaard et al. 2003).

Stable isotope ratios also provide signatures based on actual food assimilation but 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 ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios of animals and those of their diets (De Niro & Epstein 1978, 1981, Peterson & Fry 1987). Changes in ratios (i.e. fractionation) occur through metabolic processes, which cause change in the relative proportions of stable isotopes. As a result, the stable isotope composition of a consumer is indicative of and in general heavier than that of its prey. The more conservative transfer of carbon isotopic compositions (0.5‰–1‰ enrichment per trophic transfer) can be useful to trace two food sources with clear differences in their $\delta^{13}C$ values whereas nitrogen ratios (3‰-4‰ enrichment per trophic transfer) are most frequently used as trophic position indicators (Minagawa & Wada 1984, Hobson & Welch 1992, Michener & Schell 1994, Lepoint et al. 2000). However, it must be considered, that fractionation is not constant and many factors can cause variation (Gannes et al. 1997), e.g. species (e.g. De Niro & Epstein 1981), food source (Fantle et al. 1999), nitrogen dietary content (Adams & Sterner 2000) or nutritional or hydric stress (Hobson et al. 1993). Despite those problems, isotopes have been successfully applied to the Antarctic trophic web (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, Schmidt et al. 2003). Only a few stable isotopic studies have been focussed on benthic communities so far (Dunton 2001, Nyssen et al. 2002). Likewise, there are limited lipid studies of Antarctic benthic amphipods (Nelson et al. 2001, Graeve et al. 2001). More work has been conducted in the Arctic (Hobson et al. 1995, Auel et al. 2002) and on Antarctic pelagic amphipods, e.g. *Themisto gaudichaudii* (Reinhardt & Van Vleet 1986, Hagen 1988, Phleger et al. 1998).

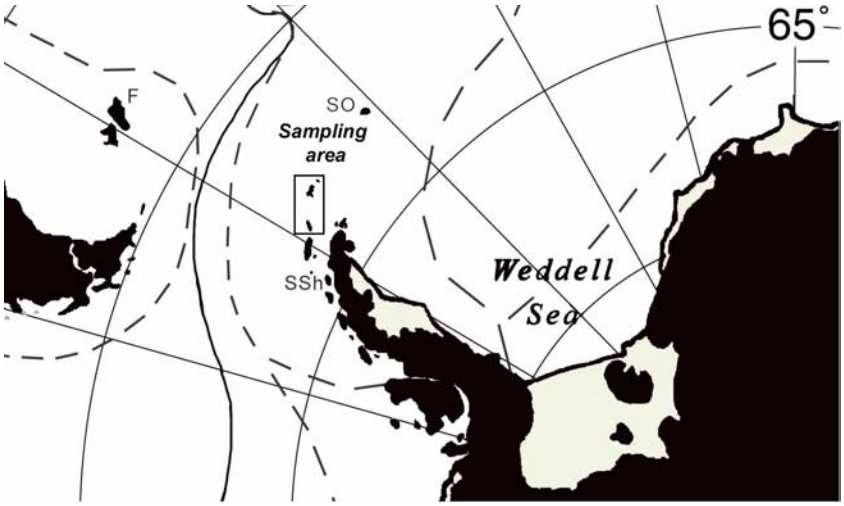
The discrepancy between the ecological significance of amphipods and our poor knowledge of their ecofunctional role calls for a more detailed investigation of their share in Antarctic trophodynamics. Furthermore, the profusion of amphipod species and the variability of their trophic spectrum in the Southern Ocean calls for a more systematic and efficient approach towards this aspect of their ecology. Our study investigates whether the combination of fatty acid and stable isotope signatures into a 2-dimensional trophic biomarker will increase accuracy in the identification of Antarctic benthic amphipod trophic position.

## 3.2. METHODS

### 3.2.1. SAMPLING AND STORAGE

The amphipods Waldeckia obesa (Chevreux 1905), Abyssorchomene plebs (Hurley 1965), Eurythenes gryllus (Lichtenstein 1822), Pseudorchomene coatsi (Chilton 1912), Epimeria similis (Chevreux 1912), Epimeria georgiana (Schellenberg 1931), Iphimediella sp, Echiniphimedia hodgsoni (Walker 1906), Eusirus perdentatus (Chevreux 1912), Djerboa furcipes (Chevreux 1906) and Ampelisca richardsoni (Karaman 1975) were caught during the cruises ANT XIX/3-4 (ANDEEP I-II), 23 January to 1 April 2002 (De Broyer et al. 2003) with RV Polarstern to the Antarctic Peninsula (Fig. 1). The animals were taken from various depths by different gear: Agassiz-trawls, bottom-trawls and autonomous traps. Immediately after sampling, individuals were sorted into species and kept for several hours in aquaria. Thereafter, individuals dedicated to isotope analyses were rinsed in distilled water and transferred into glass vials. Specimens for lipid analysis were transferred into glass vials and covered with dichloromethan:methanol (2:1, by vol.) All samples were stored at -30°C until analysis at the Alfred Wegener Institute at Bremerhaven.

**Fig.3.1. Detailed map of the Antarctic Peninsula and the sampling area: F—Falklands, SO—South Orkneys, SSh—South Shetlands.**




### 3.2.2. STOMACH CONTENT ANALYSIS

Gut contents of 20 specimens from each species preserved in 4% formaldehyde solution were examined. The digestive tract was removed from the animal, opened and the content was spread on a micro slide. The slide was examined microscopically (Leica DMLB with reflection contrast system) and every food item was determined as precisely as possible. Additional data were taken from Nyssen et al. (2002) and Dauby et al. (2001b) where the methodological details are described. Observations of feeding behaviour of the various amphipod species in aquaria provided further information on diet and feeding.

### 3.2.3. LIPID ANALYSIS

Lipid analyses carried out on all sampled amphipod species (n=11). Fatty acid data from Graeve et al. (2001) referring to the species *A. richardsoni*, *E.*

*hodgsoni*, *Oradarea edentata*, *E. georgiana* (one specimen) and *E. perdentatus* were added to our data set for comparison.

Samples stored in chloroform:methanol (2:1 by vol.) were evaporated with nitrogen to dryness and subsequently lyophilised for 48 h. Dry mass (DM) was determined gravimetrically. Total lipid mass (TL) was measured gravimetrically after lipid extraction from the freeze-dried samples using dichloromethane:methanol (2:1 by vol.), essentially after Folch et al. (1957).

Fatty acid composition was analysed by gas-liquid chromatography (Kattner & Fricke 1986). Fatty acids of the total lipid extracts were converted to their methyl esters by transesterification in methanol containing 3% concentrated sulphuric acid at 80°C for 4 hours. After extraction with hexane, fatty acid methyl esters were analysed with a Hewlett-Packard 6890 Series gas chromatograph with a DB-FFAP fused silica capillary column (30 m x 0.25 mm inner diameter; 0.25 µm film thickness) using temperature programming (160-240°C at 4°C $min^{-1}$, hold 15 min). For recording and integration Class-VP software (4.3) (Shimadzu, Germany) was used. Fatty acids were identified with commercial and natural standard mixtures and if necessary, additional confirmation was carried out by gas chromatography-mass spectrometry.

### 3.2.4. STABLE ISOTOPE ANALYSIS

Carbon and nitrogen isotopic ratios were measured in all sampled amphipod species (n=11, no isotopic data available for *O.edentata*) as well as in the brown algae *Desmarestia mensiezii*. Isotopic data for suspended particulate organic matter (SPOM) are from Nyssen et al. (2002). Muscle tissues or whole animals of small species were dried and ground with mortar and pestle into a homogenous powder. Isotopic ratios were measured individually in each specimen. Stable carbon and nitrogen isotope ratios were analysed with a nitrogen-carbon elemental analyser (Fisons, UK) directly coupled to an Optima (Micromass, UK) continuous flow isotope ratio mass spectrometer

(CF-IRMS) for combustion and automated analysis. Isotopic ratios are expressed in δ values as the proportional deviation of the sample isotope ratio from that of an international Vienna Peedee Belemnite (V-PDB) standard according to the following formula:

$\delta X$ (‰) = [Rsample-Rstandard /Rstandard] x 1000,

where X is $^{13}C$ or $^{15}N$, R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$, and the appropriate standards were Vienna Peedee Belemnite (V-PDB) and atmospheric nitrogen for carbon and nitrogen, respectively. Intercomparison materials were IAEA-N1 ($\delta^{15}N$= +0.4 ± 0.2‰) and IAEA CH-6 (sucrose) ($\delta^{13}C$= -10.4 ± 0.2‰). Experimental precision (based on the standard deviation of replicates of an atropina standard) was 0.3‰ for both carbon and nitrogen.

### 3.2.5. DATA ANALYSIS

Multivariate analyses of the fatty acid composition were performed for all individuals using the program PRIMER (Plymouth Routines in Multivariate Ecological Research), Version 5 (Clarke & Warwick 1994). Hierarchical clustering and multi-dimensional scaling (MDS) were performed based on a Bray-Curtis similarity coefficient applied to untransformed percentage composition data. No transformation was applied to the data set, because those fatty acids that contribute only to a small percentage of the total composition did not feature heavily in the diet. Giving artificial weight to these minor fatty acids by applying a transformation would therefore be inappropriate. Data from Graeve et al. (2001) referring to the species *A. richardsoni*, *E. hodgsoni*, *Oradarea edentata*, *E. georgiana* (one specimen) and *E. perdentatus* were added to our data set for comparative analysis.

The SIMPER (SIMilarity PERcentage–species contribution) routine in PRIMER was used to investigate the clusters found by both hierarchical cluster analysis and MDS.

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 (Tukey test) comparisons of means. A significance level of $p < 0.001$ was used in all tests (Scherrer 1984) except when it is mentioned.

## 3.3. RESULTS

### 3.3.1. STOMACH CONTENT & TROPHIC TYPE

Major stomach contents and corresponding trophic type of the 11 amphipod species are summarized in Table 3.1. Detailed stomach content data are provided by Dauby et al. (2001b) and Nyssen et al. (2002). Trophic type of the 11 species ranged from suspension feeder to scavenger.

**Table 3.1. Classification of 11 species of Antarctic amphipods in different trophic categories following the composition of their stomach contents (Dauby et al. 2001b, Nyssen et al. 2002, this study)**

| Species | Trophic type | Major prey |
|---|---|---|
| ***Ampelisca richardsoni*** | Suspension feeder | Phytoplancton |
| ***Djerboa furcipes*** | Herbivore | Brown Macroalgae |
| ***Epimeria similis*** | Micropredator | Hydrozoan |
| ***Epimeria georgiana*** | Deposit feeder | Detritus |
| ***Eusirus perdentatus*** | Predator | Crustaceans |
| ***Echiniphimedia hodgsoni*** | Micro predator | Sponges |
| ***Iphimediella*** sp | Predator | Crustaceans |
| ***Pseudorchomene coatsi*** | Scavenger | Carrion |
| ***Abyssorchomene plebs*** | Scavenger | Carrion |
| ***Eurythenes gryllus*** | Scavenger | Carrion |
| ***Waldeckia obesa*** | Scavenger | Carrion |

### 3.3.2. FATTY ACID COMPOSITION

The fatty acid composition, albeit different between species, showed some overall similarities (Table 3.2). The principal fatty acids of all species were 16:0, 18:1 (both isomers), 20:4(n-6), 20:5(n-3) and 22:6(n-3). High percentages of polyunsaturated fatty acids (PUFA) were found in *A. richardsoni* (58%) whereas monounsaturated fatty acids (MUFA) were most abundant in *E. gryllus*, accounting for up to 58%. The hierarchical cluster analysis separated twelve amphipod species into 5 distinct groups at the 80% similarity level (Fig. 3.2, see p.21). Clusters C1 and C5 are mono-specific and Cluster 4 is well separated into single species groupings. In Clusters C2 and C3 the individuals are not gathered by species in subgroups but more spread, although some separation was still apparent. *Iphimediella* sp. and one specimen of *E. hodgsoni* remained outside the clusters defined at the 80% similarity level: As shown by the SIMPER analysis (Table 3.3), these groupings had high, within group, similarities. The statistical treatment, using all fatty acids for each group indicated that essentially the oleic acid (18:1(n-9)) distinguished Cluster 1 (*W. obesa*) from all other clusters. The fatty acid profile of *W. obesa* was unique since oleic acid accounted for more than 44% of total fatty acids. This unusually high proportion of oleic acid is responsible for the split of scavenger species into two different clusters (C1 and C2). The SIMPER analysis revealed also that it is mainly the higher proportion of the fatty acid 18-4(n-3) which isolates Cluster 5 from the other Clusters. The highest levels of $C_{18}$ and $C_{20}$ PUFA (mainly arachidonic acid (20:4(n-6)), which is the discriminant fatty acid for this cluster) occurred in Cluster 4 (*D. furcipes* and *O. edentata*). Besides all the clusters, the isolated position of the iphimediid species in the dendrogram seems to be due to its considerably high levels of 20:1 and 22:1 fatty acids (19% in total).

**Table 3.2. Fatty acid composition (mean value ± SD) of total lipid extracted from 12 species of amphipods from the Southern Ocean. Only values ≥ 0.3% are mentioned. Number of analysed individuals in brackets. Wo—*Waldeckia obesa*, Ap—*Abyssorchomene plebs*, Eg—*Eurythenes gryllus*, Pc—*Pseudorchomene coatsi*, Es—*Epimeria similis*, Ege—*Epimeria georgiana*, Eh—*Echiniphimedia hodgsoni*, Ep—*Eusirus perdentatus*, Df—*Djerboa furcipes*, Oe—*Oradarea edentata* (data from Graeve et al. (2001), Ar—*Ampelisca richardsoni*, Iphi—*Iphimediella* sp**

| Fatty acids | *Wo* (7) | *Ap* (9) | *Eg* (2) | *Pc* (1) | *Es* (2) | *Ege* (2) | *Eh* (2) | *Ep* (1) | *Df* (2) | *Oe* (2) | *Ar* (3) | Iphi *(1)* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **14:0** | 11.3±2.9 | 3.4 ±1.0 | 1.7 ±0.9 | 6.9 | 1.3 ±0.1 | 1.1 ±0.1 | 0.7 ±0.1 | 2.1 | 1.0 ±0.1 | 1.6 ±0.1 | 5.3 ±0.2 | 3.5 |
| **15:0** | 0.8 ±0.9 | 0.3 | 0.2 ±0.1 | 0.4 | 1.2 ±0.4 | 0.9 ±0.4 | 0.7 ±0.1 | 0.4 | 0.6 ±0.1 | 0.6 ±0.2 | 0.1 | 0.4 |
| **16:0** | 12.9 ±1.6 | 12.9 ±2.0 | 11.0 ±2.9 | 22.5 | 13.4 ±3.5 | 11.4 ±1.9 | 8.9 ±1.1 | 15.3 | 16.8 ±1.1 | 14.7 | 8.8 ±0.6 | 12.5 |
| **17:0** | 0.4 ±0.3 | 0.9 ±0.8 | 0.1 ±0.1 | 0.2 | 0.5 ±0.1 | 0.3 ±0.3 | 0.1 | 0.1 | 2.0 ±2.8 | 0.1 | 0.1 | 0.4 |
| **18:0** | 1.9 ±0.8 | 1.1 ±0.3 | 1.8 ±0.2 | 2.9 | 1.1 ±0.1 | 1.1 ±0.5 | 1.1 ±0.1 | 0.9 | 1.7 ±0.1 | 0.5 ±0.1 | 1.2 ±0.2 | 3.0 |
| **16:1(n-7)** | 6.7 ±1.4 | 10.0 ±3.2 | 7.5 ±0.6 | 7.9 | 2.1 ±0.4 | 3.6 ±1.3 | 11.4 ±1.5 | 3.7 | 3.1 ±0.3 | 7.4 ±1.4 | 9.1 ±1.9 | 3.9 |
| **18:1(n-9)** | 44.1 ±2.7 | 30.5 ±4.9 | 33.9 ±2.7 | 31.1 | 20.2 ±1.6 | 21.9 ±0.2 | 19.9 ±5.2 | 22.7 | 17.7 ±1.1 | 20.9 ±0.7 | 8.3 ±0.7 | 19.7 |
| **18:1(n-7)** | 2.9 ±2.1 | 6.8 ±0.9 | 7.4 ±0.6 | 6.2 | 6.1 ±0.2 | 8.4 ±0.5 | 10.6 ±3.6 | 5.2 | 3.3 ±0.2 | 5.1 ±1.1 | 3.3 | 6.1 |
| **20:1(n-9)** | 1.1 ±0.5 | 5.1 ±2.9 | 4.9 ±0.3 | 2.6 | 1.9 | 1.8 ±0.7 | 1.1 | 1.3 | 1.0 ±1.3 | 1.6 ±0.1 | 1.4 ±0.2 | 9.3 |
| **20:1(-7)** | 0.3 ±0.1 | 0.9 ±0.3 | 1.9 ±0.7 | 0.5 | 1.0 ±0.7 | 2.3 ±0.4 | 2.8 ±0.9 | 0.7 | 0.0 | 0.3 ±0.3 | 0.6 ±0.1 | 5.8 |
| **22:1(n-11)** | 0.6 ±0.6 | 1.5 ±1.0 | 1.7 ±1.5 | 2.5 | 0.3 ±0.2 | 0.4 ±0.2 | 0.2 ±0.1 | 0.2 | 0.6 ±0.8 | 0.3 ±0.2 | 0.1 | 3.5 |
| **22:1(n-9)** | 0.1 ±0.1 | 0.6 ±0.7 | 0.5 ±0.6 | 0.1 | 0.5 ±0.4 | 0.4 ±0.1 | 0.7 ±0.4 | 0.4 | 0.0 | 0.3 | 0.1 | 0.1 |
| **16:2(n-4)** | 0.5 ±0.2 | 0.6 ±0.9 | 3.2 ±4.2 | 1.2 | 0.7 ±0.1 | 0.6 ±0.1 | 0.6 ±0.7 | 0.5 | 1.8 ±0.1 | 2.3 ±0.3 | 2.1 ±0.5 | 1.6 |
| **18:2(n-6)** | 1.0 ±0.3 | 1.8 ±0.3 | 1.8 ±0.4 | 1.1 | 1.7 ±0.1 | 1.8 ±0.3 | 4.7 ±2.2 | 2.2 | 5.4 ±0.4 | 3.6 ±0.2 | 2.0 ±0.2 | 1.2 |
| **16:3(n-4)** | 1.0 ±0.2 | 0.4 ±0.1 | 0.5 ±0.1 | 0.5 | 0.6 ±0.5 | 0.8 ±0.2 | 1.1 ±0.1 | 0.5 | 0.3 ±0.4 | 0.8 ±0.1 | 0.4 ±0.1 | 0.5 |

| Fatty acids | *Wo* (7) | *Ap* (9) | *Eg* (2) | *Pc* (1) | *Es* (2) | *Ege* (2) | *Eh* (2) | *Ep* (1) | *Df* (2) | *Oe* (2) | *Ar* (3) | Iphi *(1)* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **16:4(n-1)** | 0.1 | 0.2 ±0.1 | 0.8 ±0.8 | 0.1 | 0.0 | 0.1 | 0.1 | 0.1 | 0.0 | 0.1 | 1.4 ±0.6 | 0.1 |
| **18:3(n-6)** | 0.2 | 0.2 | 0.5 ±0.1 | 0.1 | 0.2 ±0.1 | 0.1 | 0.1 | 0.1 | 0.0 | 0.1 | 0.1 | 0.2 |
| **18:3(n-3)** | 0.2 | 0.5 ±0.1 | 0.5 ±0.2 | 0.4 | 0.5 ±0.2 | 0.5 ±0.3 | 0.8 ±0.2 | 0.8 | 3.3 ±0.5 | 2.7 ±0.3 | 1.2 | 0.3 |
| **18:4(n-3)** | 0.3 ±0.1 | 0.8 ±0.4 | 0.6 ±0.2 | 0.8 | 0.7 ±0.6 | 0.7 ±0.5 | 0.3 ±0.3 | 1.7 | 1.8 ±0.4 | 1.9 ±0.5 | 21.4 | 0.3 |
| **20:4(n-6)** | 1.3 ±0.5 | 1.4 ±1.7 | 1.4 ±0.4 | 1.1 | 8.0 ±3.3 | 8.2 ±2.7 | 2.7 ±1.2 | 2.8 | 15.0 ±0.9 | 20.0 ±1.5 | 0.7 | 1.4 |
| **20:4(n-3)** | 0.1 | 0.5 ±0.2 | 0.6 ±0.2 | 0.5 | 0.4 ±0.4 | 0.3 ±0.1 | 0.1 | 0.4 | 0.7 ±0.1 | 0.8 ±0.1 | 3.1 ±0.4 | 0.5 |
| **20:5(n-3)** | 6.1 ±1.5 | 9.1 ±2.4 | 8.7 ±2.5 | 4.3 | 19.0 ±1.6 | 19.2 ±2.0 | 16.7 ±3.2 | 19.7 | 19.9 ±1.3 | 12.4 ±0.5 | 19.2 ±0.6 | 14.6 |
| **22:5(n-3)** | 0.6 ±0.8 | 1.6 ±0.8 | 0.4 ±0.1 | 1.0 | 0.8 ±0.3 | 1.2 ±0.1 | 0.3 ±0.3 | 0.7 | 0.8 | 1.3 ±0.2 | 0.1 | 2.9 |
| **22:6(n-3)** | 6.0 ±1.0 | 8.9 ±2.1 | 8.8 ±1.7 | 5.4 | 18.1 ±2.6 | 13.2 ±0.3 | 14.9 ±11.3 | 17.7 | 2.7 ±0.3 | 0.9 ±0.1 | 10.5 ±0.8 | 8.3 |
| **sum PUFA** | 15.8 ±4.4 | 23.6 ±7.9 | 22.7 ±6.4 | 14.2 | 48.2 ±9.6 | 44.2 ±6.3 | 37.1 ±16.6 | 44.5 | 44.3 ±3.8 | 41.1 ±3.3 | 58.0 ±2.5 | 29.1 |
| **C18 ratio** | 15.0 | 4.5 | 4.6 | 5.0 | 3.3 | 2.6 | 1.9 | 4.3 | 5.4 | 4.1 | 2.5 | 3.3 |
| **sum 20:1** | 1.4 ±0.7 | 6.0 ±3.1 | 6.8 ±1.0 | 3.1 | 2.9 ±0.7 | 4.1 ±1.1 | 3.9 ±0.9 | 1.9 | 1.0 ±1.3 | 1.9 ±0.4 | 2.0 ±0.3 | 15.0 |
| **sum 22:1** | 0.7 ±0.7) | 2.1 | 2.1 ±2.1 | 2.6 | 0.8 ±0.6 | 0.8 ±0.3 | 0.9 ±0.6 | 0.6 | 0.6 ±0.8 | 0.6 ±0.3 | 0.2 | 3.6 |

### 3.3.3. STABLE ISOTOPE RATIOS

The average carbon and nitrogen isotope ratios range from –29.3‰ ($\delta^{13}C$) and 4.1‰ ($\delta^{15}N$) in *A. richardsoni* to –21.7‰ ($\delta^{13}C$) and 11.9‰ ($\delta^{15}N$) in *Iphimediella* sp (Table 3.4). The inter-species differences are significant as indicated by ANOVA and subsequent post-hoc tests (Tables 3.5a & 3.5b). Displaying the lowest isotopic ratios, *A. richardsoni* ($\delta^{13}C$ = -27.1 ± 0.9‰; $\delta^{15}N$ = 6.6 ± 0.6‰) and *D. furcipes* ($\delta^{13}C$ = -23.4 ± 0.6‰; $\delta^{15}N$ = 4.9 ± 0.3‰) resemble primary producers, i.e. the suspended particulate organic matter and the brown macroalgae *Desmarestia mensiezii*. The isotopic ratios of these primary consumers are significantly different from values of all the other species (Tukey test, $p<0.001$).

Both Epimeriidae and the species *E. perdentatus* show wide ranges of isotopic ratios. As illustrated in Figure 3.3 (see p.24), the range of values is wider for $\delta^{13}C$ than for the $\delta^{15}N$. The difference between maximum and minimum $\delta^{13}C$ is from 2.5 to 5.5‰. This difference is less pronounced for nitrogen (from 1.5 to 3‰). The species displaying the widest range of values is *E. georgiana.* The scavengers are clearly separated into two groups and this scission is essentially due to their significantly different $\delta^{13}C$ (Tukey test, $p<0.001$). The first group is composed of the lipid-rich species *A. plebs* and *E. gryllus* while the second gathers the lipid-less *W. obesa* and *P. coatsi* (Nyssen & Graeve, unpublished results).

**Table 3.4. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios of 11 species of Antarctic amphipods (mean ± SD); n: number of samples.**

| Species | N | $\delta^{13}C \pm SD$ | $\delta^{15}N \pm SD$ |
|---|---|---|---|
| ***Ampelisca richardsoni*** | 3 | -29.3 ± 0.2 | 4.1 ± 0.1 |
| ***Djerboa furcipes*** | 5 | -27.8 ± 0.6 | 4.9 ± 0.3 |
| ***Eusirus perdentatus*** | 14 | -23.4 ± 0.6 | 7.3 ± 1.0 |
| ***Epimeria similis*** | 15 | -25.0 ± 1.5 | 7.6 ± 0.5 |
| ***Epimeria georgiani*** | 17 | -23.7 ± 1.7 | 7.9 ± 0.4 |
| ***Echiniphimedia hodgsoni*** | 2 | -24.3 ± 1.3 | 10.6 ± 1.8 |
| ***Iphimediella*** sp | 4 | -21.7 ± 1.2 | 11.9 ± 0.9 |
| ***Pseudorchomene coatsi*** | 3 | -22.7 ± 0.3 | 9.3 ± 0.3 |
| ***Abyssorchomene plebs*** | 6 | -26.6 ± 0.5 | 9.5 ± 0.8 |
| ***Eurythenes gryllus*** | 9 | -27.3 ± 1.1 | 8.5 ± 0.5 |
| ***Waldeckia obesa*** | 5 | -22.8 ± 0.9 | 7.3 ± 0.7 |

The highest positioned species in the food web, *Iphimediella* sp. displays significantly different $\delta^{15}N$ to the other species (Tukey test, $p<0.001$) except from *E. hodgsoni* which belongs to the same family. However, the $\delta^{13}C$ value shows some similarity with other species, such as *W. obesa*, *E. perdentatus*, *P. coatsi and E. georgiana*.

**Table 3.3. Results of SIMPER analysis: within-group similarity (% in parenthesis), average dissimilarity (%) and separating fatty acids (FA) (most discriminant).**

| Average Dissimilarity + separating FA | CLUSTER 1 (89.1%) | CLUSTER 2 (83.7%) | CLUSTER 3 (81.8%) | CLUSTER 4 (85.3%) | CLUSTER 5 (95.0%) |
|---|---|---|---|---|---|
| CLUSTER 1 | - | 25.4%<br>18:1(n-9)/14:0 | 41.1%<br>18:1(n-9)/20:5(n-3) | 44 .3%<br>18:1(n-9)/20:4(n-6) | 50.5%<br>18:1(n-9)/18:4(n-3) |
| CLUSTER 2 | | - | 29.7%<br>18:1(n-9)/20:5(n-3) | 36.8%<br>20:4(n-6)/18:1(n-9) | 43.2%<br>18:1(n-9)/18:4(n-3) |
| CLUSTER 3 | | | - | 29.9%<br>22:6(n-3)/20:4(n-6) | 36.7%<br>18:4(n-3)/18:1(n-9) |
| CLUSTER 4 | | | | - | 44.5%<br>18:4(n-3)/20:4(n-6) |
| CLUSTER 5 | | | | | - |

**Table 3.5a. ANOVA results: post-hoc test (Tukey test) for $\delta^{13}C$. "x" indicates significant with $p < 0.001$, "x*" indicates significant with $p < 0.005$ and "ns" indicates no significant difference between means at $\alpha = 0.05$.**

| | Species | N | $\delta^{13}C$ | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *A. richardsoni* | 3 | -29.3±0.2 | | ns | x | x | x | x | x | x* | ns | x | x |
| 2 | *D. furcipes* | 5 | -27.8 ± 0.6 | | | x | x | x | x* | x | ns | ns | x | x |
| 3 | *E. similis* | 15 | -25.0 ± 1.5 | | | | x | x* | ns | x | ns | x | ns | x* |
| 4 | *E. georgiana* | 17 | -23.7 ± 1.7 | | | | | ns | ns | ns | x | x | ns | ns |
| 5 | *E. perdentatus* | 14 | -23.4 ± 0.6 | | | | | | ns | ns | x | x | ns | x* |
| 6 | *E. hodgsoni* | 2 | -24.3 ± 1.3 | | | | | | | ns | ns | x* | ns | ns |
| 7 | *Iphimediella* sp. | 4 | -21.7 ± 1.2 | | | | | | | | x | x | ns | ns |
| 8 | *A. plebs* | 6 | -26.6 ± 0.5 | | | | | | | | | ns | x | x |
| 9 | *E. gryllus* | 9 | -27.3 ± 1.1 | | | | | | | | | | x | x |
| 10 | *P. coatsi* | 3 | -22.7 ± 0.3 | | | | | | | | | | | ns |
| 11 | *W. obesa* | 5 | -22.8 ± 0.9 | | | | | | | | | | | |

**Table 3.5b. ANOVA results: post-hoc test ±Tukey test) for $\delta^{15}N$. "x" indicates significant with $p < 0.001$, "x*" indicates significant with $p < 0.005$ and "ns" indicates no significant difference between means at $\alpha = 0.05$, n: number of samples.**

| | Species | N | $\delta^{15}N$ | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *A. richardsoni* | 3 | 4.1 ± 0.1 | | ns | x | x | x | x | x | x | x | x | x |
| 2 | *D. furcipes* | 5 | 4.9 ± 0.3 | | | x | x | x | x | x | x | x | x | x |
| 3 | *E. similis* | 15 | 7.6 ± 0.5 | | | | ns | ns | x | x | x | ns | ns | ns |
| 4 | *E. georgiana* | 17 | 7.9 ± 0.4 | | | | | x | ns | x | ns | ns | ns | ns |
| 5 | *E. perdentatus* | 14 | 7.3 ± 1.0 | | | | | | x | x | x | ns | x | ns |
| 6 | *E. hodgsoni* | 2 | 10.6 ± 1.8 | | | | | | | ns | ns | ns | ns | x |
| 7 | *Iphimediella* sp. | 4 | 11.9 ± 0.9 | | | | | | | | x | x | x* | x |
| 8 | *A. plebs* | 6 | 9.5 ± 0.8 | | | | | | | | | ns | ns | x* |
| 9 | *E. gryllus* | 9 | 8.5 ± 0.5 | | | | | | | | | | ns | ns |
| 10 | *P. coatsi* | 3 | 9.3 ± 0.3 | | | | | | | | | | | ns |
| 11 | *W. obesa* | 5 | 7.3 ± 0.7 | | | | | | | | | | | |

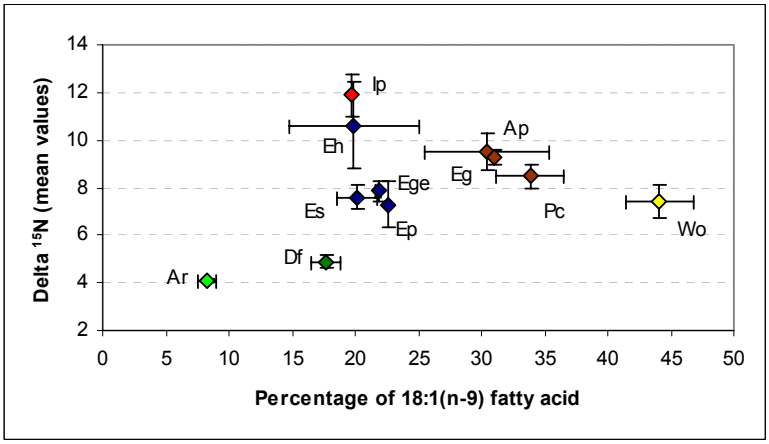
### 3.3.4. THE 2-DIMENSIONAL BIOMARKER APPROACH

In order to check whether the combination of fatty acid and stable isotope data is useful to enhance the identification of trophic positions, $\delta^{15}N$ values were plotted versus four fatty acid types which are characteristic biomarkers for certain food types or feeding strategies (Figs 3.4a to 3.4b).

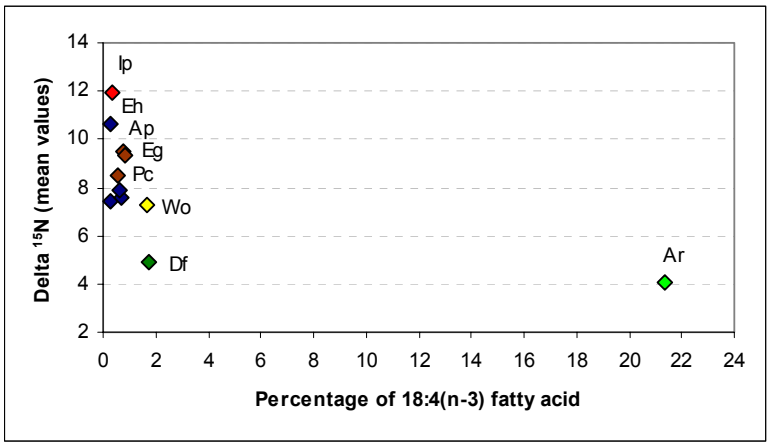
18:1(n-9) fatty acid is considered to be a signature of carnivory (Graeve et al. 2001, Auel et al. 2002). There is a general positive relationship between $\delta^{15}N$ and 18:1(n-9) (Fig 3.4a). The negative relationship between $\delta^{15}N$ and the polyunsaturated fatty acid 18:4(n-3), recognized as a biomarker of haptophytes (Graeve et al. 1994a, b), is illustrated in Figure 3.4b. The distinction between primary consumers food preferences is evident from comparison of Figures 3.4b and 3.4c. Finally, the plot of 20:1 and 22:1 fatty acids, synthesized only by calanoid copepods (Graeve et al. 1994a, b, Hagen et al. 1993, 2000, Kattner et al. 1994), against $\delta^{15}N$ shows a clear positive correlation (Fig. 3.4d).

**Figs.3.4a to 3.4d. Nitrogen isotopic ratios plotted *vs* concentration of fatty acid biomarkers (% of total fatty acids) of 11 species of Antarctic amphipods: Wo—*Waldeckia obesa*, Ap—*Abyssorchomene plebs*, Eg—*Eurythenes gryllus*, Pc—*Pseudorchomene coatsi*, Es—*Epimeria similis*, Ege—*Epimeria georgiana*, Ep—*Eusirus perdentatus*, Ip—*Iphimediella* sp., Eh—*Echiniphimedia hodgsoni*, Ar—*Ampelisca richardsoni*, Df—*Djerboa furcipes*.**

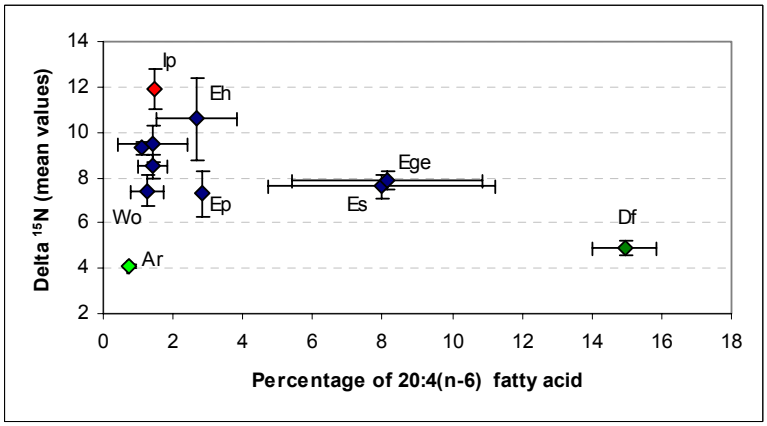
3.4a



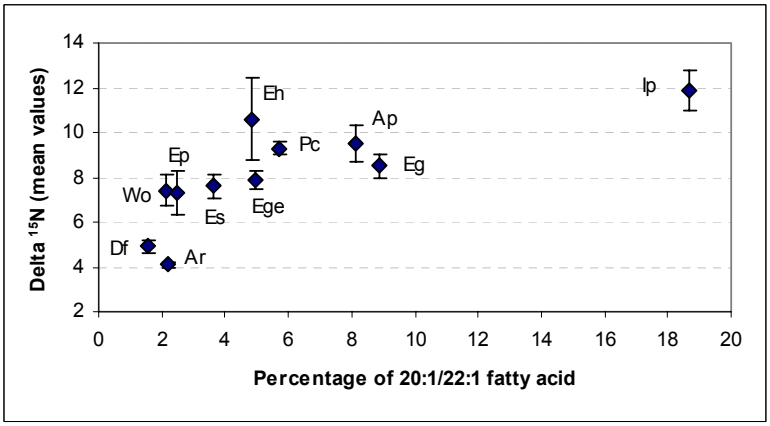
3.4b


Delta ¹⁵N (mean values)
Percentage of 18:4(n-3) fatty acid
Ip
Eh
Ap
Eg
Pc
Wo
Df
Ar

3.4c


Delta ¹⁵N (mean values)
Percentage of 20:4(n-6) fatty acid
Ip
Eh
Ege
Es
Ep
Wo
Df
Ar

3.4d

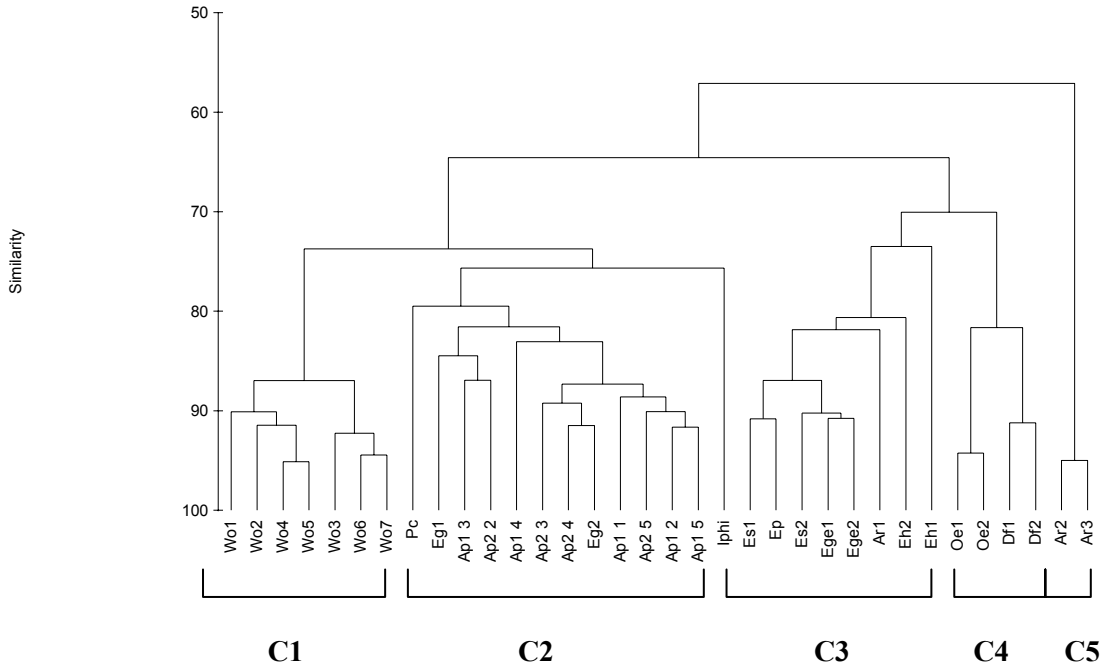

Delta ¹⁵N (mean values)
Percentage of 20:1/22:1 fatty acid
Ip
Eh
Ap
Pc
Eg
Ep
Wo
Es
Ege
Df
Ar

## 3.4. DISCUSSION

SIMPER analysis involving all fatty acids revealed essentially the oleic acid, to distinguish Cluster 1 from all other clusters. The fatty acid signature of *W. obesa* is characterized by extremely high levels of 18:1(n-9) and high levels of 14:0 compared to all other species. This unusual amount of 18:1(n-9) has already been recorded by Graeve et al. (2001) for the same species. Oleic acid is a major end product of the fatty acid biosynthesis in vertebrates and invertebrates. For example, Iverson et al. (2002) have reported concentrations of more than 30% of this fatty acid in Alaskan eulachon (*Thaleichthys pacificus*). In Antarctic waters, the notothenioid fishes, such as the icedevil, *Aethotaxis mitopteryx*, and the silverfish, *Pleurogramma antarcticum*, also display rather high levels of 18:1(n-9) fatty acid (about 25% of the total fatty acid composition) (Hagen et al. 2000) but none of them have ever been found to contain concentrations as high as those recorded in scavenging amphipods. The fatty acid 18:1(n-9), typically occurring in metazoans, is generally considered as a signature of carnivorous feeding (Sargent & Henderson 1986, Falk-Petersen et al. 1990, Graeve et al. 1994b, 1997, Hagen & Kattner 1998, Auel et al. 2002). Plotted against $\delta^{15}N$, which is a trophic indicator, a general positive correlation is observed, and an accumulation of 18:1(n-9) from the diet could be suggested. However, a particularly high *de novo* biosynthesis of 18:1(n-9) could also explain those high concentrations in Lysianassidae in general and *W. obesa* in particular. These fatty acids could have been synthesized by amphipods in response to short periods of satiety followed by long periods of starvation, a common situation for scavengers. Cluster 2, comprising the other scavengers, *A. plebs*, *E. gryllus* and *P. coatsi*, is also characterized by high levels of 18:1(n-9) but to a lesser extent compared to *W. obesa*. This difference, associated with the different levels of 14:0 fatty acid, is responsible for 40% of the separation of scavenger amphipods in two different clusters.

Considering the isotopic results, the species *A. plebs* and *E. gryllus* are characterized by particularly low $\delta^{13}C$ values compared to the other scavengers *W. obesa*, and *P. coatsi*. This depletion in carbon is probably due to the higher lipid content of *A. plebs* and *E. gryllus* (Nyssen & Graeve, unpublished results). Lipids are isotopically lighter than proteins and so high lipid content generally results in a decrease of the $\delta^{13}C$ of the whole body (DeNiro & Epstein 1977, Tieszen et al. 1983, Wada et al. 1987, Pinnegar & Polunin 1999, Nyssen et al. 2002).

**Fig 3.2. Hierarchical cluster analysis of fatty acid composition (%) of the total lipid extracted from 12 species of Antarctic amphipods: Wo—*Waldeckia obesa*, Ap—*Abyssorchomene plebs*, Eg—*Eurythenes gryllus*, Pc—*Pseudorchomene coatsi*, Es—*Epimeria similis*, Ege—*Epimeria georgiana*, Eh—*Echiniphimedia hodgsoni*, Ep—*Eusirus perdentatus*, Df—*Djerboa furcipes*, Oe—*Oradarea edentata* (data from Graeve et al. (2001)), Ar—*Ampelisca richardsoni*, Iphi—*Iphimediella* sp.**



All these scavenging amphipods belong to the family of the Lysianassidae and the conservation of a similar fatty acid composition in all of these congeners is particularly striking. A potential link between phylogeny and fatty acid composition in Lysianassids would be an interesting topic in itself. Indeed, the fatty acid composition of another Antarctic scavenger, the isopod Natatolana sp., is distinctly different despite its almost identical feeding strategy and prey spectrum (Nyssen, unpublished data).

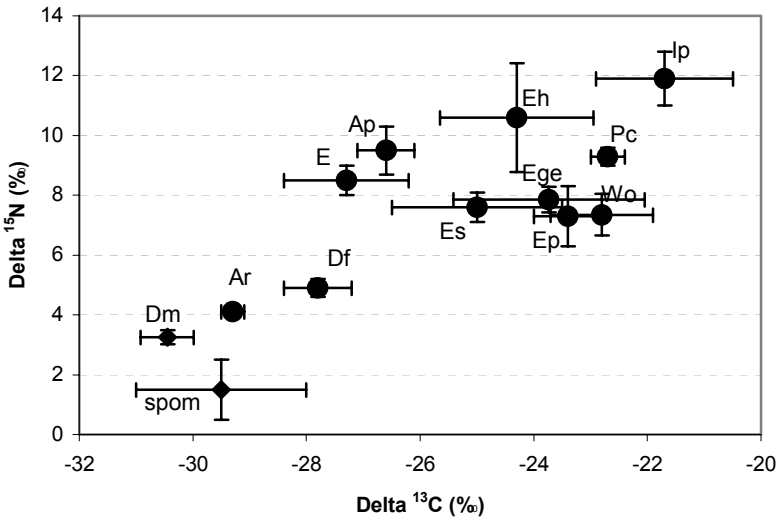
The high levels of $C_{18}$ and $C_{20}$ PUFAs (mainly arachidonic acid 20:4(n-6)) recorded in *D. furcipes* and *O. edentata* (Cluster 4, Fig 3.2) are well in accordance with their herbivorous diet. High concentrations of $C_{18}$ and $C_{20}$ polyunsaturated fatty acids have been shown to be typical of many macroalgae (Kayama et al. 1989, Cook et al. 2000, Graeve et al. 2001, Kharlamenko et al. 2001). Furthermore, judging by stomach content results, the brown alga *Desmarestia menziesii* seems to be preferentially consumed by these herbivorous amphipods. The results are corroborated by the fatty acid composition of the macroalgae, which are dominated by 20:4(n-6), 18:1(n-9) and $C_{18}$ PUFAs (Nyssen, unpublished results). When plotted against the $\delta^{15}N$ of all species, the percentage of 20:4(n-6) displays a negative correlation; its concentration increases with decreasing ranking of the various species in the food web (Fig. 3.4c). Although they are not macroherbivore, both Epimeriidae species accumulate significant quantities of 20:4(n-6) with up to 8%. Although Graeve et al. (2002) suggested arachidonic acid as indicating a macroalgal origin; other authors have suspected protists in the sediment to be one of the sources of 20:4(n-6) (Bell & Sargent 1985, Fullarton et al. 1995, Howell et al. 2003). The presence of sediment in the stomach of *E. similis* and *E. georgiana* has already suggested at least a partial deposit feeding behaviour and 20:4(n-6) levels could reflect some assimilation of the sediment-associated micro-organisms. Furthermore, even with a significant amount of arachidonic acid, the intermediate nitrogen ratios of both Epimeriidae provide additional evidence of the distance to this fatty acid signature source. These species do probably not belong to a well-defined

trophic category but are able to modulate their feeding behaviour in response to food availability. The combination of the different approaches used here enables the classification of those epimeriid species into the wrong trophic category to be avoided. This omnivory is corroborated by the wide range of their $\delta^{13}C$ which could reflect the large spectrum of organic matter sources upon which they can rely.

The SIMPER analysis also revealed that it is mainly the higher concentration of 18:4(n-3) fatty acid which isolates *A. richardsoni* from the other amphipods. These levels attest to a major dietary input of material originating from phytoplankton such as cryptophytes and/or haptophytes (Harrington et al. 1970, Nichols et al. 1991, Graeve 1993, Graeve et al. 1994a, b, Swadling et al. 2000, Graeve et al. 2001). Figure 3.4b clearly illustrates the drastic decrease of $\delta^{15}N$, indicator of the trophic position, along with the increase of the proportions of 18:4(n-3), a biomarker for the assimilation of fatty acid of phytoplankton origin (Harrington et al. 1970, Nichols et al. 1991, Graeve 1993, Graeve et al. 1994a, b, Swadling et al. 2000, Graeve et al. 2001). In this case, confusion would have been caused by the use of stable isotopes alone to determine trophic links. If the $\delta^{15}N$ values indicate *A. richardsoni* and *D. furcipes* as primary consumers, their respective fatty acid profiles reveal that they do not rely on the same primary producers at all.

The rather isolated position of *Iphimediella* sp. (Fig.3.2) seems to be due to the significant proportions of both isomers of the long-chain monounsaturated 20:1 and 22:1 fatty acids. These long-chain monounsaturates are typical components of dominant Antarctic copepod species *Calanoides acutus* and *Calanus propinquus* (Hagen et al. 1993, Kattner et al. 1994, Hagen et al. 2000). The significance of these copepod biomarkers in the fatty acid pattern would put *Iphimediella* sp. in the zooplankton feeder group. However, its $\delta^{15}N$ value (highest value in Fig.3.4d) as well as its known predatory behaviour strongly indicates that there exists a trophic level between copepods and *Iphimediella* sp.

**Fig.3.3. Carbon and Nitrogen isotopic ratios of 11 species of Antarctic amphipods: Wo—*Waldeckia obesa*, Ap—*Abyssorchomene plebs*, Eg—*Eurythenes gryllus*, Pc—*Pseudorchomene coatsi*, Es—*Epimeria similis*, Ege—*Epimeria georgiana*, Ep—*Eusirus perdentatus*, Ip—*Iphimediella* sp., Eh—*Echiniphimedia hodgsoni*, Ar—*Ampelisca richardsoni*, Df—*Djerboa furcipes*, spom—suspended particulate organic matter (data from Nyssen *et al.* 2002), Dm—brown macroalgae *Desmarestia mensiezii*.**




As illustrated in Figure 3.3 where $\delta^{15}N$ is plotted against $\delta^{13}C$, the other iphimediid species, *E. hodgsoni*, topped the trophic food web together with *Iphimediella* sp. With a diet essentially composed of sponges (Dauby et al. 2001b, Nyssen unpublished results), the high trophic position of *E. hodgsoni* is unexpected. Stable isotope ratios of Antarctic sponges can be quite high (–22.3 and 12.5 ‰ for $\delta^{13}C$ and $\delta^{15}N$ respectively (Nyssen et al. 2002). This may be due to assimilation of rapidly sedimenting and isotopically heavy aggregates of sea ice origin (Dunton 2001) or to assimilation of resuspended matter that was cycled repeatedly through the microbial loop (Hobson et al. 1995, Nyssen et al. 2002 and references therein). The fatty acid profile of *E. hodgsoni* did not show any sign of particular reliance on special food items. Its profile is dominated by 20:5(n-3) and 22:6(n-3) which are typical for marine organisms and predominant

in membrane lipids (Sargent & Whittle 1981, Sargent & Henderson 1986, Albers et al. 1996, Graeve et al. 2001).

In conclusion, our study demonstrates 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 lead to misinterpretations with serious implications. The combination of the two approaches creates a 2-dimensional biomarker assay with higher accuracy and better trophic resolution.

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# CHAPTER 4: ANTARCTIC AMPHIPODS FEEDING HABITS INFERRED BY GUT CONTENTS AND MANDIBLE MORPHOLOGY

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To be submitted

# ABSTRACT

In this work, we have investigated the possibility to infer amphipod feeding type from morphology of amphipod mandible combined to the gut content composition. Ten species mouthparts have been dissected and examined with scanning electron microscopy (SEM). From gut content composition, four main trophic categories were distinguished: (micro- and macro-) herbivores, opportunistic predator, specialist carnivore and opportunistic scavenger. Macro-herbivores (*Djerboa furcipes*, *Oradarea* n. sp., *Oradarea walkeri*) show a rather similar mandible morphology which does not differ very much from the amphipod mandible basic plan. Their diet essentially composed of macroalgae required strong and well toothed incisors to cut fragments of thallus. The suspension-feeder (*Ampelisca richardsoni*) shows few molar ridges and poorly developed, the small phytoplanktonic components requiring less triturating process to be ingestible compared to tough algae. The opportunistic predator (*Eusirus perdentatus*) shows mandible morphology close to the basic model excepted for the molar which is tall, narrow and topped by a reduced triturative area. This could facilitate a fast ingestion. The species revealed as specialised carnivores (*Epimeria similis* and *Iphimediella cyclogena*) have been compared with other Antarctic species which also feed exclusively on the same item and the mandible morphology presented numerous dissimilarities. Finally, the molar development of scavenger species (*Tryphosella murrayi* and *Parschisturella carinata*) suggests that these animals rely on a broader dietary regime than carrion only. In any case, the smooth and sharp incisor of these lysianassoids seems adapted for feeding on meat. Indeed, opportunistic carrion feeding seems to require little specialisation of the mouthparts.

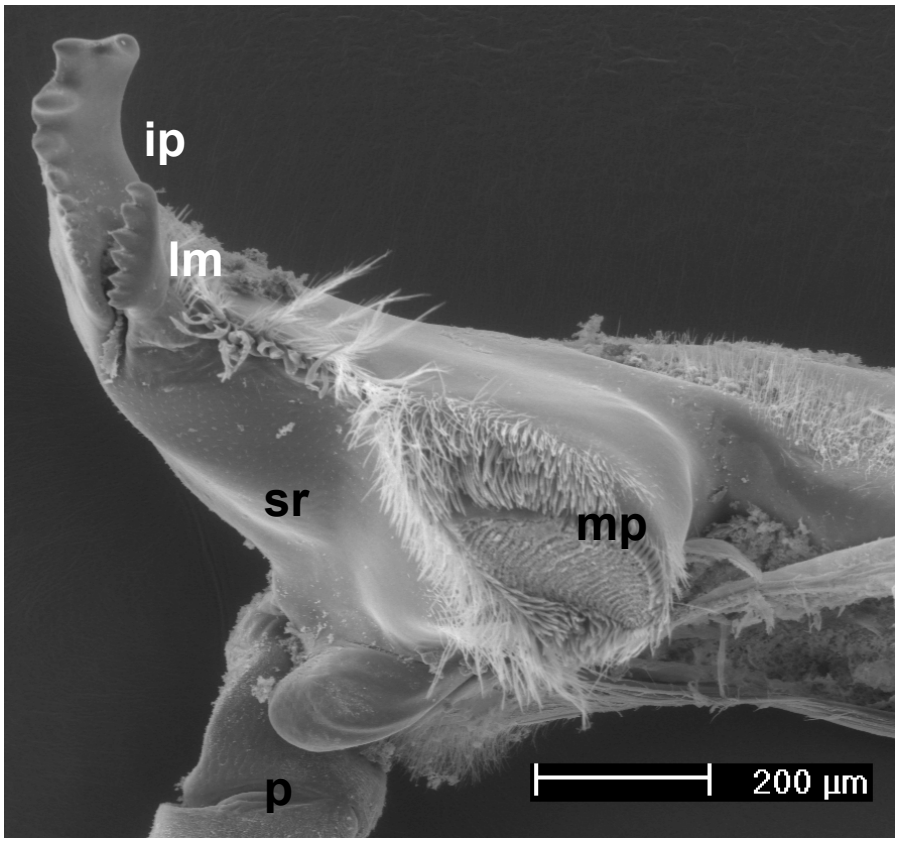
Regarding the discrepancies in the mandible morphology for species that are supposed to feed on the same items, one can conclude that, unfortunately, the morphology of amphipod mandibles is not characteristic enough to be a reliable method to distinguish the different trophic type. The evolution of amphipod mouthparts morphology has not only been guided by their functionality but others factors did interfere also in this process.

# 4.1. INTRODUCTION

Despite a relatively low biomass Amphipoda constitute a significant group in terms of energy flux in the Antarctic shelf ecosystems (Jarre-Teichmann et al. 1997, Dauby et al. 2001b). Among Antarctic zoobenthos, these crustaceans represent one of the most speciose groups and probably the most diversified with respect to lifestyles, trophic types, habitats and size spectra (De Broyer & Jazdzewski 1996, Dauby et al. 2001a, Chapelle & Peck 1999, Nyssen et al. 2002).The ecofunctional and specifically the trophic role of those Antarctic amphipods is still poorly known. Constant and predictable environmental conditions as well as the high diversity (Knox and Lowry 1977) lead to an expectation of close niche adaptation and consequently the presence of many specialists to exploit the full spectrum of resources. The highly specialized mouthparts of many Antarctic amphipods widely illustrated by Coleman's work on Iphimediidae (1989a, b, c, 1990a, b) support the hypothesis of close niche adaptation to a preferred food source. The structure of the mandibles in particular has been sometimes interpreted as an adaptation to the presumed food source (Watling 1993).

The structure and function of crustacean mandibles have extensively been described by Manton in 1977. The basic gammaridean amphipod mandible is of the type observed in the genus *Gammarus* and most other gammaridean families (Barnard 1969). This basic morphology consists of a mandible body where four main structures are typically to be found, starting distally and going to the mouth opening: the **incisor process**, generally provided with cusps and teeth; the ***lacinia mobilis***, inserted close to the incisor and generally in line with; the **spine-row**, filling the space between incisor and molar and probably involved in the transfer of the food to the mouth opening by forming a kind of bridge; and the **molar process**, a plane surface provided with diverse triturative structures (Watling 1993).

**Figure 4.1. mandible basic morphology (*Oradarea* n. sp. left mandible). ip: incisor process, mp: molar process, lm: *lacinia mobilis*, p: mandibular palp, sr: spine row.**



A large panel of modifications to the basic pattern can be observed among peracarids. In his review of the functional morphology of the amphipod mandible, Watling (1993) divided the larger amphipod families into four groups in function of the degree of the modification of their mandible from the basic plan. As modifications, reduction of the incisor process, disappearance of the spine-row, reduction or complete loss of the molar process are observed in the different families. Most of those morphological changes appear as evolutionary patterns resulting from different feeding strategies as predation and/or scavenging feeding behavior. Several species of Iphimediidae and Lysianassoidea are good illustrations of some of those morphological adaptations (Dahl 1979, Sainte-Marie 1984, Coleman 1989b, c, 1990b, 1991, Watling 1993).

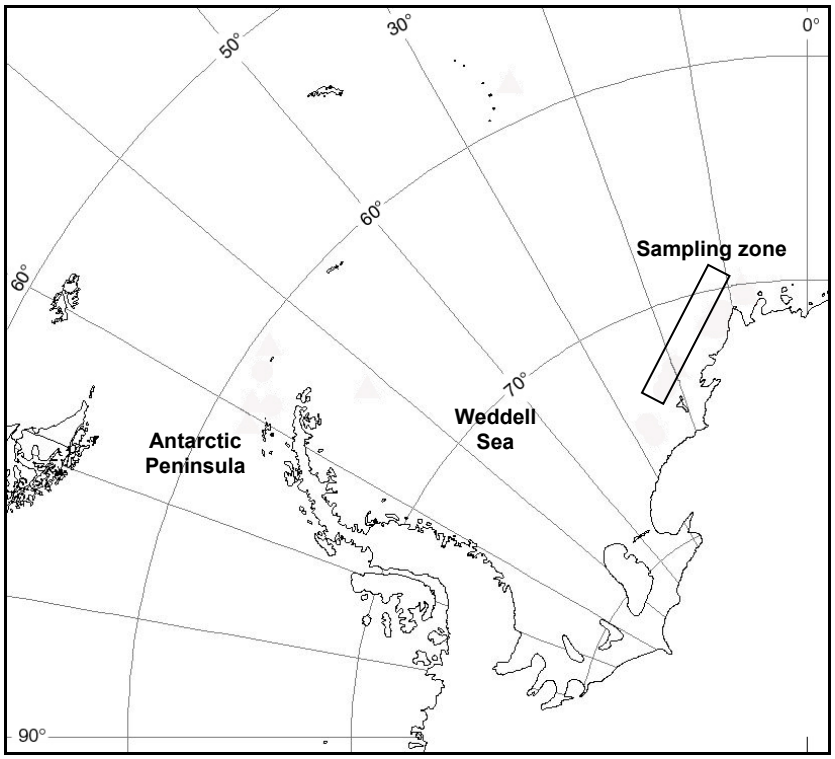
As a part of a multidisciplinary study of the amphipod ecological roles in Antarctic benthic systems (De Broyer et al. 2002), amphipod trophic patterns have been investigated (Dauby et al. 2001a, Graeve et al. 2001, Nyssen et al. 2002, De Broyer et al. 2004). The mandible morphology of ten species of Antarctic gammaridean amphipods has been studied and combined to gut contents analyses in an attempt to correlate mandible structure and feeding strategies.

# 4.2. MATERIAL AND METHODS

## 4.2.1. SAMPLING AND STORAGE

Amphipods (except three species) were collected from benthic and suprabenthic samples taken in the eastern Weddell Sea during three Antarctic summer cruises of RV "Polarstern": EPOS leg 3 (1989; Arntz et al. 1990; De Broyer & Klages 1990), EASIZ I (1996; Arntz & Gutt 1997; De Broyer et al. 1997) and EASIZ II (1998; Arntz & Gutt 1999; De Broyer et al. 1999). Gears used included Agassiz, benthopelagic and bottom trawls, dredges and baited traps (Fig 4.2).

**Fig.4.2. Map displaying sampling zone (rectangle) in the Eastern Weddell Sea**



Catches of *Oradarea* n. sp., *Oradarea walkeri* and *Djerboa furcipes* were achieved in the upper part of the infralittoral of Admiralty Bay (King George Island, South Shetland Islands, Antarctic Peninsula) during spring tides and also by dredging in shallow water in the vicinity of the Polish base "Henryk Arctowski" during the summer season 1993 (Fig 4.3). All sampled species are listed in Table 4.1.

**Fig.4.3. Map of Admiralty Bay, King George Island, Antarctic Peninsulaμ**

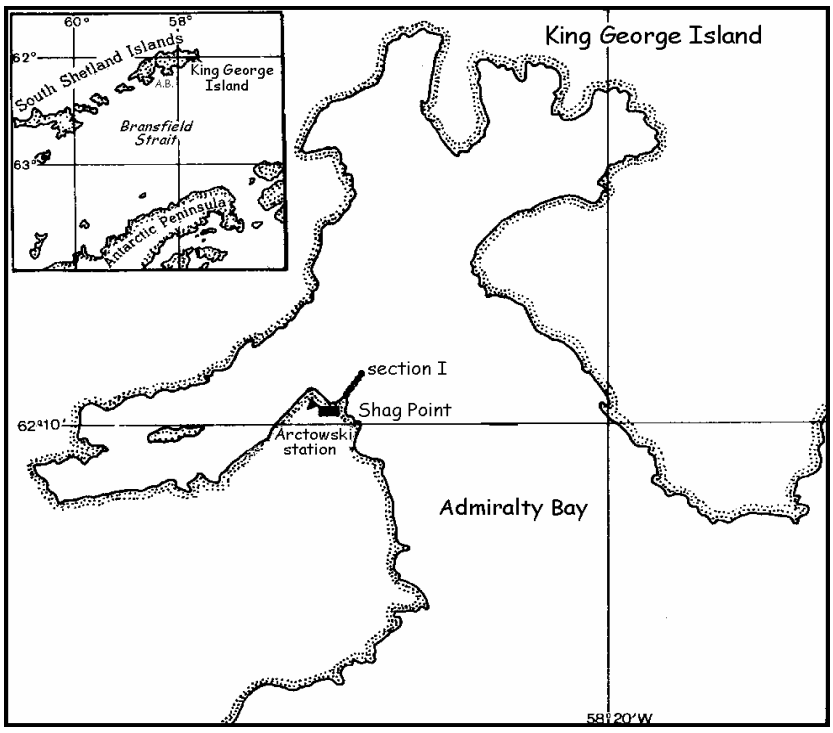


**Table 4.1. List of sampled species, sampling sites and years, sex, size and feeding types**

| Family | Species | sampling | Site | Sex / size | Feeding type |
|---|---|---|---|---|---|
| Ampeliscidae | *Ampelisca richardsoni* | 1998 | E. Weddell Sea | Fem / 22mm | Suspension feeder |
| Eusiridae | *Oradarea* n. sp. | 1994 | S.Shetlands | Fem / 25mm | Herbivorous |
| Eusiridae | *Oradarea walkeri* | 1993 | S.Shetlands | Fem / 19mm | Herbivorous |
| Eusiridae | *Djerboa furcipes* | 1993 | S.Shetlands | Fem / 19mm | Herbivorous |
| Eusiridae | *Eurirus perdentatus* | 1998 | E. Weddell Sea | Fem / 38mm | Predator |
| Iphimediidae | *Iphimediella cyclogena* | 1998 | E. Weddell Sea | Fem / 35mm | Micro-predator |
| Epimeriidae | *Epimeria similis* | 1996 | E. Weddell Sea | Fem / 36mm | Micro-grazer |
| Epimeriidae | *Epimeria georgiana* | 1998 | E. Weddell Sea | Male / 26mm | Deposit feeder |
| Lysianassidae | *Parschisturella carinata* | 1998 | E. Weddell Sea | Fem / 20mm | Opport. scavenger |
| Lysianassidae | *Tryphosella murrayi* | 1996 | E. Weddell Sea | Fem / 25mm | Opport. scavenger |

### 4.2.2. GUT CONTENT ANALYSIS

Analyses of gut contents were performed on 20 specimens from each species preserved in 4% formalin solution. Macroscopic dissections were conducted under a binocular dissecting microscope (Leica MZ12), using forceps and scissors. The digestive tract was cut at the oesophagus level and removed together with the midgut glands. Afterwards, it was separated from the midgut glands, opened and the content was spread on a micro slide. All the surface of the slide has been examined under optical microscope Leica DMLB (equipped with reflection contrast system). Every item has been identified as precisely as possible. The optic system was equipped with a video camera (JVC KY-F50) connected to a computer and pictures of the different food items were taken.
For several species, the gut contents results have been completed by Dauby *et al.* (2001a) wherein the methodological details can be found.

### 4.2.3. MORPHOLOGICAL ANALYSIS

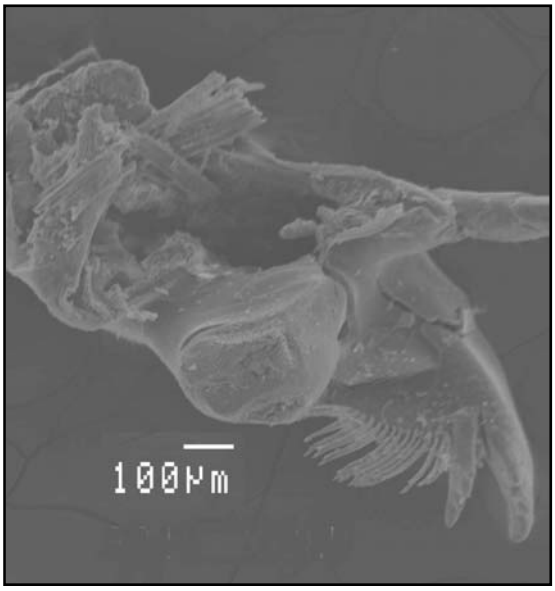
Each species mouthparts were dissected (maxillipeds, maxillae 1 and 2, mandibles, upper and lower lips). Afterwards structures were dehydrated through an alcohol series, critical point dried and sputter-coated with carbon then gold to be observed with scanning electron microscopy (SEM). In this study, only the morphology of mandibles has been considered.

## 4.3. Results

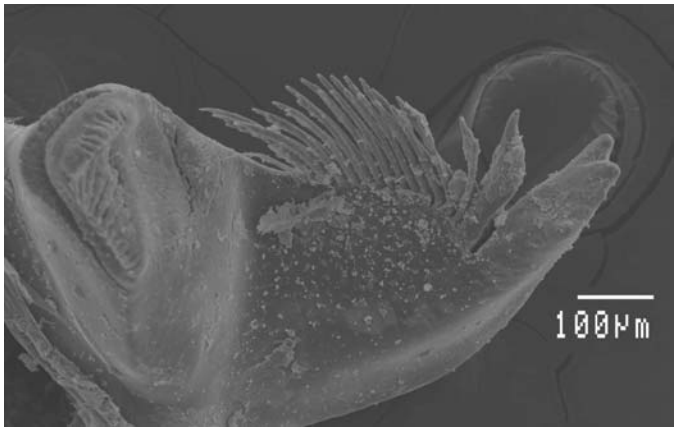
***Ampelisca richardsoni* Karaman, 1975 (suspension feeder)**

*Examination of foregut and gut contents* (see Dauby et al. 2001a). Food consists essentially of planktonic items (mainly diatoms) embedded in unidentified organic material (see picture on the left).

*Mandible morphology*. Both mandibles bear well developed incisor and molar processes. Both incisors bear 5 rounded cusps but, whereas the left one (see picture on the right) is equipped by a strong 5-toothed *lacinia mobilis*.

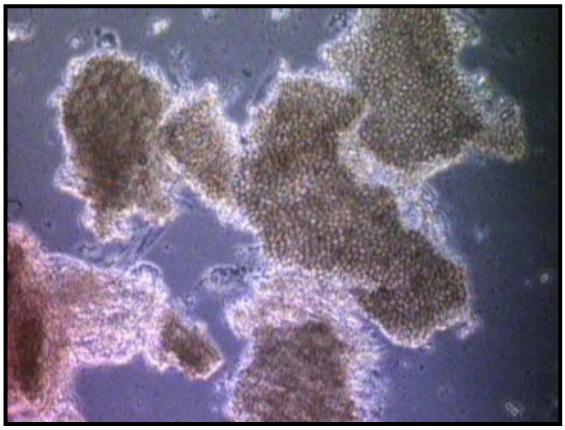


The right *lacinia mobilis* is smaller and more spine-like (see picture below). The molars are prominent and some smooth ridges are visible. The most striking feature of those mandibles is the development of the spine rows: on both side the row is composed of about 15 serrate spines nearly as long as the *lacinia mobilis* which could, by joining each other, form a kind of bridge between the tip of the mouthparts and the mouth itself.

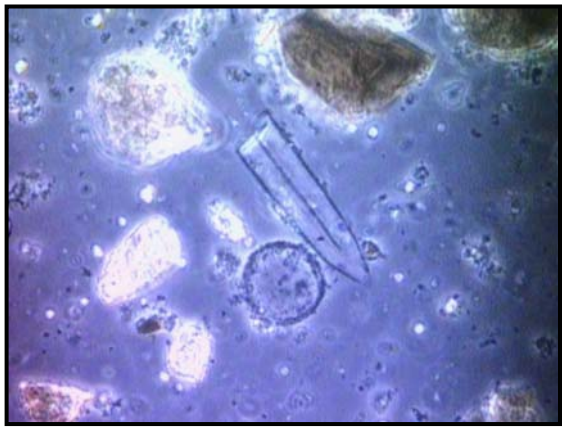



***Oradarea* n. sp. (macroherbivore)**

*Examination of foregut and gut contents*. The foregut and gut of 20 adult animals (female and ovigerous females) were examined. Those specimens were sampled by traps (400 meters depth) baited with different macroalgae (*Desmarestia mensiezi* and *Iridea* sp.) and following the present algae species, gut composition were totally different.

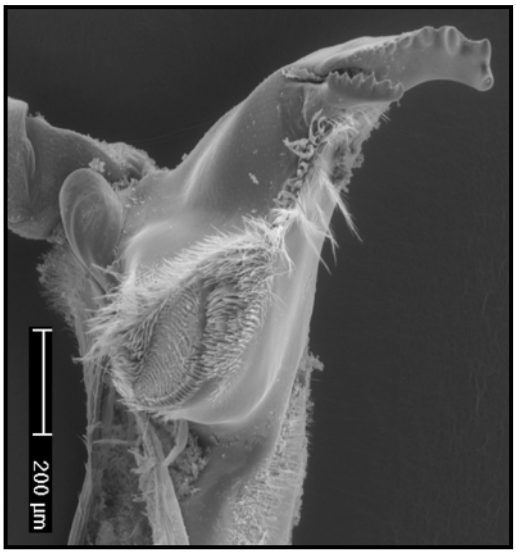


When baits consisted of pieces of the brown algae *D. menziesii*, 95% of the gut volume was filled with fragments of this algae (see picture on the left, magnification X20).

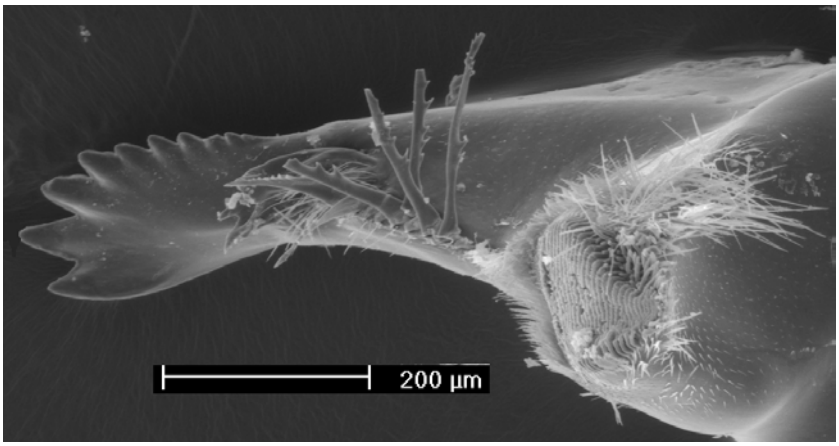


When baits consisted of pieces of algae belonging to the genus *Iridea*, (see picture on the left, magnification X80) the gut content was composed of: mineral particles, frustules of different kind of diatoms, chitinous structures and in some specimens, a very few amount of pieces of the macroalgae *Iridea* sp.

*Mandible morphology*. The mandibles are asymmetrical, although differing only in morphology of the *lacinia mobilis*. Incisor bears 10 rounded cusps. The left *lacinia* (see picture on the right) is similar to incisor although reduced in size and with only 7 more acute cusps.

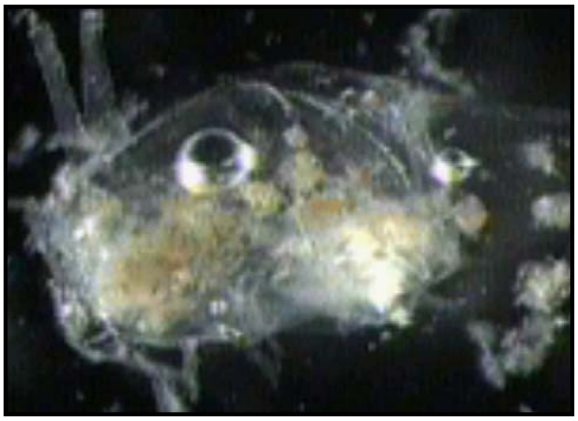


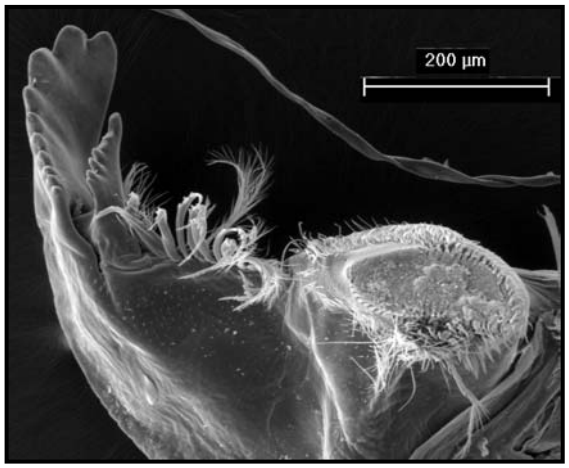
The right *lacinia* (see picture below) is slender. The spine row consists of stout serrate spines plus on the left mandible only a parallel row of plumose slender setae. The molar process is massive, sub columnar, and the triturative area is closely surrounded by short and thick setae and topped by a dense crown of setae. The grinding surface is provided with densely set short spinules and ridges with serrate distal margin.




***Oradarea walkeri* Shoemaker, 1930 (macroherbivore)**

*Examination of foregut and gut contents*. 20 adult sampled by trawls (20-35m depth) were dissected. According to observation, 90% of gut contents were composed of pieces of macroalgae. The 10% left consisted of diatoms of different types and inorganic material. The picture on the left represents the stomach of *O. walkeri* where pieces of macroalgae can be distinguished (green parts).



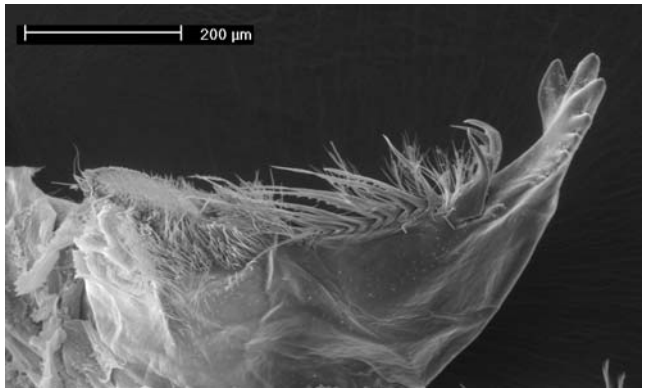



*Mandible morphology*. The morphology is nearly identical to that of *O.* n.sp. (see left mandible on the picture on the left). Both incisors are well developed and bear 10 strong teeth. The rather flat *corpus mandibulae* is bordered ventrally by a double row of stout serrate setae and of slender plumose setae. The large and tall molars are topped by a dense fringe of setae and bear a large triturative area provided with ridges and other rasplike structures. Both mandibles are flanked with a *lacinia mobilis*, strong and toothed (7 teeth) on the left mandible and weaker and spine-like on the right mandible.

***Djerboa furcipes* Chevreux, 1906 (macroherbivore)**

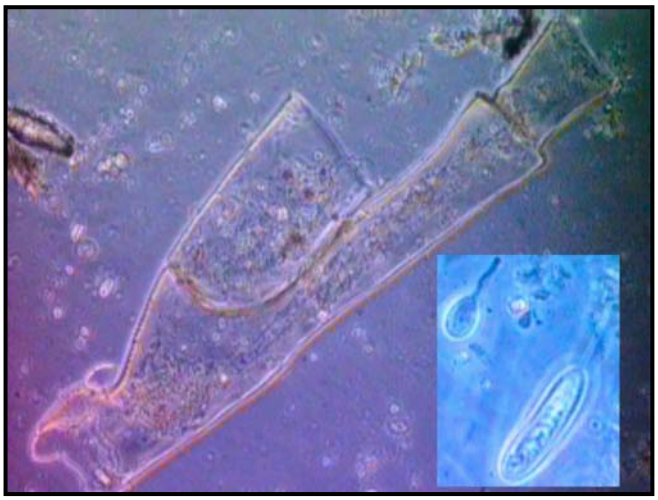
*Examination of foregut and gut contents*. Examination of the gut contents of 20 animals collected by trawls (20-35 m depth) allowed distinguishing – from the most to the less abundant item - : pieces of macroalgae thalli, pennate diatoms and a small amount of chitinous parts. All dissected specimens had also a significant amount of mineral particles in their gut.

*Mandible morphology*. As both species of the genus *Oradarea*, *D. furcipes* displays basic amphipod mandibles (in the sense of Watling 1993); toothed incisor (10 teeth), left *lacinia mobilis* with 10 teeth, only three on the right one (next page on top, see right mandible); large molar (but smaller than in genus *Oradarea*), cylindrical and triturative, crowned by a dense fringe of small setae; spine-row composed of two sort of setae.

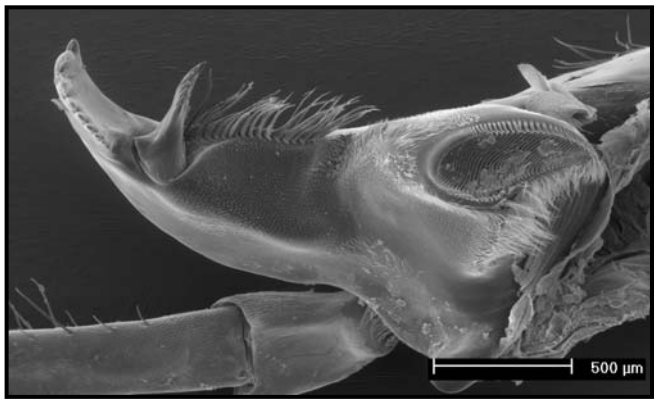



***Epimeria similis* Chevreux, 1912 (micropredator)**

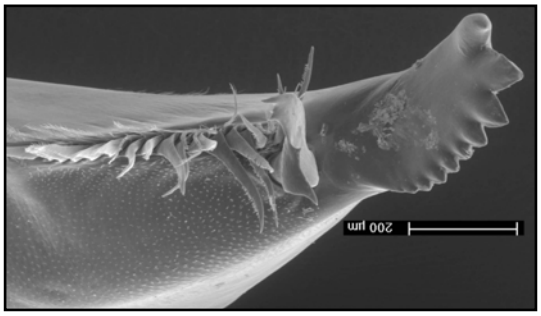
*Examination of foregut and gut contents*. The gut content of *Epimeria similis* was dominated by hydroid perisarc fragments (see picture below) and cnidocysts of different shape and size (see small insert). The rest of the gut consisted of sponge spicules, microalgae (mainly centric diatoms and fragments of *Chaetoceros* sp.) and pieces of polychaetes.



*Mandible morphology*. Both mandibles bear strong ten-toothed incisor and tall sub columnar molar provided with well-developed and smooth ridges. The molar is surrounded by a raw of stubby setae and fringed with bundles of hairs at dorsal margin.

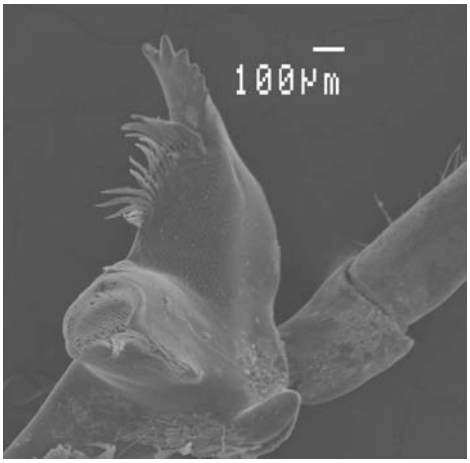



The left *lacinia mobilis* is armed with 7 cusps (see left mandible on the picture above) whereas the right one is smaller, bifurcated and spine-like (see the right mandible on the opposite picture). The spine-row is composed by stout denticulate setae, flanked on the ventral side by slender setae.




***Epimeria georgiana* Schellenberg, 1931 (deposit feeder)**

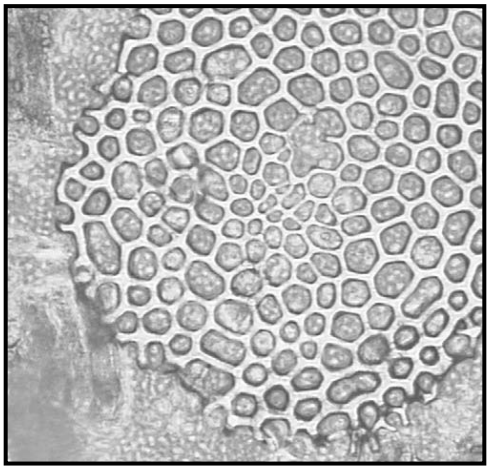
*Examination of foregut and gut contents*. The gut content of *E. georgiana* revealed a wide variety of food items: parts of crustaceans (mysids and amphipods), polychaetes, holothurian ossicles and hydrozoan perisarcs and planktonic items as diatoms, radiolarians and foraminifers. Sponge spicules and mineral particles complete the food (see Dauby et al. 2001).

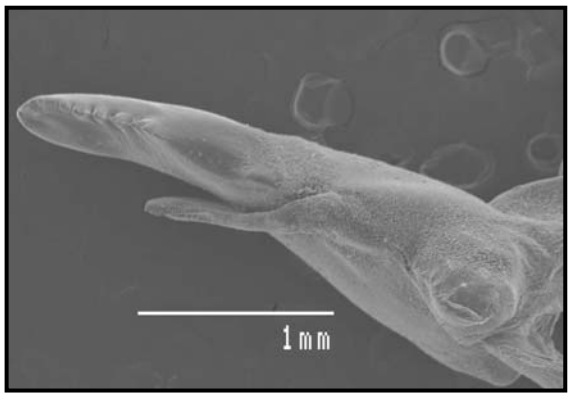



*Mandible morphology*. Both mandibles bear strong six-toothed incisor and as currently observed in this genus, the molars are prominent and provided with well developed ridges. The triturative area of molar is surrounded by a raw of stubby setae and topped backward by bundles of hairs. The left *lacinia mobilis* is toothed (5 cusps) whereas the right one is smaller and narrower (see right mandible on the picture above). The spine-row is composed by thick denticulate setae.

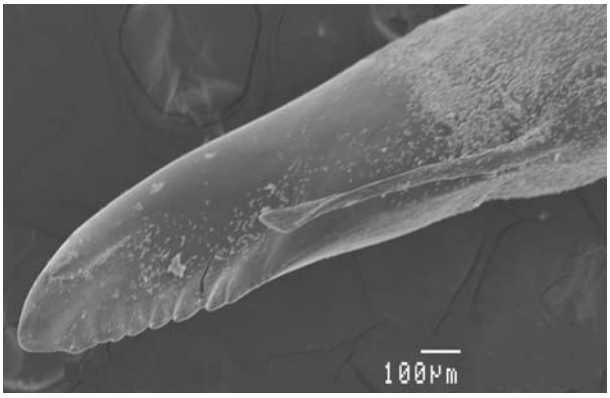
***Iphimediella cyclogena* K.H. Barnard, 1930 (micropredator)**

*Examination of foregut and gut contents*. The main food items observed in *I. cyclogena* gut were holothurian ossicles (see picture below) and polychaetes remains. In regard to the size of holothurians, it is more probable that this species scavenges instead of actually preying on it. *Iphimediella cyclogena* is considered as an opportunist consumer switching from predation to scavenging following the availability of food.



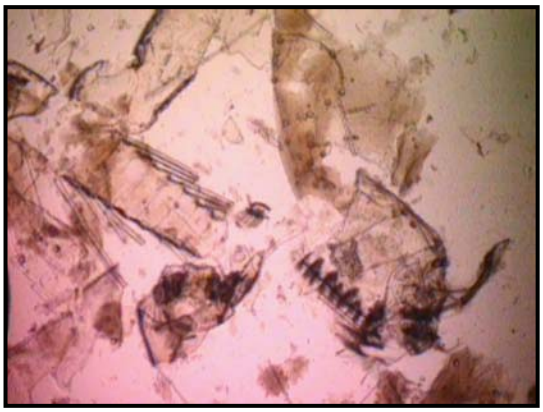



*Mandible morphology*. (see left mandible on picture on the left). The mandibular body is elongate tapering into the incisor that is much narrower than in all other species considered in this work. Both incisor processes are toothed (10 cusps) and bear a long *lacinia mobilis* which is inserted near a molar process reduced to a small fleshy cone. The *lacinia mobilis* is thick and strongly chitinised on the left mandible and reduced to a thinner twiggy structure on the right mandible (see right mandible on picture below).



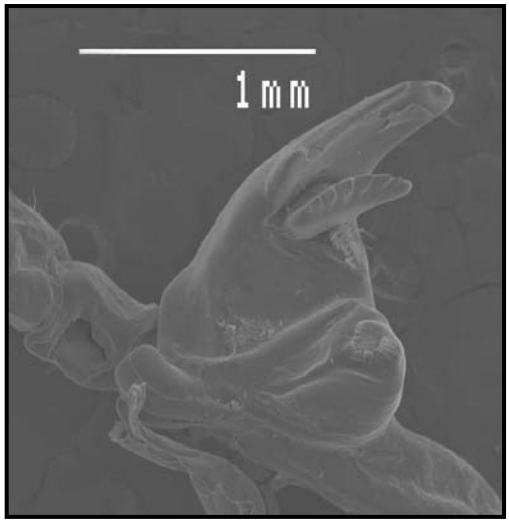

A major modification is the change in the orientation of the incisor, cutting in the vertical front plane. The position of the teeth along the incisor suggests a cutting in a scissor-like fashion.

***Eusirus perdentatus* Chevreux, 1912 (predator)**



*Examination of foregut and gut contents*. Crustacean hard parts and pieces of polychaetes form more than 50 percent of the gut contents (see picture on the left). Other food items consist of diatoms, sponge spicules and inorganic material. These observations corroborated the conclusion of Klages & Gutt (1990) wich said that *E. perdentatus* was a passive predator mainly feeding on crustaceans and polychaetes.

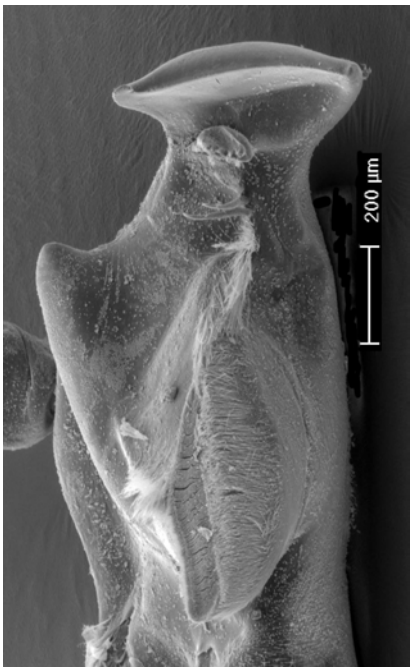
*Mandible morphology*. Mandibles bear strong incisors and molar processes. On the left mandible the large *pars incisiva* bears dorsal and ventral cusps and is flanked with a denticulated (7 teeth) *lacinia mobilis* (see picture on the right). The right *lacinia mobilis* is armed with two teeth. The short spine-row is composed of about 10 spines.




The apex of the tall sub columnar molar bears a small triturative area provided with rasp-like structures (see picture on the left). The reduced crushing area could explain the non-chewed state of some food items.

***Tryphosella murrayi* (Walker, 1903) (opportunistic necrophage)**

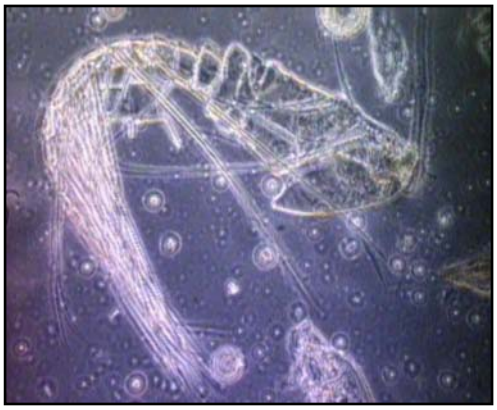
*Examination of foregut and gut contents*. Different items were observed in the digestive tract: pieces of crustaceans (antennae, buccal appendages, feathered setae, pleopods and ommatidia), pieces of polychaetes, very frequent fragments of flesh without any structure and some sponge spicules. The picture on the right presents a mid-gut full of fish flesh, parts of digestive caeca are also visible.



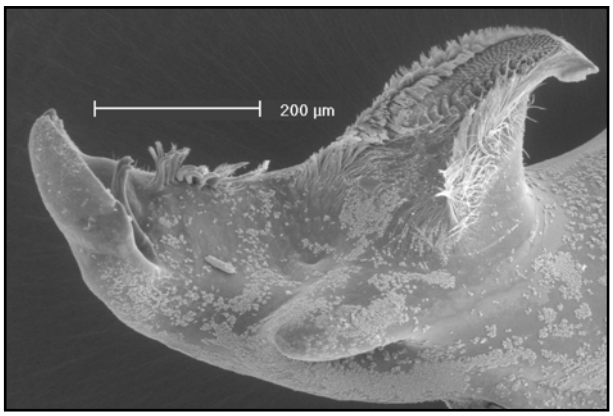

*Mandible morphology*. The proximal part of the incisors is narrow and the structure is broadening distally. The cutting edge is smooth and bears dorsal and ventral cusps. The *lacinia mobilis* is present on both mandibles. The spine-row is composed of 3 spines followed by a dense string of hairy setae which borders the corpus mandibulae. The molar is oval shaped and surrounded by a ventral fringe of setae that partly overlap the triturative area (see picture on the left).

***Parschisturella carinata*** **(Schellenberg, 1926) (opportunistic necrophage)**

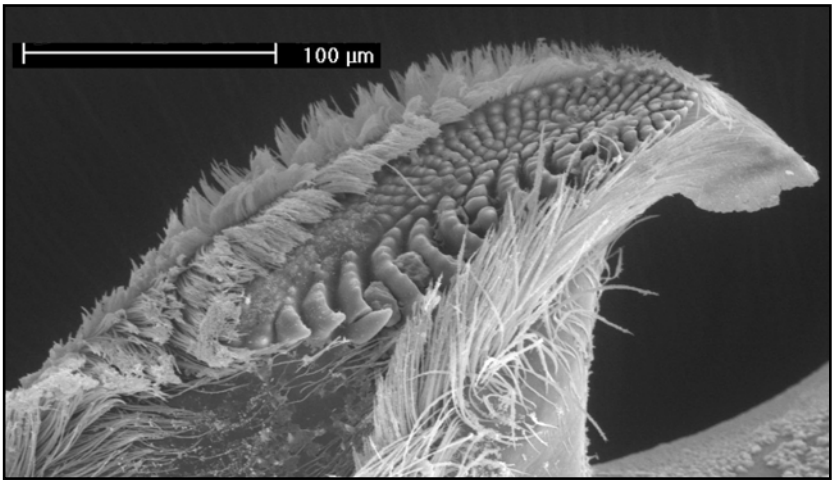
*Examination of foregut and gut contents*. Gut content observations revealed a diet composed mainly of crustaceans (see picture on the right). Nevertheless, this species is commonly observed in baited traps and is this case has the gut full of bait. This suggests a necrophage tendency, at least in an opportunistic way.



*Mandible morphology*. Incisor process is smooth and its edge is rather sharp and flanked by a single cusp at each end. The slightly concave *corpus mandibulae* is bordered by a row of (7-8) thick spines. The left mandible bears a weak digitifom apically bidentated *lacinia mobilis* (see picture on the right).




Tall molars are highly provided with setae and the oval triturative area displays impressive series of deep toothed ridges and rasp-like structures (see picture below).



## 4.4. Discussion

The feeding type of any organism can be assessed in different ways, according to the chosen approach. Regarding the gut composition, distinction can be made among herbivory, detritivory and carnivory. Regarding the size of the ingested food, it is possible to distinguish between microphagy and macrophagy. The third way to assess the trophic category depends on the feeding behaviour of the organisms and, it is possible, for example, to discriminate between predation and necrophagy among carnivores.

**Herbivorous species**

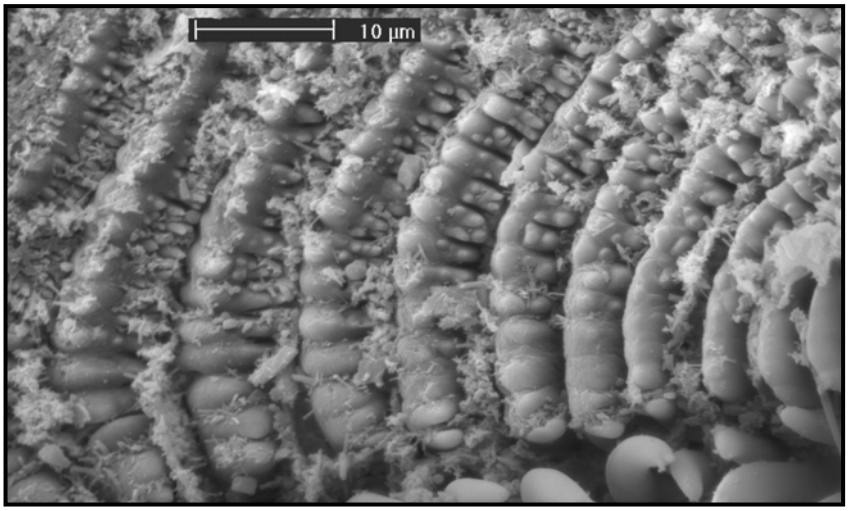
Among the species considered in this work, four of them can be classified in the herbivores: *A. richardsoni*, *O.* n.sp.*, O. walkeri* and *D. furcipes*.

The first species is a microphage feeding mainly on phytoplankton items whereas the three other species consuming essentially macroalgae tissues are categorized as macrophages. These macroherbivores show a rather similar mandible morphology which does not differ very much from the amphipod mandible basic plan. Their diet essentially composed of macroalgae required strong and well toothed incisors to cut fragments of thallus. The left mandible of the three species is also provided with a strong denticulate *lacinia mobilis* which probably works as an additional cutting edge.

Recently, the origin, function and phylogenetics implication of *lacinia mobilis* have been reconsidered. In 1982, Dahl & Hessler reaffirmed Boas' (1883) hypothesis of a spine-row origin for Peracarida *lacinia mobilis*. In 2002, Richter et al. approved it for the right mandible but for the left mandible, a separation from the incisor process could be more probable - although an origin from the spine row could not be totally excluded. In typical peracaridan biting, the right incisor process enters the gap between the left incisor and the left lacinia, which glides into the gap left between the right incisor and the right lacinia, where the latter is present. The function of

the lacinia in biting appears to be three- or possibly fourfold. It contributes to cutting, it helps guide the incisor processes into the right planes and to lock them into their final closing position. Probably a toothed or spiny lacinia also helps to hold food particles in place during the bite (Dahl & Hessler 1982, Watling 1993).

In macroherbivores, the molar area is provided with strongly denticulate ridges, necessary to triturate the tough macroalgal tissue. The picture below shows *Oradarea* n. sp. molar details.




The diatom consumer, *A. richardsoni*, has a less incurved and elongated incisor process which is also stouter. The molar ridges are few and poorly developed, the small phytoplanktonic components requiring less triturating process to be ingestible compared to tough algae.

Following their diet composition, the new species of the genus *Oradarea* seems to feed preferentially on brown macroalgae. Indeed, a clearly different diet composition has been observed following the offered baits in the traps. When the bait consisted of pieces of algae of the genus *Desmarestia*, the gut was completely filled with plant fragments. Meanwhile, when pieces of the

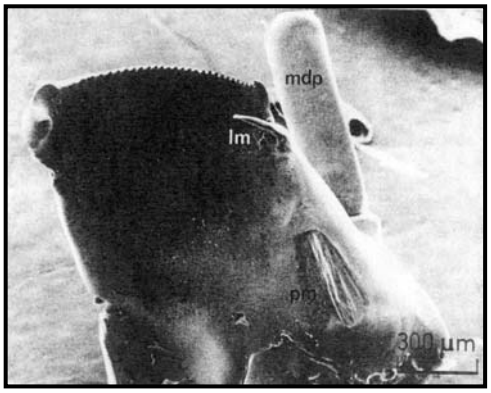
red algae (*Iridea* sp.) were offered, the gut content was only composed of mineral particles and diatoms. This preferential consumption of *Desmarestia* is not surprising as Amsler et al. (1998) have demonstrated the development of chemical defenses against herbivory for the species *Iridea cordata*. Furthermore, as the repartition area of Desmarestiales (down to 90-100 meters depth, the limit of the phytal zone) is deeper than the one of the genus *Iridea* (from 0 to 10 meters depth), the probability to find those brown algae at 400 meters depth (the sampling depth) is higher. So, the presence of herbivore species in rather deep zones (400 meters depth) is not surprising as the contribution of drifted macroalgae to the organic matter in the deep basins of Admiralty bay is rather high (Fischer & Wiencke, 1992).

**Specialist carnivore species**

According to their gut contents, *Epimeria similis* and *Iphimediella cyclogena* are both specialist consumers. The first is considered as a cnidarian-feeder (gut contents essentially composed of cnidocysts and hydroid perisarc fragments), and the second consumes mainly holothurians (high amount of ossicles in gut). However, if each species mandibles are compared with those of other Antarctic species which also feed exclusively on cnidarians or holothurians, as respectively, the iphimediid *Maxilliphimedia longipes* and the stilipedid *Bathypanoploea schellenbergi* (Coleman 1989a, 1990b), totally different morphologies are observed. These different morphologies are summarized in the following Table as well as *M. longipes* and *B. schellenbergi* mandibles are illustrated in pictures provided by Coleman (1989a, 1990b).

From these observations, one could conclude that to classify an animal as a cnidarian feeder is not restrictive enough, this phylum being composed by organisms with very different structures. In this case, *E. similis* and *M. longipes* must be classified respectively as consumers of hydrozoans and anthozoans respectively. In the latter, gut contents are characterised by the

presence of nematocysts: spirocysts - typical of Hexacorallia, and mastigophores which can frequently be found in Anthozoa and Hydrozoa (Coleman 1989a) whereas *E. similis* gut is essentially composed of perisarc fragments and nematocysts of hydrozoans. The discrepancies in mandible morphology could be explained by the consumption of these different organisms.

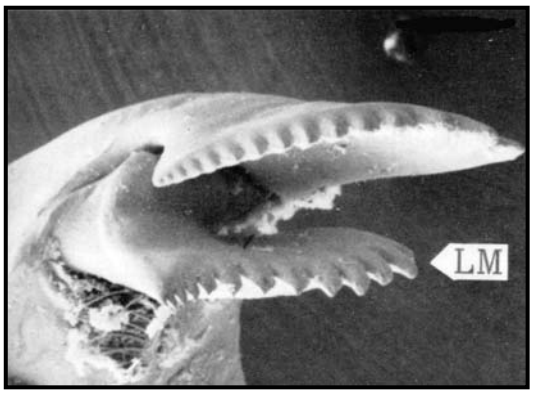



In *M. longipes* (see picture on the right from Coleman, 1989a), the remarkable absence of hair-like setae and the smooth aspect of the setae present could be an adaptation to the food source. Setose mouthparts and feather-like setae would easily be embedded together by the mucus of anthozoans. Furthermore the long cutting edge of their incisor processes can cut larger pieces of prey and the rudimentary molars are not able to triturate food. This could point to very soft food (Coleman 1989a). On the other hand, *E. similis* well-toothed incisors and tall and strongly ridged molars are more adapted to harder kind of food as hydrozoans perisarcs.

The dissimilarities in mandible morphology of both holothurian feeders considered in this work: *B. schellenbergi* and *I. cyclogena* is also surprising. Holothurians are a quite uncommon food source for invertebrates. Their integument is leathery with embedded ossicles. On the other hand, their reduced motility makes them a rather ideal prey for other slow predators. Some seastars and among the gastropods, some genera of the prosobranch

family Eulimidae have been observed feeding on holothurians (see references in Coleman 1990b).

*B. schellenbergi* appeared to be the first "food specialist" feeding on holothurians in the Antarctic. Its mouthparts are interpreted to be highly adapted to cope with the tough tissues of these echinoderms (Coleman 1990b). Its mandibles are remarkably stout. The incisors are strongly serrate, both bearing a *lacinia mobilis*; the left one, also well-toothed, might act as a third cutting edge. This highly integrated cutting mechanism would enable *Bathypanoplea* to cut such firm tissue as the body wall of holothurians. In this species, the molar is reduced so that the reduction of the food in little pieces relies solely on the actions of the incisors and their laciniae. The picture on the left displays the left incisor process and its *lacinia mobilis*.




Although they seem to rely mainly on the same food source, *Iphimediella* mandible morphology is completely different. As summarized in Table 3.2., the mandibular body is elongated and the incisors are much narrower. Both incisor processes are toothed (10 cusps) and bear a *lacinia mobilis*. But, with such a smooth structure, none of the *lacinia mobilis* could help in cutting tissue as tough as holothurian body wall is. Furthermore, in view of the reduced molar process, the food reduction can not rely only on them. The question is: how do they feed on holothurians? One hypothesis could be that they actually scavenge on rotting holothurians and that the process of decomposition make the tissues softener and easier to cut.

**Table 4.2. Summary of the mandible morphological differences between specialist consumers**

| | CNIDARIAN CONSUMERS | | HOLOTHURIAN CONSUMERS | |
|---|---|---|---|---|
| | ***E. similis*** | ***M. longipes*** | ***I. cyclogena*** | ***B. schellenbergi*** |
| **Mandible** | - stout | - stout | - elongated | - stout |
| **Incisor & *lacinia mobilis* (*l.m*)** | - normal<br>- strong teeth<br>- strong and toothed left *l. m*<br>- weak right *l. m*<br>- seta row | - broadened<br>- weak teeth<br>- both *l.m.* are vestigial<br>- no seta row | - very narrow<br>- longitudinally toothed<br>- strong and smooth left *l.m*<br>- weak right *l. m.*<br>- no seta row | - normal<br>- strongly serrate<br>- strong and toothed left *l. m*<br>- weak right *l. m.*<br>- seta row |
| **Molar** | - strong<br>- smooth ridges<br>- fringe of setae | - vestigial | - small fleshy lobe without any ridges and setae | - reduced |

**Opportunistic predator**

According to its gut contents and feeding behaviour observations, ***Eusirus perdentatus*** is a true predator which seems to be able to switch its diet following the food availability (crustaceans, polychaetes). The most characteristic feature of *E. perdentatus* mandibles is their tall molar bearing a high and small triturative area provided with rasplike structures. The reduced crushing area could explain the rather large food items observed in the gut contents. This ability to ingest big parts of prey could facilitate a fast predation.

**Opportunistic necrophages**

Besides all other food sources, there is strong evidence that large food falls play a significant role in the vertical flux to the sea bottom, too. On the one hand, there are reports of the encounter of such large food items on the sea floor such as big marine mammal carcasses, fishes, large pelagic invertebrates or their remains (Smith *et al.* 1989, Jones *et al*. 1998, Klages *et al.* 2001). On the other hand, well developed associations of highly mobile scavengers (mainly lysianassoid amphipods) are present on shelf and deep sea bottoms throughout the world oceans. In this context lysianassoids have evolved morphological, physiological and behavioral traits which seem to enable them to rely on this food source. According to Dahl (1979), three adaptations are necessary for efficient carrion feeding. The first adaptation is the development of efficient chemoreceptors to detect and locate carrion. Secondly the ability to feed on large, muscular food items, such as squid, fish or marine mammals by the use of adapted mandibles characterised, briefly, by a wide and sharp incisor edge, a bowl-shape *corpus mandibulae* and a non-triturative molar (Dahl 1979, Sainte-Marie 1984). Lastly, necrophage lysianassoids seem to solve the starvation problem due to the rarity of their food sources by storing large quantities of carrion in capacious guts.

The scavenging lysianassoids have evolved along two divergent lines represented by the genera *Hirondellea-Eurythenes-Paralicella* and *Orchomene* (Dahl 1979). The former group appears to be the strict (obligate?) necrophage group, the latter being more opportunistic in their feeding. Regarding their mandible morphology, although the basic plan is similar, their mandible features are quite different, and their gut contents analysis, the lysianassoid species considered in this work, *T. murrayi* and *P. carinata*, would belong more probably to the second group. Although it has been classified as a true necrophage by Dauby et al. (2001), our new gut content analyses of *P. carinata* (several individuals were full of crustaceans' remains) and furthermore the extreme development of its molar (tall and strongly ridged) obviously enabling this species to feed on other items than carrion, suggest a more opportunistic feeding behaviour. Besides its necrophagous behaviour, *T. murrayi* is also a predator and has already been observed killing and eating others crustaceans and even fishes (Dauby et al. 2001).

So, for both species the molar development suggests that these animals rely on a broader dietary regime. In any case, the smooth and sharp incisor of lysianassoids seems adapted for feeding on meat. Indeed, opportunistic carrion feeding seems to require little specialisation of the mouthparts.

Regarding the discrepancies in the mandible morphology for species that are supposed to feed on the same items, one can conclude that, unfortunately, the morphology of amphipod mandibles is not characteristic enough to be a reliable method to distinguish the different trophic type. The evolution of amphipod mouthparts morphology has not only been guided by their functionality but others factors did interfere also in this process.

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# CHAPTER 5: THE CRUSTACEAN SCAVENGER GUILD IN ANTARCTIC SHELF, BATHYAL AND ABYSSAL COMMUNITIES

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After De Broyer C, Nyssen F, Dauby P (2004) Deep-Sea Research, Part II: 51: 1733-1752

# Abstract

Peracarid crustaceans form a significant part of the macrobenthic community which is responsible for scavenging on large food falls onto the sea floor. Although several studies are available about scavengers from tropical and temperate seas, very little information has been published about such species living in Antarctic waters, particularly at greater depths. The present paper is based on a collection of 31 baited trap sets deployed in the Weddell Sea, Scotia Sea and off the South Shetland Islands, and presents results on the geographical and bathymetric distribution of the different taxa and on the ecofunctional role of scavengers.

Some 68,000 peracarid crustaceans from 62 species were collected. About 98% of individuals belonged to the amphipod superfamily Lysianassoidea, and 2% to the isopod family Cirolanidae. Of these species, 31, including 26 lysianassoids (1,400 individuals), were collected deeper than 1000 m.

High species richness was discerned for the eastern Weddell Sea shelf compared with other Antarctic areas. The Antarctic slope also seems to be richer in species than other areas investigated in the world, while in the abyss, scavenger species richness appears to be lower in Antarctica. A richness gradient was thus observed from the shelf to the deep. For amphipods, a number of species extend their distribution from the shelf to the slope and only one to the abyssal zone.

Amphipod species showed degrees of adaptation to necrophagy. The functional adaptations of the mandible and the storage function of the gut are discussed. Feeding experiments conducted on lysianassoid species collected at great depths and maintained in aquaria showed a mean feeding rate of about 1.4 to 4.1 % dry body weight.day$^{-1}$, which is consistent with data obtained from other species.

## 5.1. Introduction

The scavenger guild plays a key role in deep-sea benthic communities by rapid recycling and dispersing organic falls of all sizes, from small plankters to whales (e.g. Gage and Tyler 1991, Britton and Morton 1994).

In the Antarctic seas, the existence of an abundant and active scavenger fauna was noticed by early Antarctic marine investigators. Observing the large catch of lysianassid amphipods attracted quickly to baited nets at Cape Adare during the National Antarctic Expedition 1901-1904, Hodgson (in Walker 1907) wrote: "*The trap contained about 10,000 of these amphipods.... Four fish were in the trap, one of them had been reduced to an absolute skeleton; on another the amphipods hung by their 'teeth' in a compact mass, completely concealing their victim. Its skin had disappeared, and I judged also a millimetre of flesh.... the other two fish were presumably waiting their turn.*"

These early collections were mostly opportunistic. With the establishment of permanent coastal Antarctic stations, baited traps have been used more systematically to collect necrophagous invertebrates (*e.g.* Hurley 1965, Arnaud 1970, Bruchhausen et al. 1979, Rakusa-Suszczewski 1982, Nagata 1986, Presler 1986, Slattery and Oliver 1986, Moore 1994). These catches have provided data on the composition, ecology and biology of scavengers, as well as the discovery of species new to science (e.g. Hurley 1965, De Broyer 1985a, Nagata 1986). Most of this sampling was done at depths shallower than 150 m. Attempts to collect scavengers on the deep Antarctic continental shelf, which extends to an average depth of 450 m and, in places, to over 1000 m depth (Clarke and Johnston, 2003), have been relatively few (Arnaud 1970, De Broyer and Klages 1990, De Broyer et al. 1997, 1999, Takeuchi et al. 2001).

Baited trap sampling led to the discovery of an unexpected vagile benthic fauna of fish and crustaceans under the Ross Ice Shelf at a distance of 400

km from the sea, under ice 415 m thick (Bruchhausen et al. 1979, Lipps et al. 1979, Stockton 1982).

In the deep sea, bathyal and abyssal trap sampling was initiated by the Prince of Monaco as early as 1888 and provided new, and sometimes giant, species of crustaceans and fishes (Richard 1934, Chevreux 1935, De Broyer and Thurston 1987). Much later, baited cameras revealed the existence of a very active guild of mobile necrophages in the deep sea which attracted much interest (e.g. Isaacs and Schwartzlose 1975, Hessler et al. 1978, Gage and Tyler 1991, Britton and Morton 1994). In the Antarctic deep sea, attempts at baited trap collecting have, so far, been extremely few: two operations were reported by Bowman and Manning (1972) from north of Amundsen Sea at depths of 4930 and 5045 m and one single operation at 3186 m off Queen Maud Land was undertaken by Takeuchi et al. (2001).

During the *Polarstern* EASIZ campaigns (1996 & 1998) in the Weddell Sea baited traps were used systematically to complement the catches made by other gears in order to obtain a more complete representation of the shelf and slope assemblages at the so-called "integrated stations" (Arntz and Gutt 1997, 1999, De Broyer et al. 1997, 1999). These trap operations collected mobile scavengers (sometimes in large number) that were not, or only rarely, sampled by other gears such as trawls, dredges, epibenthic sledges, box-corers and deep plankton nets.

In addition, investigations of the Antarctic deep sea have recently been conducted during the *Polarstern* ANDEEP cruises in 2002 in the Scotia Sea, the western Weddell Sea and the South Sandwich Trench (Brandt et al. 2003, De Broyer et al. 2003). These bathyal and abyssal investigations involved a series of successful deep-sea trapping operations.

The results of these *Polarstern* campaigns in terms of composition and bathymetric distribution of the crustacean scavenger guild are reported herein and Antarctic shelf and deep sea faunules are compared. In addition, to investigate the role of the scavenger guild in Antarctic shelf communities and

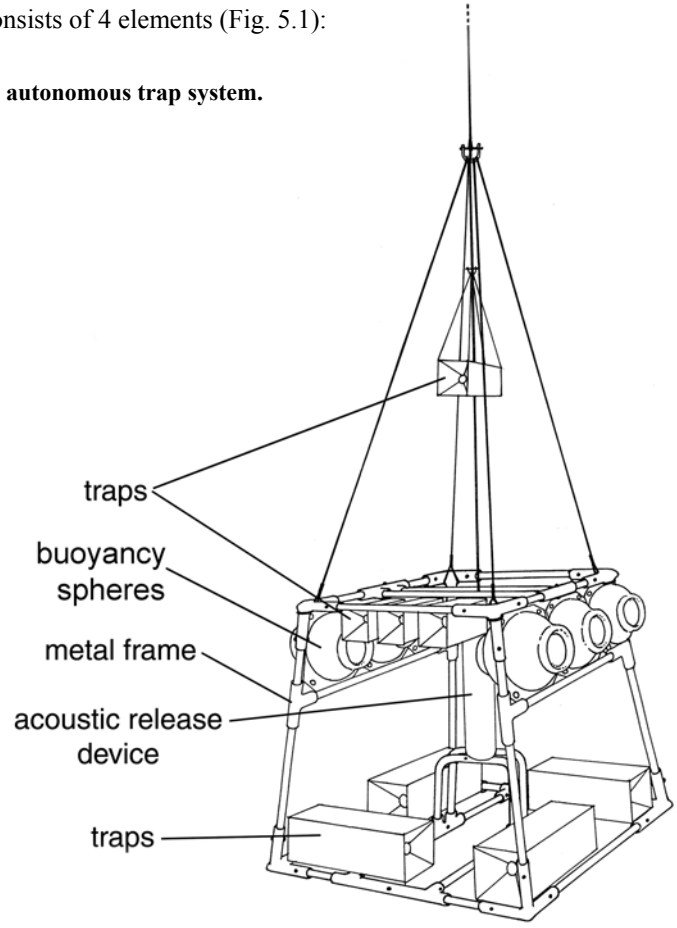
to complement data previously obtained from gut content analyses (Dauby et al. 2001a, b), results of feeding experiments on necrophagous amphipods are presented.

## 5.2. Material and Methods

### 5.2.1. THE AUTONOMOUS TRAP SYSTEM

All scavengers were sampled using an 'autonomous trap system' (ATS), based on the system developed at IFREMER, Brest (Guennegan and Martin 1985). It consists of 4 elements (Fig. 5.1):

**Fig. 5.1. The autonomous trap system.**



1. A brass trapezoidal frame (about 1 $m^3$) on which are fixed various baited traps, either in direct contact with bottom or held one metre above. “Box traps” are metal rectangular frames of different sizes (7 or 22 l), covered with nylon gauze of 500 µm, with two inverse conical openings (diameter: 2 or 4 cm). Their upper side can be opened for rapid retrieval of collected animals.
2. A buoyancy package made of sets of high pressure 10" or 17" glass balls (50 and 260 N buoyancy, respectively) attached directly to the frame and a few metres above it.
3. A deep-sea acoustic release (Ix-Sea Oceano Instruments, Brest, France).
4. Disposable ballast made of iron plate and anchor chains.

Traps were baited (preferably) with notothenioid fish when available, or with other fish or beef meat (from about 200 to 600 g, depending on trap size). Bait was usually wrapped in nets (5 mm mesh) in order to prevent too rapid consumption and so increase the time over which it remained attractive. The system was deployed and retrieved after 1 to 5 days (preferably 48 h) on the bottom (Table 5.1). A low-frequency acoustic signal sent from the ship activated release of the ballast and the ATS was returned to the surface by the buoyancy.

The ATS has provided healthy individuals of necrophagous species that could be reared in aquaria and kept alive for as long as two years.

### 5.2.2. SAMPLING SITES

The material was collected with the ATS during several cruises of the German icebreaker *Polarstern* in the Southern Ocean:

2 operations (using classical line mooring traps) during the EPOS leg 3 cruise, January-February 1989, in the eastern Weddell Sea (De Broyer and Klages,1990);

6 operations during the EASIZ I cruise, January-March 1996, in the eastern Weddell Sea (De Broyer et al. 1997);

15 operations during the EASIZ II cruise, January-March 1998, in the eastern Weddell Sea and off South Shetland Islands (De Broyer et al. 1999). In addition to ATS catches, two samples were collected from a classical fish trap, at stations 152 and 266.

6 operations during the cruises ANDEEP 1 and ANDEEP 2, January-March 2002, in the southern Drake Passage, the western Weddell Sea and the Scotia Sea (De Broyer et al. 2003).

Sampling data are presented in Table 5.1. and sampling locations are shown in Fig. 5. 2.

**Fig.5.2. Location of the 29 trap deployments. Circles and triangles indicate stations lower and deeper than 1000 m, respectively.**

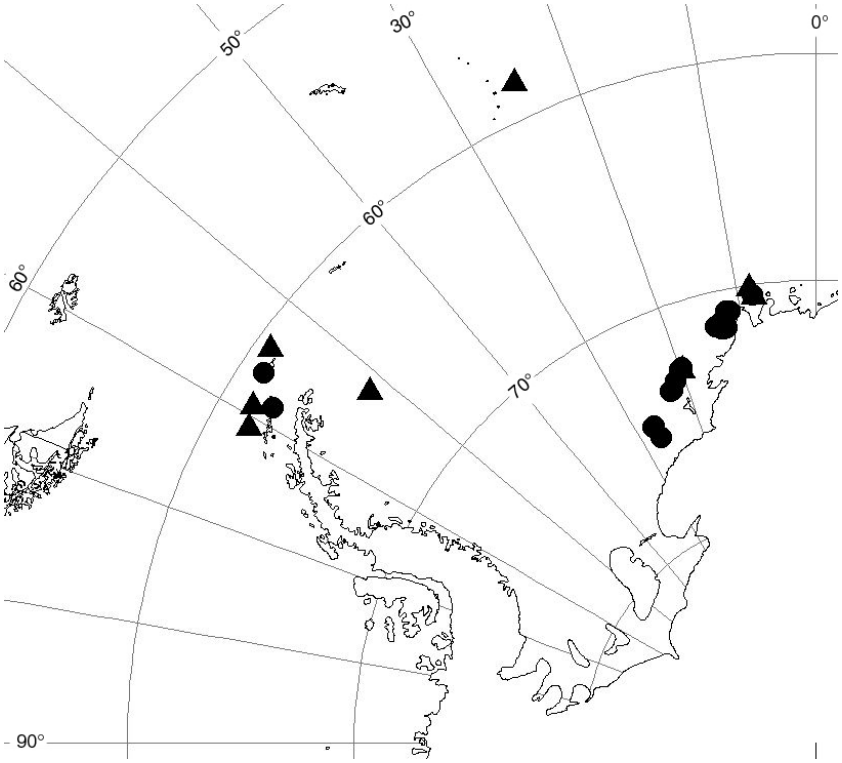


**Table 5.1.**
**Station data for 29 autonomous trap system operations and two fish traps. Italic rows correspond to stations deeper than 1000 m.**

| Cruise | Station | Date | Area | Location | | Depth | Soak Time | Number |
|---|---|---|---|---|---|---|---|---|
| | | | | °S | °W | (m) | (h) | of specimens |
| **EPOS** | 228 (T2) | 28.01.89 | Halley Bay | 75°14.4' | 26°42.1' | 399 | 70 | 3500 |
| | 275 (T4) | 15.02.89 | Kapp Norvegia | 71°39.5' | 12°04.4' | 236 | 50 | |
| **EASIZ I** | 04 (T4) | 20.02.96 | Kapp Norvegia | 71°40.6' | 12°31.0' | 421 | 132 | 2924 |
| | 05 (T1) | 06.02.96 | Kapp Norvegia | 71°40.2' | 12°45.3' | 223 | 23 | 576 |
| | 06 (T2) | 07.02.96 | Kapp Norvegia | 71°31.5' | 13°31.4' | 234 | 74 | 2619 |
| | 12 (T3) | 13.02.96 | Vestkapp | 73°15.7' | 21°04.8' | 791 | 65 | 769 |
| | 28 (T5) | 26.02.96 | Kapp Norvegia | 71°29.6' | 12°21.2' | 219 | 74 | 2848 |
| | *30 (T6)* | *01.03.96* | *Atka Bay* | *70°01.0'* | *08°16.5'* | *2009* | *86* | *818* |
| **EASIZ II** | 11/25 (T1) | 26.01.98 | Drescher Inlet | 72°50.8' | 19°55.5' | 377 | 38 | 25365 |
| | 27/76 (T2) | 28.01.98 | Kapp Norvegia | 71°19.0' | 12°24.2' | 171 | 103 | 10528 |
| | 38/75 (T3) | 29.01.98 | Kapp Norvegia | 70°59.0 | 11°09.1 | 389 | 82 | 765 |
| | 094/119 (T4) | 05.02.98 | Vestkapp | 73°35.7' | 22°23.4' | 813 | 50 | 788 |
| | 102/122 (T5) | 05.02.98 | Vestkapp | 73°36.0' | 22°00.5' | 396 | 46 | 516 |
| | 138/155 (T6) | 09.02.98 | Halley Bay | 74°39.8' | 27°13.1' | 798 | 39 | 3434 |
| | 152 (FT) | 11.02.98 | Halley Bay | 74°36.8' | 26°53.9' | 597 | | |
| | 160/179 (T7) | 11.02.98 | Halley Bay | 74°40.0' | 26°57.9' | 403 | 38 | 4188 |
| | 202/233 (T8) | 18.02.98 | Kapp Norvegia | 70°57.0' | 11°40.6' | 808 | 58 | 401 |

| Cruise | Station | Date | Area | Location | | Depth | Soak Time | Number |
|---|---|---|---|---|---|---|---|---|
| | | | | °S | °W | (m) | (h) | of specimens |
| | 203/234 (T9) | 18.02.98 | Kapp Norvegia | 70°58.8' | 11°39.4' | 442 | 58 | 787 |
| | 251/267 T10) | 22.02.98 | Drescher Inlet | 72°47.8' | 19°31.4' | 895 | 66 | 1820 |
| | *255/268 (T11)* | *23.02.98* | *Drescher Inlet* | *72°48.4'* | *19°39.6'* | *1453* | *58* | *1642* |
| | 266 (FT) | 25.02.98 | Drescher Inlet | 72°50.5' | 19°21.8' | 419 | | |
| | *279/283 (T12)* | *28.02.98* | *Atka Bay* | *70°24.1'* | *07°52.2'* | *1136* | *48* | *75* |
| | 280/284 (T13) | 28.02.98 | Atka Bay | 70°27.4' | 07°55.9' | 550 | 48 | 2085 |
| | 291/312 (T14) | 14.03.98 | King George Isl. | 62°16.6' | 58°15.8' | 798 | 57 | 451 |
| | 292/315 (T15) | 14.03.98 | King George Isl. | 62°11.3' | 58°20.2' | 414 | 58 | |
| **ANDEEP 1** | *46* | *29.01.02* | *Elephant Isl.* | *60°39'* | *53°59'* | *2926* | *14* | *44* |
| | 83 | 07.02.02 | Elephant Isl. | 61°07' | 56°09' | 349 | 72 | 8597 |
| | *100* | *13.02.02* | *King George Isl.* | *61°25'* | *58°54'* | *2280* | *57* | *171* |
| | *114* | *17.02.02* | *King George Isl.* | *61°46'* | *60°45'* | *2754* | *54* | *36* |
| **ANDEEP 2** | *131* | *05.03.02* | *N-W Weddell Sea* | *65°19'* | *51°35'* | *3070* | *71* | *129* |
| | *139* | *19.03.02* | *South Sandwich Trench* | *58°18'* | *24°29'* | *3739* | *71* | *1000* |

### 5.2.3. FEEDING EXPERIMENTS

Directly after collection, animals were transferred to a cool laboratory (maintained at -1 ± 1°C), sorted by species and counted. They were then distributed, by groups of 40 to 150, among different aquaria (15 to 200 l) continuously provided with clean fresh sea water.

Several experiments were performed in order to evaluate the feeding rate of four common scavenging Antarctic amphipod species (all lysianassoids, see Table 6). Animals were starved for periods of 9 to 15 days to maximize foregut clearance (as checked from dissected individuals). During this fast, faeces and exuvia were removed daily. After starvation, weighted (and calibrated for dry *vs* wet weight) food items (pieces of squid or fish) were given *ad lib* every day during experiments lasting 7 to 29 days. Uneaten food was removed after 24 hours, oven-dried and weighed, enabling calculation of mean daily ingestion rates. At the end of last day of experiment, amphipods were sacrificed and oven-dried to obtain their mean invidual weight. Results are expressed as $g_{food\text{-}DW} \cdot g_{animal\text{-}DW}^{-1} \cdot day^{-1}$ x 100 (or $\%.day^{-1}$).

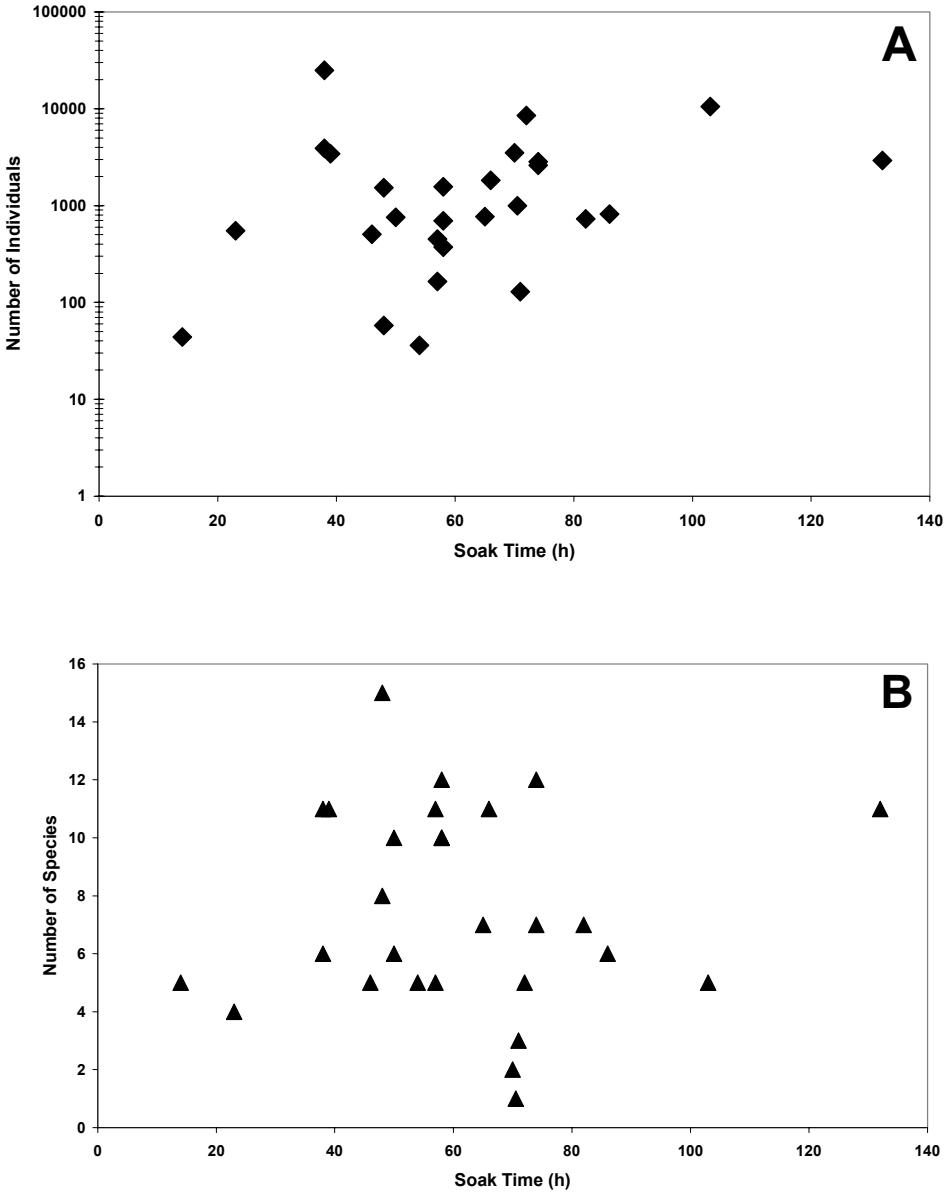
Egestion rates were estimated, in parallel to some feeding experiments, with *Waldeckia obesa* (Chevreux 1905). After a single 24 hour feeding period, a group of animals was placed in nylon gauze baskets (mesh size 2 mm) which allowed faecal pellets to pass through, so to avoid coprophagy. Animals were kept unfed for 5 to 9 days, and faeces were collected twice daily, dried and weighed as above.

## 5.3. Results and discussion

### 5.3.1. SAMPLING METHODOLOGY

The ATS is a sampling device which collects roughly "what is scavenging around", *i.e.* the necrophagous organisms able to detect and track the bait odour and living at a distance corresponding to the food odour plume in the water, itself influenced by the direction and velocity of the local bottom current (Sainte-Marie and Hargrave 1987). Several factors, such as bottom topography and related benthic biological community structure, are likely to affect the number and composition of the fauna attracted to bait. Sample size and composition not only depend on these environmental factors, but also on structural ones related to the trap design (mouth opening, mesh size) and relative position of the trap on or above the sea floor. Finally, bait quality and type may attract preferentially some species. The duration of trap deployment has been reported to influence the number of individuals caught, at least initially, when a positive correlation is found (Stockton 1982). However, in our study there was no relationship between the number of individuals or species and soak time for ATS deployments ranging from about 10 to 135 hours (Fig. 5.3.). Possible causes include escape from traps, bait exhaustion, interspecific predation or cannibalism inside the traps (behaviours we observed in restricted aquarium conditions), tidal effects, or simply the local density of the scavenging fauna. Thus the ATS can be considered at best only a semi-qualitative sampler.

**Fig. 5.3. Numbers of collected individuals (A) and species (B) *vs* soak time of the autonomous trap system.**



## 5.3.2. COMPOSITION OF THE SCAVENGER GUILD

The 31 trap sets reported here captured a total of about 70,000 invertebrates from 76 species and 10 specimens of fish from 4 species (Table 5.2).

**Table 5.2. Comparison between the number of species and individuals of the different taxonomic groups collected by the autonomous trap system and fish traps at shelf and deep-sea depths.**

| | ***ANTARCTIC SHELF*** | ***ANTARCTIC DEEP SEA*** | |
|---|---|---|---|
| | ***(< 1000m)*** | ***(>1000m)*** | |
| | | **EASIZ** | **ANDEEP** |
| | | Eastern Weddell Sea | South Shetland Islands |
| **Campaign** | **EPOS / EASIZ I & II** | South Shetland | Scotia Sea |
| Locality | Eastern Weddell Sea | Islands | South Sandwich Trench |
| Depth range | 171- 895 m | 1139- 2009 m | 2280- 3739 m |
| N trap operations | **20** | **3** | **5** |
| | **N spp (N ind.)** | **N spp (N ind.)** | |
| **CRUSTACEA** | | | |
| ***Amphipoda*** | | | |
| Lysianassoidea | **37 (~ 65 000)** | | **26 (1374)** |
| Iphimedioidea | **2 (4)** | | **2 (2)** |
| Eusiridae | **2 (7)** | | |
| Melphidippidae | **1 (1)** | | |
| Stegocephalidae | | | **2 (3)** |
| ***Isopoda*** | | | |
| Cirolanidae | **3 (1547)** | | **1 (4)** |
| ***Leptostraca*** | **2 (23)** | | |
| ***Ostracoda*** | **2 (1500)** | | |
| ***Copepoda*** | **2(4)** | | **2 (2)** |
| ***Mysidacea*** | **1 (13)** | | |
| ***Decapoda*** | **1(1)** | | |
| **MOLLUSCA** | | | |
| ***Gastropoda*** | | | **1 (1)** |
| **ECHINODERMATA** | | | |
| ***Asteroidea*** | **1(1)** | | |
| ***Ophiuroidea*** | **3(4)** | | |
| **PISCES** | **3 (7)** | | **3 (3)** |

Twenty one trap sets at shelf depths (less than 1000 m) in the eastern Weddell Sea and around South Shetland Islands captured more than 68,000 specimens of crustaceans belonging to 53 benthic and benthopelagic species, 5 specimens of echinoderms and 7 specimens of 3 fish species.

In the deep sea, 8 trap operations on the slope of the eastern Weddell Sea and at bathyal and abyssal depths in the western Weddell Sea, the Scotia Sea and the South Sandwich Trench provided about 1400 crustaceans of 33 species, 1 specimen of a gastropod and 3 specimens of fish.

While the trap samples can be considered representative of the crustacean scavenger fauna, this is not the case for the fish as the traps were suboptimal in terms of size and entrance diameter for collecting them.

Both at shelf depth and in the deep sea (slope and abyssal plain) the bulk of the catches consisted of amphipod crustaceans, in particular lysianassoids. The second dominant group, the cirolanid isopods, was not represented significantly in the deep-sea samples. A few representatives of other amphipod families (Epimeriidae, Iphimediidae, Eusiridae, Melphidippidae, Stegocephalidae) were collected as well as other crustacean groups, namely Leptostraca, Ostracoda, Copepoda, Mysidacea and Decapoda.

The detailed taxonomic composition of the amphipods collected is presented in Tables 5.3. and 5.4. Complete taxonomic references and zoogeographical characterization of the species can be found in De Broyer and Jazdzewski (1993). Within the very diverse superfamily Lysianassoidea, species have been allocated to the different family groups recognized by a recent cladistic analysis (Lowry pers. comm.). On the shelf, a total of 37 lysianassoid species have been collected belonging to 17 different genera. Lysianassoid amphipods are known to comprise a number of scavenger species (e.g. Thurston 1990, Lowry and Stoddart 1989, 1994). Representatives of *Adeliella* and *Allogaussia* were taken in traps for the first time but may be accidental (one unique specimen in each case). Part of the collected species remains to be precisely identified. One new species has been found in each of

the genera *Allogaussia, Paracallisoma*, *Pseudorchomene, Stephonyx* and *Tryphosella*.

**Table 5.3. Amphipod species collected with the autonomous trap system and fish traps at depths shallower than 1000 metres; occurrence by station and depth ranges.**

| | EPOS | EASIZ I | EASIZ II | Depth range |
|---|---|---|---|---|
| **LYSIANASSOIDEA** | | | | |
| **Lysianassidae and Uristidae** | | | | |
| *Abyssorchomene charcoti* (Chevreux, 1912) | | T2 | | 234 |
| *Abyssorchomene nodimanus* (Walker, 1903) | T4 | T2-4-5 | T2-4-13 | 171-813 |
| *Abyssorchomene plebs* (Hurley, 1965) | T2 | | T1-5-7-13-14-15 | 377-798 |
| *Abyssorchomene rossi* (Walker, 1903) | | T4-5 | T1-7-9-13 | 219-550 |
| *Adeliella sp.A* | | | **152** | 597 |
| *Allogaussia n.sp.1* | | [2] | T4 | 813 |
| *Cheirimedon crenatipalmatus* Stebbing, 1888 | | T3 | **152** | 389-597 |
| *Hippomedon sp.A* | | T2-5 | T6-7-8-9-10-13, **152** | 219-895 |
| *Orchomenopsis cavimanus* (Stebbing, 1888) *var.A* | | T4-5 | T1 to 10, 13-14, **152** | 171-895 |
| *Orchomenopsis kryptopinguides* (Andres, 1983) | | | T3 | 389 |
| *Orchomenopsis pinguides* (Walker, 1903) | T4 | T2-5 | T2-7 | 171-403 |
| *Parschisturella carinata* (Schellenberg, 1926) | | T1-2-3-4-5 | T3-4-5-6-8-10, **152** | 219-895 |
| *Pseudorchomene coatsi* (Chilton, 1912) | T4 | T4-5 | T1-10,13-14-15, **266** | 171-895 |
| *Pseudorchomene n.sp.1* | | | T4-6-10 | 798-895 |
| *Stephonyx n.sp.1* | | T3 | T4-6-8-10-13 | 791-895 |
| *Tryphosella cf analogica* K.H. Barnard, 1932 | | T3 | T6-10 | 791-895 |
| *Tryphosella bispinosa* (Schellenberg, 1931) | | T2 | | 234 |
| *Tryphosella intermedia* (Schellenberg, 1926) | | | T6-7-8-9-10, **152** | 403-895 |
| *Tryphosella longiseta* Ren, 1991 | | | T8 | 808 |
| *Tryphosella macropareia* (Schellenberg, 1926) | | T4 | T4-8 | 421-813 |
| *Tryphosella murrayi* (Walker, 1903) | T4 | T1-2-4 | T1-3-7-9-10-13, **266** | 223-895 |
| *Tryphosella n.sp.1* | | | T6 | 798 |
| *Tryphosella sp.A* | | | T4 | 813 |
| *Tryphosella sp.B* | | | T7 | 403 |
| *Tryphosella sp.C* | | | T7 | 403 |

| | EPOS | EASIZ I | EASIZ II | Depth range |
|---|---|---|---|---|
| *Tryphosella sp.D* | | | T9 | 442 |
| *Tryphosella sp.E* | | T2-3 | | 234-791 |
| *Tryphosella sp.F* | | T4 | | 421 |
| *Tryphosella sp.G* | | T4 | | 421 |
| *"Tryphosella" cicadopsis* Schellenberg, 1926 | | | T7-9-13 | 403-550 |
| *"Tryphosella" n.sp.2* | | | T6-13, **152** | 550-798 |
| *Uristes gigas* Dana, 1849 | | | T13, **152** | 550-597 |
| *Uristes stebbingi* (Walker, 1903) | T4 | T2 | T2-4 | 171-813 |
| *Waldeckia obesa* (Chevreux, 1905) | T2-4 | T1-2-3-4-5 | T1, 3 to 10, 13, **152** | 219-895 |
| **Eurytheneid family group** | | | | |
| *Eurythenes gryllus* (Lichtenstein, 1822) | | T3 | T13-14 | 550-798 |
| **Hirondelleid family group** | | | | |
| *Hirondellea antarctica* (Schellenberg, 1926) | | T1-2-3 | T8-13, **152** | 223-808 |
| **Scopelocheiridae** | | | | |
| *Paracallisoma n.sp.1* | | | T14 | 451 |
| **IPHIMEDIOIDEA** | | | | |
| **Epimeriidae** | | | | |
| *Epimeria similis* Chevreux, 1912 | | | T10-13, **152** | 550-895 |
| **Iphimediidae** | | | | |
| *Iphimediella bransfieldi* K.H. Barnard, 1932 | | | **266** | 419 |
| **EUSIROIDEA** | | | | |
| **Eusiridae** | | | | |
| *Eusirus cf antarcticus* Thomson, 1880 | | T2-5 | T3-9, **152** | 219-597 |
| *Eusirus bouvieri* Chevreux, 1911 | | T4 | T7 | 403-421 |
| **Melphidippidae** | | | | |
| *Melphidippa antarctica* Schellenberg, 1926 | | | **152** | 597 |

**Table 5.4. Amphipod species collected with the autonomous trap system and fish traps at depths greater than 1000 metres; occurrence by station and depth ranges.**

| | EASIZ I | EASIZ II | ANDEEP | Depth range |
|---|---|---|---|---|
| **LYSIANASSOIDEA** | | | | |
| **Lysianassidae and Uristidae** | | | | |
| *Abyssorchomene rossi* (Walker, 1903) | | T11 | | 1453 |
| *Abyssorchomene scotianensis* (Andres, 1983) | T6 | T11-12 | 100,114,131 | 1136-3070 |
| *Abyssorchomene sp.A* | | | 114 | 2754 |
| *Hippomedon sp.A* | T6 | | | 2009 |
| *Hippomedon sp.B* | | T11 | | 1453 |
| *Orchomenopsis cavimanus* (Stebbing, 1888) *var.A* | | T11-12 | 100,131 | 1136-3070 |
| *Orchomenopsis n.sp.1* | | | 46 | 2926 |
| *Parschisturella carinata* (Schellenberg, 1926) | | T11-12 | | 1136-1453 |
| *Pseudorchomene coatsi* (Chilton, 1912) | | T11 | 100 | 1453-2280 |
| *Pseudorchomene n.sp.1* | | T11 | | 1453 |
| *Stephonyx n.sp.1* | | T11-12 | | 1136-1453 |
| *Tryphosella cf analogica* K.H. Barnard, 1932 | | T11-12 | | 1136-1453 |
| *Tryphosella sp.C* | | T12 | | 1136 |
| *Tryphosella sp.H* | | | 100 | 2280 |
| *Tryphosella sp.I* | | | 100 | 2280 |
| *Tryphosella sp.J* | | | 100 | 2280 |
| *"Tryphosella" n.sp.2* | | T11 | | 1453 |
| *Tryphosinae gen. sp.A* | | T11 | | 1453 |
| **Alicellid family group** | | | | |
| *Alicella n.sp.1* | | | 100 | 2280 |
| *Paralicella cf caperesca* Shulenberger & Barnard, 1976 | | | 46 | 2926 |
| *Paralicella n.sp.1* | | | 100,114 | 2280-2754 |

| | EASIZ I | EASIZ II | ANDEEP | Depth range |
|---|---|---|---|---|
| **Eurytheneid family group** | | | | |
| *Eurythenes gryllus* (Lichtenstein, 1822) | T6 | T11-12 | 46,100,114, 131,139 | 1453-3739 |
| **Hirondelleid family group** | | | | |
| *Hirondellea antarctica* (Schellenberg, 1926) | | T12 | | 1136 |
| *Hirondellea n.sp.1* | | | 100 | 2280 |
| **Scopelocheridae** | | | | |
| *Paracallisoma n.sp.1* | | | 100 | 2280 |
| *Scopelocheirus sp.A* | | | 46,100,114 | 2280-2926 |
| **IPHIMEDIOIDEA** | | | | |
| **Epimeriidae** | | | | |
| *Gen. sp.A* | | | 46 | 2926 |
| **Iphimediidae** | | | | |
| *Iphimediella sp.A* | T6 | | | 2009 |
| **Stegocephalidae** | | | | |
| *Gen.sp.C* | T6 | | | 2009 |
| *Gen.sp.D* | T6 | | | 2009 |

In the deep sea, 26 lysianassoid species from 15 genera were found, with one new species in each of the following genera: *Alicella, Hirondellea, Orchomenopsis, Paralicella* and *"Tryphosella"* in addition to the 4 new species occuring also in the shelf zone.

Single species of Epimeriidae and Iphimediidae have been found in each depth zone. There is no previous record of Epimeriidae in baited traps except for *Epimeria cf cornigera* (Jones et al. 2003) and *Epimeria similis* (Dauby et al. 2001a). Stomach content analysis of the latter species by the same authors revealed the presence of various food items such as cnidocysts of hydrozoans and actiniids, sponge spicules, polychaete setae and planktonic cells (diatoms and foraminifers) but also of pieces of fish flesh in individuals captured in traps. Iphimediidae have never been taken in baited traps and their trophic ecology generally characterises them as being specialist micropredators (Coleman 1989a, 1989b, Dauby et al. 2001a). They were probably caught accidentally in traps.

Few Eusiridae are regular scavengers (e.g. Chevreux 1935, Vader 1972, Bowman 1974). Some *Eusirus* species have been recorded in traps in Admiralty Bay, King George Island (De Broyer unpubl.) and on the shelf off Enderby Land (Takeuchi et al. 2001). Examination of feeding behaviour and stomach contents showed that *E.* cf *antarcticus,* for instance, is a selective macropredator able to feed partially on carrion (Dauby et al. 2001a).

*Melphidippa antarctica* is a passive suspension feeder (Dauby et al. 2001a) and the unique specimen was quite probably collected accidentally in trap.

Stegocephalidae are mostly micropredators associated with diverse benthic sessile invertebrates, while some species have been reported to be occasional scavengers (Berge and Vader 2003). They are, however, not taken commonly in traps except for some species of *Andaniotes* and *Austrocephaloides* (Berge and Vader 2001, Berge *pers. comm.*). Takeuchi et al. (2001) found *Parandania boecki* (Stebbing 1888) and *Euandania gigantea* (Stebbing 1883) in their abyssal trap off Enderby Land. Both species are meso- or

bathypelagic and rarely if ever taken in baited traps. Some specimens of *Euandania* were also found by Thurston (*pers. comm*.) in bathyal and abyssal trap catches in the Atlantic Ocean.

Species diversity is high in the scavenger guild on the Antarctic shelf (eastern Weddell Sea), in particular in crustaceans, i.e. in comparison with catches at shallower depths, such as those reported by Presler (1986) in the sublittoral of King George Island, who found 5 species of amphipods and 2 of isopods. Nemerteans, gastropods, and echinoderms (asteroids, ophiuroids, echinoids and holothuroids) occur frequently in traps at depths of less than 100 m (*e.g.* Arnaud 1970, Presler 1986, De Broyer *unpubl*.). These groups were not represented in our catches at shelf, slope or abyssal depths except for five specimens of echinoderms and a single gastropod respectively found on the Weddell Sea shelf and slope.

The higher species richness seems also to hold true when eastern Weddell Sea shelf data are compared with other Antarctic catches at similar depths (e.g. Arnaud 1970, Stockton 1982, Nagata 1986, Takeuchi et al. 2001). Arnaud (1970), for instance, found only a few tens of amphipods of two species (*Abyssorchomene plebs* and *A. rossi*), one specimen of two species of pycnogonid and of one species of fish at a depth of 320 m off Terre Adélie. Stockton (1982) recorded five species of amphipods (among which four lysianassoids) and one mysid under the Ross Ice Shelf, while Nagata (1986) collected only four species of lysianassoids near Syowa Station (Lützow-Holm Bay, East Antarctica). Takeuchi et al. (2001) found 7 species of amphipods (6 lysianassoids, 1 eusirid), 2 of isopods (Cirolanidae, Gnathiidae), 1 mysid, 3 ostracods, 1 copepod, 1 leptostracan and 2 species of nototheniid fish in two trapsets on the shelf (171 and 353 m) off Enderby Land. The general composition of the scavenger fauna thus appears quite similar between the eastern Weddell Sea and Enderby Land but more amphipods have been recorded in the former, which may at least partly be due to the larger number of trapsets analysed from the Weddell Sea (18 *vs* 2).

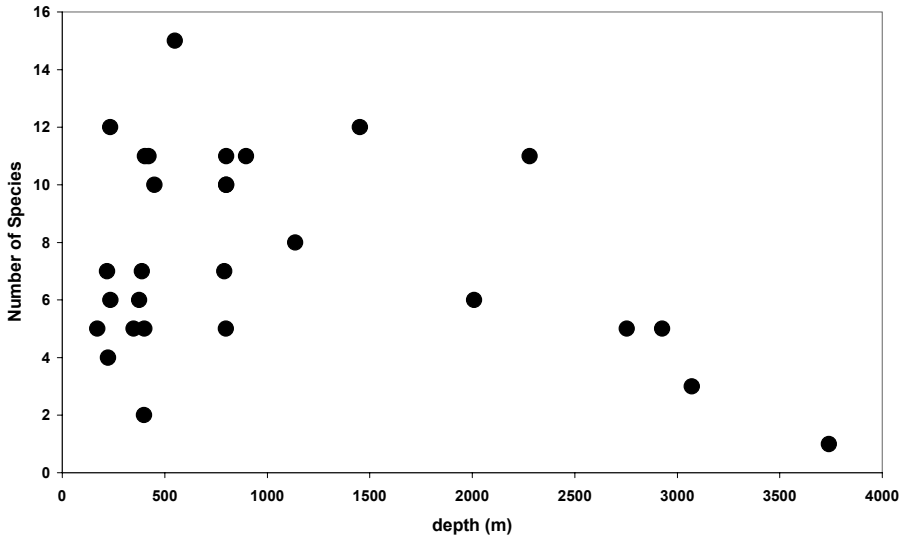
In the Antarctic abyssal waters (3000 m or deeper) the species richness of the scavenger guild appears to be less than documented from abyssal trap collections elsewhere in the world. The three ANDEEP trapsets close to or deeper than 3000 m provided only 5 species of necrophagous amphipods (Table 4) and Takeuchi et al. (2001) reported 5 amphipod and 1 isopod species. In comparison, the 44 trap-sets at 3144-5940 m in the northeastern and tropical Atlantic Ocean analysed by Thurston (1990) yielded 15 different species (13 lysianassids, 1 scopelocheirid, 1 valettiettid), which constitute the largest abyssal trap record. Thurston's record, however, concerned several distinct abyssal plains and a much wider bathymetric range, prospected with many more trap-sets.

On the other hand, the Antarctic slope (1000-3000 m) appears to be richer in scavenger species than elsewhere in the world at similar depth range. Thirty one amphipod species have been collected (18 in the eastern Weddell Sea) versus e.g. 6 amphipods species (all lysianassoids) on the Gulf of Biscay slope (200-1800 m depth; Desbruyères et al., 1985), 11 amphipod species (9 lysianassoids, 1 eusirid, 1 tironid) found in baited traps by Vinogradov (1997) on the slope of the Norwegian Sea (1690 m) or 5 amphipod species (4 lysianassoids, 1 epimeriid) collected by traps in the deep Cretan Sea (1511-2485 m depth; Jones et al. 2003).

It must be kept in mind in such comparisons that trap sampling is by no means quantitative, as remarked above, and that repeated sampling may yield more species.

The relation between species richness of necrophagous amphipods and depth is shown in Fig. 5.4. This figure clearly shows the variability of amphipod richness in coastal and shelf traps and its reduction from the shelf down-slope to the abyssal zone.

**Fig. 5.4. Relation between species richness of necrophagous amphipods and depth.**




A number of species occurred on both the shelf and the slope showing in some cases a quite extended level of bathymetry: *Abyssorchomene rossi* (219-1453 m), *Eurythenes gryllus* (550-3789 m), *Hippomedon* sp.A (389-2009 m), *Hirondellea antarctica* (223-1136 m), *Orchomenopsis cavimanus* var.A (171-3070 m), *Paracallisoma* n.sp.1 (451-2280 m), *Parschisturella carinata* (219-1453 m), *Pseudorchomene coatsi* (171-2280 m), *Pseudorchomene* n.sp.1 (798-1453 m), *Stephonyx* n.sp.1 (791-1453 m), *Tryphosella* cf *analogica* (791-1453 m), *Tryphosella* sp.C (403-1136 m), *"Tryphosella"* n.sp.2 (550-1453 m). In the Southern Ocean, *E. gryllus* is the only scavenger species found on the shelf, the slope and in the abyssal zone (see also Takeuchi et al. 2001). The latter species is a panoceanic bathyal (on seamounts, as shallow as 1440 m, Bucklin et al. 1987), abyssal and hadal stenotherm species which can occur far above the sea floor (Thurston 1990). It has been found in both polar regions at bathyal and abyssal depths (*e.g.*

Bowman and Manning 1972, Paul 1973, Hargrave et al. 1992, De Broyer et al. 1999) and in bird stomachs (see Rauschert 1985).

Arnaud (1970) observed some seasonality in the presence or abundance of several scavengers in the Terre Adélie catches (16 to 120 m): *Waldeckia obesa* was much more abundant in traps in winter than in summer and this could indicate a seasonal shift in diet or a migration. *W. obesa* was abundant in the Weddell Sea at shelf depths (171-895 m) during summer, suggesting migration or local movement as a most like cause (see Bregazzi 1972, Slattery and Oliver 1986).

### 5.3.3. MORPHOLOGICAL ADAPTATIONS TO NECROPHAGY

Morphological analysis of the amphipod species collected in traps (Tables 5.3. and 5.4.) has shown several types and degrees of adaptation to a necrophagous mode of life, thus confirming previous observations and interpretations (Dahl 1979, Thurston 1979, De Broyer 1983). The typical eco-functional adaptations to necrophagy are summarized briefly in Table 5.5. No attempt is made here to document detailed differences in chemosensory organs (in particular callynophores, see Lowry 1986, Meador 1981) or mechanoreceptors (Klages et al. 2002). The focus is on the morphology of the mandible and the digestive tract.

**Table 5.5. Morphological and physiological adaptations of scavenging amphipods with respect to behavioural constraints.**

| ***Typical behavioural sequence of scavengers*** | ***Morphological and physiological adaptations*** |
|---|---|
| Detecting and locating carrion source | Chemosensory organs (callynophores) |
| | Mechanoreception organs |
| Arriving (quickly) to carrion | Good swimming ability |
| Ingesting (quickly) | Cutting mandible |
| Storing food | Enlarged foregut or midgut |

| ***Typical behavioural sequence of scavengers*** | ***Morphological and physiological adaptations*** |
|---|---|
| Feeding opportunities | |
| Unpredictable | Resistance to starvation |
| | Reduced metabolism |

Mandible morphology appears of primary importance in amphipod evolution in general and in the scavenger feeding types in particular (Dahl 1979, De Broyer 1985b, Barnard and Karaman 1991, Watling 1993). The evolutionary trend toward necrophagy is marked by several transformations of the mandible from the relatively basic type found in the opportunistic scavengers *Orchomenopsis (e.g. O. obtusa*; see Olerod, 1975) or *Abyssorchomene* to the types found in the deep sea species that are obligate scavengers *Eurythenes, Hirondellea* and *Paralicella* (Dahl 1979, Thurston 1979, De Broyer 1983). The following morphological transformations are considered adaptations to necrophagy:

- widening and sharpening of the incisor cutting edge;
- modification of the molar process from a relatively basic subcolumnar type with oval triturative surface (*Orchomenopsis;* see Olerod 1975, Fig. 62 & 63) to the ridge-shaped type with elongate and reduced triturative surface (*Abyssorchomene;* see Dahl 1979, Fig. 9), and ultimately to the non triturative semitubular or "flap-like" setiferous molar found in *Hirondellea* or *Eurythenes* respectively (see Dahl 1979, Fig. 5 & 6);
- transformation of the flat mandibular body found in *Orchomenopsis* to the strongly bowl-shaped type found in *Eurythenes* or in *Alicella* (see De Broyer and Thurston 1987). Together with the development of the raker spine row and the setal row prolonging the molar, and the widening of the incisor, this adaptation allows relatively large fragments or ships of food to be passed directly into the oesophagus (Thurston 1979, De Broyer and Thurston 1987). In common with the present deep sea material, all the abyssal scavenger species recorded by Thurston (1990) with the exception of *Valettietta gracilis*

have a mandibular molar considerably modified from the basic gammaridean pattern.

Another important adaptation to necrophagy is the development of the storage capacity of either the foregut, *e.g.* in *Abyssorchomene* or the midgut in *Eurythenes, Hirondellea* or *Paralicella* (Dahl 1979, De Broyer 1983). The "storing stomodeum" extending along the whole length of the pereion has been found in most lysianassid and uristid species we collected from shelf and deep-sea traps: *Abyssorchomene, Hippomedon, Parschisturella, Pseudorchomene, Tryphosella, Uristes* and *Waldeckia.* In *Orchomenella* (*Orchomenopsis)* it extends to the fourth pereionite.

Because several steps can be detected along the evolutionary pathway to the necrophagous mode of life in amphipods, it seems obvious from the morphological comparison of the different scavenger groups (in particular: eurytheneids, hirondelleids, alicellids, scopelocheiridae) that these adaptations arose independently several times during the evolution within the Lysianassoidea.

Previous studies have shown that baited traps attracted facultative, opportunistic scavengers as well as (presumed) obligate scavengers (*e.g.* Arnaud 1970, Britton & Morton 1994, Dauby et al. 2001a). The distinction between the two categories on the basis of morphological traits is by no means straightforward in amphipods. Mandible and gut morphology can help indicate scavenger status, but only within certain limitations. Eurytheneids, alicellids, some Lysianassidae such as *Waldeckia obesa* are considered to be exclusive scavengers. Within the genus *Hirondellea*, for instance, which has a typical advanced scavenger-type mandible, deep-sea species probably are exclusive scavengers (Hessler et al. 1978). However, the shelf species *H. antarctica* is collected regularly in traps but is supposed to be mainly a micropredator on hydrozoans and sea anemones (Dauby et al. 2001a). *Abyssorchomene plebs* is frequently taken and sometimes is extremely abundant in bottom traps (*e.g.* Rakusa-Suszczewski 1982, De Broyer and

Klages 1990). This species, as well as the less common *A. rossi*, are typical benthopelagic species that are also able to prey on copepods, salps and coelenterates in the water column (Dauby et al. 2001a). These *Abyssorchomene* species can feed on phytoplankton and microzooplankton organisms (Hopkins 1985, 1987) presumably aggregated prior to ingestion (see Riebesell et al. 1991) as these species have no filtering appendages.

Stomach content studies of animals from trap collections, as well as fatty acid and stable isotope analyses (Graeve et al. 2001, Nyssen et al. 2002), have revealed that the opportunistic scavengers may be primarily predators (*e.g. Eusirus antarcticus, E. bouvieri, Hirondellea antarctica, Tryphosella murrayi)* or mainly deposit feeders (*e.g. Uristes gigas*).

### 5.3.4. BATHYMETRIC DISTRIBUTION

The bathymetric distribution of amphipods collected in traps in the eastern Weddell Sea is given in Fig. 5.5 (next page). The chart is not representative of the complete bathymetric distribution of these species as it does not include depth records from other gears.

In terms of bathymetric distribution, the trap results (Fig. 5.5, next page) may indicate a faunal break for scavenger amphipods at a depth of about 800 to 1000 m in the eastern Weddell Sea that may be related to the shelf break depth. The same faunal limit is suggested by the scavenger isopod distribution (Fig. 5.6).

**Fig. 5.6. Bathymetric distribution of cirolanid isopods collected with the autonomous trap system in the eastern Weddell Sea.**

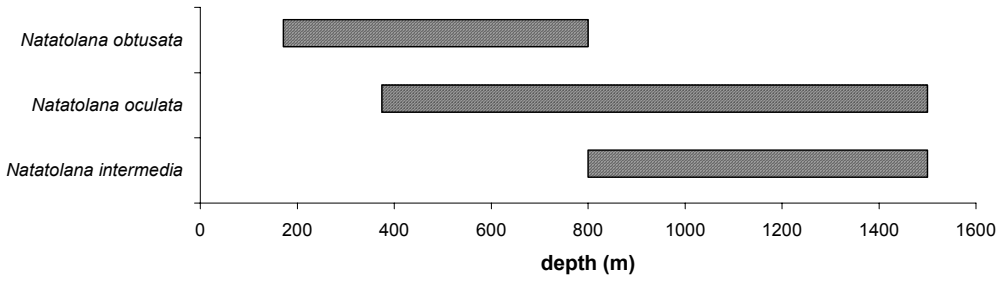
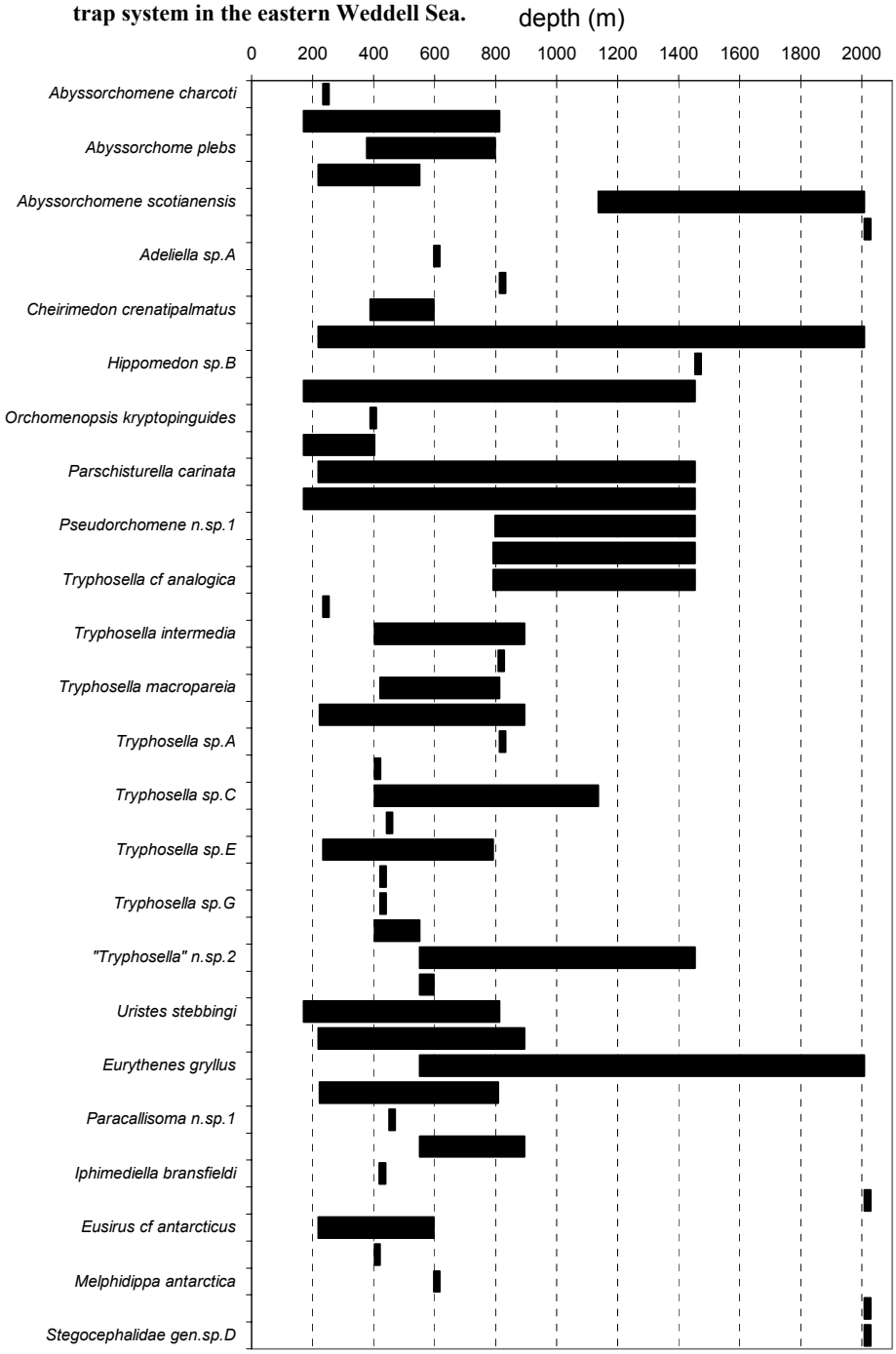


**Fig. 5.5. Bathymetric distribution of amphipods collected with the autonomous trap system in the eastern Weddell Sea.**



### 5.3.5. FEEDING EXPERIMENTS

Table 5.6 gives the mean (and range) of the average feeding rates (in % dry weight.day$^{-1}$) measured during several experiments for the 4 studied species of Lysianassoidea. The egestion rate and digestion efficiency (both in % of ingested food) are given for *Waldeckia obesa*. Available data for other Lysianassoidea are also reported.

**Table 5.6. Estimated and reported feeding rates of scavenging lysianassoid amphipods. F: given food, N: number of experiments, FR: feeding rate (%body dry weight.day-1), MS: meal size (% body weight), ER: egestion rate (% food.day-1), DE: digestion efficiency (% food)**

| species | F | N | FR | MS | ER | DE | reference |
|---|---|---|---|---|---|---|---|
| *Abyssorchomene nodimanus* | squid | 5 | 4.1 (2.5 – 5.1) | | | | *this study* |
| *Parschisturella carinata* | squid | 5 | 1.9 (1.3 – 2.7) | | | | ″ ″ |
| *Tryphosella murayi* | fish | 8 | 2.1 (0.4 – 4.5) | | | | ″ ″ |
| | squid | 14 | 1.4 (0.9 – 4.5) | | | | ″ ″ |
| *Waldeckia obesa* | fish | 3 | 3.1 (2.6 – 10.4) | | 33 | 67 | ″ ″ |
| | squid | 10 | 2.2 (1.0 – 7.7) | | | | ″ ″ |
| *Eurythenes gryllus* | fish | | | 30 – 60 | | | Hargrave, 1985 |
| | fish | | | up to 150 | | | Meador, 1981 |
| *Anonyx sarsi* | squid | | | 10 – 37 | | | Sainte-Marie, 1987 |
| *Anonyx* sp. | squid | | | 10 – 18 | | | Sainte-Marie et al., 1989 |
| *Orchomenella pinguis* | squid | | | 11 – 33 | | | Sainte-Marie et al., 1989 |
| *Onisimus litoralis* | squid | | | 9 – 11 | | | Sainte-Marie et al., 1989 |
| *Alicella gigantea* | fish | | | 12 | | | De Broyer and Thurston, 1987 |

It appears that feeding rates (averaged for each single experiment) encompass relatively large variations, ranging from 0.4 to 10.4 %.day$^{-1}$. These variations could be explained partly by the differences in the duration of the experiments (from 7 to 29 days, see Fig. 8), and by the fact that the number of experiments differed from species to species. The mean rate (averaged over all the different experiments), however, was not very different among the four species. The type of food given (squid *vs* fish) influences this rate but the difference is not statistically significant. However, it has been shown (Moore 1994) that *Orchomenopsis zschaui* digested soft tissues far more rapidly than epidermal material.

**Fig. 5.7. Day-to-day variations of the mean feeding rate (in % dry weight.day$^{-1}$) of the scavenging lysianassid *Abyssorchomene nodimanus* (group of 50 individuals) during an aquarium experiment. Day 1 is the day following the starvation period.**

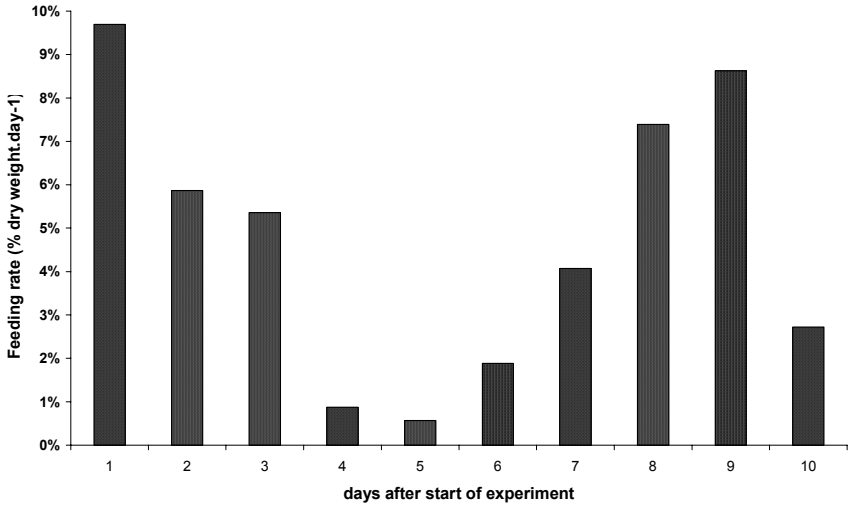
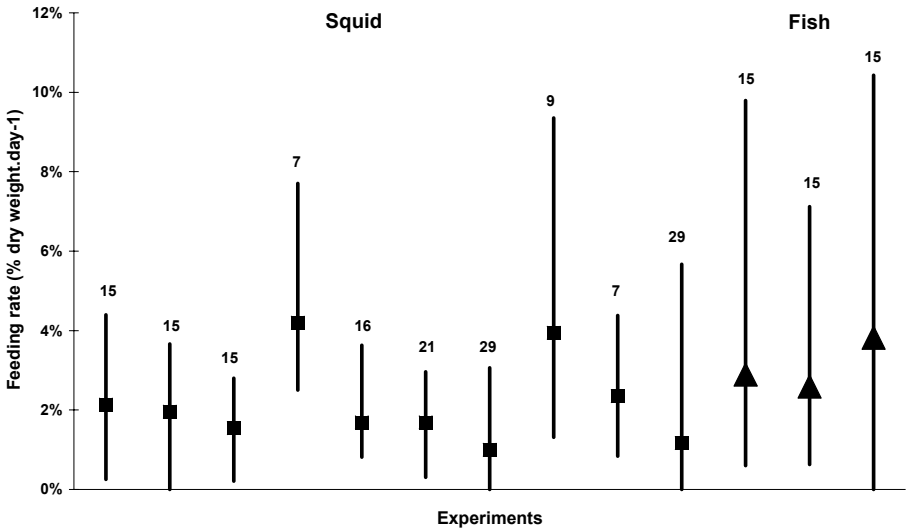


**Fig. 5.8. Between experiment variations of the feeding rate (in % dry weight.day$^{-1}$) of a scavenging lysianassid (*Waldeckia obesa*). Lines show the range of the day-to-day variations; symbols show the mean values (square: fed with squid; triangles: fed with fish). Numbers above the lines give the durations (in days) of experiments.**




It is difficult to compare our estimates with literature data, as the latter are expressed in a different way, usually refering to meal size (*vs* body mass) often inferred from *in situ* camera observations (*e.g.* Hargrave 1985). This kind of estimate is made by offering scavengers a large quantity of bait and evaluating the ingested mass over short periods of time. It does not take into account eventual periods of lower feeding activity, such as we observed in aquaria (see below), and is thus a measure of instantaneous ingestion capacity rather than an estimate of feeding rate over longer periods. This may explain the differences between the two sets of values.

The feeding rate of a group of individuals from a given species varied strongly from day to day (Fig. 5.7). Following starvation, lysianassids feed initially at a high rate (up to 15%.day$^{-1}$ for some species) but afterwards, this

rate decreases gradually over a period of 4 to 8 days, depending on species. A subsequent increase rate is observed, followed again by a decrease. This kind of rhythm, alternating between periods of intense feeding activity and periods of quasi fasting, may be related to the time needed for digesting part of the ingested food or at least for clearance of the foregut. This behaviour could also suggest that tested scavenging amphipods are "topping up" whenever food is available, which would be consistent with a low level of dependency on necrophagy and a plug-flow feeding/digestion strategy (see Penry and Jumars 1987). At the opposite, the gluttonous feeding reported for *e.g. Eurythenes* or *Anonyx* in the literature (Table 5.6) is consistent with a high level of dependency on necrophagy and a batch feeding/digestion strategy. It must be pointed out, however, that on the basis of digestive tract observations (Dauby et al. 2001a) species such as *Abyssorchomene nodimanus, Parschisturella carinata* or *Waldeckia obesa* have been reported to be obligate –or at least preferential– necrophages.

On the other hand, feeding rates can vary by a factor of 4 to 5 among different experiments on the same species (Fig. 5.8). A huge food intake of bait may occur in the trap (see Table 5.6, meal size), that might be responsible for satiation of some collected animals and for a low feeding rate in aquarium experiments, even after a week-long starvation period. Animals maintained in aquaria can survive unfed for months (Chapelle et al. 1994).

The mean feeding rates, based on our experiments, vary between 1 and 5 % dry weight.day$^{-1}$, regardless of species. Very few data on digestion and assimilation rates of scavenging lysianassoid amphipods exist in the literature. Sainte-Marie (1992), assuming complete assimilation of the food bolus, calculated that for *E. gryllus* between 8.3 and 17.8 days would be required for complete digestion and assimilation of one meal. Hargrave et al. (1995) estimated from exponential curves fitted to decreases in gut contents of the same species, that digestion would be 95% complete within 15-46 h in the Canada Basin, and within 99-255 h in the Nares and Sohm Abyssal Plain.

Comparing the organic matter in bait and in well-digested gut contents, they estimated a digestion efficiency of 85%, which is not very different from the value we obtained for *W. obesa*, *i.e.* 67%, using another method. Rapid digestion, associated with liquefaction of food, would enable amphipods to regain mobility as soon as possible after feeding, which is advantageous for these opportunistic feeders in food-poor environments (McKillup and McKillup 1994, Hargrave et al. 1995).

Considering the numerous and diverse benthic fauna recorded on the Antarctic shelf (see Gutt *et al*. 2000) it appears that relatively few species, mostly lysianassoid amphipods, are attracted to baited traps. Similar observations were made in the high Arctic (Legezynska et al. 2000). Some species may occur in huge numbers (*e.g.* Slattery and Oliver 1986, who claimed 264,000 *Abyssorchomene plebs* in a single trap) indicative either of high local densities that are difficult to precisely evaluate, or of low chemosensory thresholds and high mobility allowing some species to congregate from large areas of bottom. The apparently significant role of the scavenger guild in the rapid dispersal of organic matter over the Antarctic shelf and deep-sea bottoms remains to be quantified more precisely.

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# CHAPTER 6: AMPHIPODS AS FOOD SOURCES FOR HIGHER TROPHIC LEVELS IN THE SOUTHERN OCEAN: A SYNTHESIS

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After Dauby P, Nyssen F, De Broyer C (2003) In: Huiskes AHL, Gieskes WWC, Rozema J, Schorno RML, van der Vies SM, Wolff WJ (eds) Antarctic Biology in a Global Context. Backhuys Publ, Leiden, p 129-134

# ABSTRACT

With more than 820 different species, among which about 75% endemics, the amphipod crustaceans form one of the richest animal group of the Southern Ocean. They have colonized most habitats and exhibit very diverse life styles and trophic types. They moreover show a broad size spectrum, with numerous giant species. Despite their importance in terms of biodiversity, very few is known about the role of amphipods in Antarctic trophodynamics. Based on an exhaustive literature survey (more than 300 references), we tried to delineate their importance as potential food for higher trophic levels. About 200 different predators were recorded: 33 invertebrates (from 12 orders), 101 fishes (19 families), 48 birds (11 families) and 10 mammals. Using this vast dataset (total amount of citations close to 1500) and published values about predators' standing stocks and feeding rates, an attempt was made to build up a small model, distinguishing between benthic and pelagic species of both amphipods and predators. The total amount of consumed amphipods was estimated to 60 millions of tons per year for the whole Southern Ocean, *i.e.* the second animal group in importance after euphausiids.

# 6.1. INTRODUCTION

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 molluscs and polychaetes, and the predominance of crustaceans. Among the latter, amphipods form obviously the richest group with more than 820 species recorded in the Antarctic and Subantarctic regions (De Broyer & Jazdzewski 1993, 1996). These peracarids have colonised 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 specialised modes like micro-predatory browsing on invertebrate colonies (Dauby et al. 2001a; Nyssen et al. 2002).

The important faunal diversity of amphipod taxocoenoses is likely to indicate a worthwhile significance of these crustaceans in total benthic or pelagic biomasses, and thus their major role in the trophodynamics of Antarctic ecosystems, as well as consumers than as preys. Total biomass data, and *a fortiori* relative data on amphipods are more than scarce, only available for some restricted areas like the eastern Weddell Sea shelf where amphipods should count for about 5% of the benthic biomass (Gerdes et al. 1992). In the same area, their impact as predators on benthic material has been arbitrarily estimated by Jarre-Teichmann et al. (1997) who supposed they feed for about 80% on detritus. This view was recently revised by Dauby et al. (2001b) who showed, from an extensive study of stomach contents of the most representative species, that their diet was far more complex, planktonic bodies and crustaceans forming the major part of it.

On another hand, the importance of amphipods, either benthic or pelagic, for Southern Ocean higher trophic levels has never been analysed in a global context. If numerous papers have been published on the diet composition of Antarctic top predators (some of which preying on amphipods to a more or

less large extent) very few (Duarte & Moreno 1981, Jazdzewski 1981, Jazdzewski & Konopacka 1999) took the "prey point of view" into account, i.e. the actual role of these crustaceans as food source. The present paper is the first attempt to summarize the available information about Amphipoda as preys. It is based on an exhaustive dataset collected from about 310 published articles wherein amphipods are mentioned to be included in the diet of Antarctic invertebrates, fishes, seabirds or marine mammals.

## 6.2. RESULTS & DISCUSSION

The bibliographic investigation covers a period running from 1905 till present and concerns the whole Southern Ocean *sensu lato i.e.* including the Sub-Antarctic islands (south of the Sub-Tropical Convergence) but excluding the Magellanic Region. All the collected papers cannot be used in the same way as the included information is not comparable. Old documents were purely qualitative but may be worthy as some amphipod species (such as *e.g. Waldeckia obesa*, Chevreux 1905) were first described from Antarctic fish stomach analyses. Papers since about the fifties were more informative as they contained data about the partition of the different faunal groups in the predator diet, usually as frequency of occurrence (O). More recently appeared more useful articles wherein prey breakdown was expressed in terms of number of items (N), volume (V) or mass (M) fractions. In the last years, finally, papers were published going into more details about prey species identification and their mass repartition in the predator diets. Owing to the editorial policy of the present volume, the set of 310 references will not be listed hereafter.

An amount of about 1500 "records" were registered in the whole dataset. A "record" is defined as the occurrence, in a reference, of a pair [predator species – amphipod species (or family, or sub-order, depending on how precisely preys were determined)]. Several records (up to 60 in *e.g.* Olaso et al. 2000) can thus be found in the same paper.

A total of 176 amphipod species were listed in top predator stomach contents, *i.e.* more than 20% of the species known for this area. The best represented (super-) families are: lysianassoids, eusirids and epimeriids for gammarideans, and hyperiids and vibiliids for hyperideans (Table 6.1). Curiously, some families well represented in the Antarctic Ocean, like iphimediids, are not commonly found, maybe because of their particular

spinose morphology which should protect them from a heavy predation (Brandt 2000).

**Table 6.1: Numbers of species in the different families of Gammaridea, Caprellidea and Hyperiidea found in the digestive tract of the Southern Ocean amphipod predators, and corresponding 'records' (see text) in the literature. (+n.d.) indicates non-determined species.**

| FAMILY | n species | n records |
|---|---|---|
| Ampeliscidae | 5 (+n.d.) | 11 |
| Amphilochidae | 1 | 1 |
| *Ceradocus* group | 1 (+n.d.) | 6 |
| Colomastigidae | 1 | 1 |
| Corophiidae | 2 (+n.d.) | 6 |
| Dexaminidae | 2 | 10 |
| Eophliantidae | 0 (+n.d.) | 2 |
| Epimeriidae | 8 (+n.d.) | 32 |
| Eusiridae | 36 (+n.d.) | 179 |
| Gammarellidae | 4 (+n.d.) | 16 |
| Hyalidae | 2 (+n.d.) | 7 |
| Iphimediidae | 2 (+n.d.) | 10 |
| Ischyroceridae | 4 (+n.d.) | 18 |
| Leucothoidae | 1 (+n.d.) | 5 |
| Liljeborgiidae | 2 (+n.d.) | 10 |
| Lysianassoidea | 29 (+n.d.) | 200 |
| Melphidipiidae | 1 | 1 |
| Oedicerotidae | 3 (+n.d.) | 12 |
| Pardaliscidae | 1 | 1 |
| Phoxocephalidae | 3 (+n.d.) | 15 |
| Podoceridae | 1 (+n.d.) | 4 |
| Sebidae | 1 | 1 |
| Stenothoidae | 5 (+n.d.) | 17 |
| Synopiidae | 2 (+n.d.) | 8 |
| *undetermined* | | 155 |
| **Total GAMMARIDEA** | | **728** |
| Phtisicidae | 1 (+n.d.) | 4 |
| *undetermined* | | 10 |
| **Total CAPRELLIDEA** | | **14** |
| Brachyscelidae | 1 | 1 |
| Hyperiidae | 13 (+n.d.) | 315 |
| Lanceolidae | 1 (+n.d.) | 2 |
| Phrosinidae | 2 (+n.d.) | 28 |
| Phronimidae | 1 (+n.d.) | 5 |
| Platyscelidae | 1 | 1 |
| Proscinidae | 0 (+n.d.) | 2 |
| Scinidae | 1 (+n.d.) | 1 |
| Vibiliidae | 6 (+n.d.) | 102 |
| *undetermined* | | 62 |
| **Total HYPERIIDEA** | | **519** |

Concurrently, 192 different predators were identified belonging to various zoological groups (Table 6.2). The most numerous records concern fishes

(101 species from 19 families, especially from the notothenioid ones) and seabirds (48 species from 12 families, mainly procellariids and penguins).

**Table 6.2: Numbers of species of amphipod predators in the different taxa (from classes to families, depending on groups), and corresponding 'records' (see text) in the literature.**

| | | n species | n records |
|---|---|---|---|
| ANNELIDA | Polychaeta | 2 | 10 |
| MOLLUSCA | Cephalopoda | 6 | 9 |
| CRUSTACEA | Amphipoda | 5 | 8 |
| | Decapoda | 2 | 2 |
| | Isopoda | 4 | 6 |
| | Mysidacea | 1 | 1 |
| ECHINODERMATA | Asteroidea | 3 | 6 |
| | Echinoidea | 2 | 7 |
| | Holothuroidea | 4 | 4 |
| | Ophiuroidea | 4 | 13 |
| CHAETOGNATHA | | 1 | 1 |
| TUNICATA | Thaliacea | | 1 |
| PISCES (101) | Achiropsettidae | 1 | 1 |
| | Artetidraconidae | 14 | 124 |
| | Bathydraconidae | 10 | 43 |
| | Bathylagidae | 1 | 1 |
| | Bovichthyidae | 1 | 1 |
| | Centrolophidae | 1 | 1 |
| | Channichthyidae | 7 | 35 |
| | Congiopodidae | 1 | 6 |
| | Cyclopteridae | 4 | 5 |
| | Gadidae | 2 | 3 |
| | Harpagiferidae | 3 | 38 |
| | Macrouridae | 2 | 2 |
| | Muraenolepidae | 2 | 9 |
| | Myctophidae | 11 | 57 |
| | Notacanthidae | 1 | 1 |
| | Nototheniidae | 33 | 450 |
| | Rajidae | 4 | 7 |
| | Scombridae | 1 | 6 |
| | Zoarcidae | 2 | 8 |
| AVES (48) | Anatidae | 2 | 5 |
| | Chionididae | 2 | 3 |
| | Diomedeidae | 4 | 30 |
| | Laridae | 5 | 33 |
| | Muscicapidae | 1 | 1 |
| | Oceanitidae | 2 | 15 |
| | Pelecanoididae | 2 | 30 |
| | Phalacrocoracidae | 3 | 7 |
| | Procellariidae | 17 | 164 |
| | Spheniscidae | 8 | 241 |
| | Stercorariidae | 2 | 9 |
| | *undetermined* | | 7 |
| MAMMALIA (10) | Cetacea | 5 | 22 |
| | Pinnipeda | 5 | 17 |

Amongst invertebrates, the more important amphipod predators are species of polychaetes and echinoderms (starfishes, urchins and brittle stars) in the benthos, and several species of squids in the water column. Very few informative data (Table 6.3) are however available in order to estimate their impact on amphipod populations.

**Table 6.3: Examples of predation percentages on amphipods by some selected predators. Amphipod types: Gb: benthic Gammaridea; Gp: pelagic Gammaridea; H: Hyperiidea. Diet estimations: V: per volume; O: per occurrence; N: per number; M: per mass (see text).**

| Taxa | | Predator species | Amphi type | % in diet |
|---|---|---|---|---|
| ANNELIDA | Polychaeta | *Harmothoe spinosa* | Gb | 99 V |
| MOLLUSCA | Cephalopoda | *Alluroteuthis antarcticus* | H | 50 O |
| | | *Galiteuthis glacialis* | H | 100 O |
| ECHINODERMATA | Asteroidea | *Labidiaster rupicola* | Gb | 38 N |
| | Echinoidea | *Sterechinus neumayeri* | Gb | 4 V |
| PISCES | Bathydraconidae | *Gerlachea australis* | Gb | 13 M |
| | | *Cygnodraco mawsoni* | Gb | 1-12 M |
| | Artetidraconidae | *Artetidraco mirus* | Gb | 4-72 M |
| | | *Artetidraco orianae* | Gb | 2-80 M |
| | | *Pogonophryne marmorata* | Gb | 3-81 M |
| | Harpagiferidae | *Harpagifer bispinis* | Gb | 2-96 M |
| | | *Harpagifer antarcticus* | Gb | 2-82 M |
| | Nototheniidae | *Gobionotothen gibberifrons* | Gb–H | 0-38 M |
| | | *Notothenia coriiceps* | Gb–H | 0-88 M |
| | | *Lepidonotothen nudifrons* | Gb–H | 3-38 M |
| | Channichthyidae | *Champsocephalus gunnari* | H | 5-83 M |
| | Myctophidae | *Electrona carlsbergi* | H | 4-27 M |
| | | *Protomyctophum choriodon* | H | 0-11 M |
| AVES | Diomedeidae | *Diomedea chrysostoma* | H | 3-17 O |
| | Laridae | *Sterna vittata* | Gb–Gp | 3-30 M |
| | | *Larus dominicanus* | Gp–H | 1-38 O |
| | Oceanitidae | *Oceanites oceanicus* | Gp–H | 1-45 M |
| | Pelecanoididae | *Pelecanoides urinatrix* | H | 0-17 M |
| | Procellariidae | *Fulmarus glacioides* | Gp–H | 0-5 M |
| | | *Pachiptila desolata* | H | 0-16 M |
| | | *Pterodroma* spp | Gp–H | 0-5 M |
| | Spheniscidae | *Eudyptes chrysocome* | H | 0-3 M |
| | | *Eudyptes chrysolophus* | Gp–H | 2-67 M |
| | | *Pygoscelis papua* | Gb–Gp– | 0-4 M |
| MAMMALIA | Cetacea | *Balaenoptera borealis* | H | →45 M |
| | Pinnipeda | *Leptonychotes weddelli* | Gb | 3-29 O |

Many species of the different notothenioid families feed on amphipods to a more or less broad range (Table 6.3). Bottom species such as dragonfishes (bathydraconids) and plunderfishes (artetidraconids and harpagiferids) actively prey upon benthic amphipods, sometimes to a very large extent (up to 96% of diet mass). Most of the species that feed in the water column, like icefishes (channichthyids), consume rather few amphipods, mainly hyperiids. Finally, members of the family Nototheniidae (rockcods) show a more complex behaviour, feeding on both benthic and pelagic animals; gammarideans as well as hyperideans are usual preys, forming up to 88% of diet mass in *e.g. Notothenia coriiceps*. Beside notothenioids, many other fish families were reported to consume amphipods, the most important one being the myctophids (lanternfishes). These small-sized, meso- or bathypelagic fish prey to a relatively small extent on different hyperidean families but, owing to their abundance and to their peculiar swarming behaviour, maybe represent the largest group of amphipod consumers in the Southern Ocean (see below).

All the Antarctic and Sub-Antarctic seabird families have been reported to feed on (pelagic) amphipods. If the latter constitute only a small fraction in the diet of albatrosses and gulls, they may form up to 30% of diet mass in terns, which forage closer to the shores. Diving and storm petrels (pelecanoidids and oceanitids) feed at a minor extent too on amphipods, except the Wilson's storm petrel (*Oceanites oceanicus*) for which these crustaceans can form up to 45% of food bulk. Most of the procellariids (petrels, prions and shearwaters) also feed occasionally on amphipods which usually constitute less than 5% of their diet mass. Finally, all the Southern Ocean penguins (sphenicids) have been reported to prey on hyperiids and pelagic gammariids, but to a very small extent (about 1% in mass); macaroni penguins (*Eudyptes chrysolophus*), however, seem to feed more frequently on amphipods (up to 67% in mass); typically benthic amphipod species are

also found in the diet of gentoo penguins (*Pygoscelis papua*), denoting that these birds feed near to the shorelines.

Among marine mammals, 10 species –4 baleen whales, 1 dolphin and 5 seals– have been found with amphipods in their stomach. The presence of these crustaceans in the diet of plankton-feeding cetaceans is not surprising as hyperiids like *Themisto gaudichaudii* are known to swim often at the vicinity of krill swarms (Pakhomov & Perissinotto 1996). The sei whale (*Balaenoptera borealis*) in particular seems to feed preferentially on this hyperiid which can form up to 45% of its diet mass (Kawamura 1974), while for the other whales the occurrence of amphipods is more anecdotal. Amphipods are also found in the diet of many Antarctic seal species, where they form only a few ‰ in mass, but most of the authors claim it should be an artifact, amphipods coming from the stomach of ingested fish.

To synthetize the dataset, a tentative 'box-model' was built up which shows the relative importance of both pelagic and benthic amphipods in the diet of the Southern Ocean top predators. To construct this model, various published data were used: (i) the mean quantitative values of amphipod mass fractions in predators' diet, (ii) the standing stocks of the main groups of predators in the Southern Ocean, (iii) the feeding rates of these predators. Available data are presented in Table 4; for some groups, namely both benthic and pelagic (squids) invertebrates, consistent biomass values are lacking, causing the total amount of preyed amphipods to be underestimated. The diagram (Fig. 1) shows the estimates of the different predation fluxes, expressed in millions of tons per year ($Mt.yr^{-1}$). It clearly appears that pelagic fishes (myctophids) are responsible for the biggest flux (50 $Mt.yr^{-1}$), which can easily be understood when considering the area and depth ratios of the oceanic *vs* neritic zones. The second group in importance is represented by benthic and benthopelagic fish (notothenioids mainly), whose predation on pelagic amphipods was not estimated but is likely at least one order of magnitude smaller than on benthic ones (8.6 $Mt.yr^{-1}$). The other predator groups (birds and mammals) consume

a lower amount of amphipods (from 0.1 to 1.7 $Mt.yr^{-1}$) as their relative biomass is far weaker than that of fish. The total amphipod mass ingested per year is thus estimated at roughly 60 Mt. These values must however be cautiously regarded as they are tainted with biases and approximations for several reasons: (i) predator biomass data are usually widely scattered, available only either for areas of intensive scientific research or for species of commercial significance; (ii) just a few (characteristic) fish families were taken into account, while other ones (such as *e.g.* zoarcids or muraenolepids) are also well represented in the Southern Ocean but less studied; (iii) seasonal variations in either predator standing stocks or feeding rates are likely to occur, the importance of which can hardly be weighed; (iv) the proportion of amphipods in predators' diet may considerably vary with respect to several parameters like *e.g.* age, sex or geographical location; (v) some maybe significant groups (*i.e.* benthic and pelagic invertebrates) were totally omitted; (vi) the circumscription of what is the 'Southern Ocean' (south of the Antarctic Convergence, south of the Sub-Tropical Front, including or not the Sub-Antarctic islands) is not clearly defined in the literature. This notwithstanding, values presented in Fig. 1 can be considered to represent a rather realistic working hypothesis about the importance of amphipods for Southern Ocean top predators.

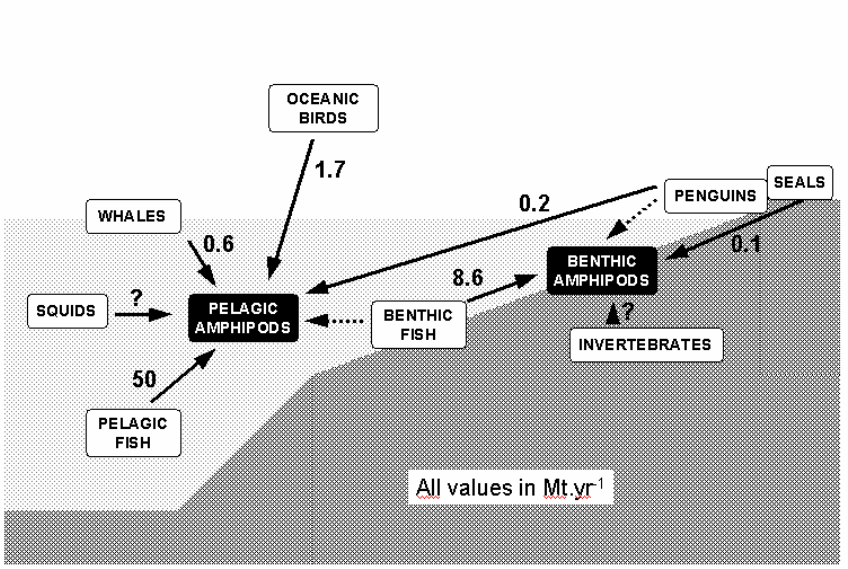
**Table 6.4: Values of the different parameters used to estimate the predation rates on amphipods by the main Southern Ocean predator groups.**

| Parameters | Values | References |
|---|---|---|
| Southern Ocean Area | $37\ 10^6\ km^2$ | Stonehouse 1989 |
| Continental Shelf Area (Continent) | $2\ 10^6\ km^2$ | |
| Continental Shelf Area (Islands) | $0.5\ 10^6\ km^2$ | |
| Demersal Fish Biomass (Continent) | $0.9\ T.km^{-2}$ | Kock 1992 |
| Demersal Fish Biomass (Islands) | $20\ T.km^{-2}$ | *estimated from* Kock 1992 |
| Myctophid Biomass | 140 MT | Lubimova *et al.* 1987 in Kock 1992 |
| Fish Mean Daily Ingestion Rate | $2\ \%.day^{-1}$ | various authors in Kock 1992 |
| Penguin Annual Ingestion Rate | $17\ MT.yr^{-1}$ | various authors in Williams 1995 |

| Parameters | Values | References |
|---|---|---|
| Other Seabirds' Annual Ingestion Rate | 35 MT.yr$^{-1}$ | *extrapolated from* Croxall & Prince 1987 |
| Sei Whale Antarctic Population | 24000 ind. | *mean from various sources* |
| Sei Whale Feeding Period | 130 days.yr$^{-1}$ | |
| Sei Whale Daily Ingestion | 900 kg.day$^{-1}$ | Kawamura 1974 |
| Seal Mean Daily Ingestion Rate | 7 kg.km$^{-2}$.day$^{-1}$ | Joiris 1991 |

| Amphipods in Diet | Mean (%) | |
|---|---|---|
| Demersal Fish (Notothenioids) | 10 | *this study* |
| Pelagic Fish (Myctophids) | 5 | *"* |
| Penguins | 1 | *"* |
| Oceanic Seabirds | 5 | *"* |
| Whales | 20 | *"* |
| Seals | 2 | *"* |

**Fig. 6.1: Scheme of the different predation fluxes on amphipods (in MT.yr$^{-1}$) by the main Southern Ocean predator groups.**



## 6.3. CONCLUSIONS

The exhaustive analysis of the literature dedicated to the diet of Southern Ocean top predators revealed the importance of amphipods in the trophodynamics of the higher food web. The integration of available data with published values about predators' biomasses and feeding rates allowed to estimate that about 60 millions of tons of these crustaceans are consumed each year in the area, *i.e.* about 1.6 $t.km^{-2}.yr^{-1}$. By comparison, the consumption of krill by all its predators in the Southern Ocean has been estimated to about 250 $Mt.yr^{-1}$ (Everson 1977, Miller & Hampton 1989), while annual fish consumption by warm-blooded predators has been estimated to be up to 15 Mt (Everson 1977, Laws 1985). Amphipods are thus likely to be the second group of animal prey in importance after euphausiids. The present review also emphasizes the major role of hyperiids (and especially of *Themisto gaudichaudii*) in Antarctic food webs.

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# 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 bentho-pelagic 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 ± SD, ‰) of all animals sampled on the shelf of the Antarctic Peninsula; *TL* corresponds to estimated trophic level**

| PHYLUM | Class / Species | $\delta^{13}C$ | $\delta^{15}N$ | *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 |
| | *Laetmonice producta* | -23.7 ± 0.5 (2) | 8.9 ± 1.0 (2) | 4,5 |
| MOLLUSCA | **Cephalopoda** | | | |
| | *Paraledone turqueti* | -24.2 ± 0.4 (7) | 9.6 ± 0.7 (7) | 4,8 |
| | *Paraledone charcoti* | -25 ± 0.0 (1) | 8.6 ± 1.0 (1) | 4,4 |
| | *Paraledone* sp. | -24.7 ± 0.0 (1) | 8.5 ± 0.0 (1) | 4,4 |
| | *Megaledone setosus* | -21.5 ± 0.0 (1) | 9.5 ± 0.0 (1) | 4,8 |
| | **Bivalvia** | | | |
| | *Limopsis marionensis* | -24.3 ± 1.6 (5) | 7.7 ± 0.8 (5) | 4,0 |
| ARTHROPODA | **Isopoda** | | | |
| | *Glyptonotus antarcticus* | -22.9 ± 0.0 (1) | 6.3 ± 0.0 (1) | 3,5 |
| | *Seratoserolis trilobitoides* | -22.9 ± 1.2 (2) | 7.5 ± 0.2 (5) | 4,0 |
| | *Natatolana* 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 | | | |
| | *Themisto* sp | -25.1 ± 0.7 (2) | 2.9 ± 0.7 (2) | 2,0 |
| | Gammarid | | | |
| | *Ampelisca richardsoni* | -29.3 ± 0.2 (3) | 4.1 ± 0.1 (3) | 2,5 |
| | *Byblis* sp | -24.8 ± 1.2 (3) | 6.1 ± 0.3 (3) | 3,4 |
| | *Eusirus perdentatus* | -23.4 ± 0.7 (19) | 7.3 ± 1.0 (19) | 3,9 |
| | *Djerboa furcipes* | -27.8 ± 0.6 (5) | 4.9 ±0.3 (5) | 2,9 |
| | *Echiniphimedia echinata* | -21.5 ± 2.1 (3) | 6.2 ± 1.0 (3) | 3,4 |
| | *Echiniphimedia hodgsoni* | -24.3 ± 1.3 (2) | 10.6 ± 1.8 (2) | 5,3 |
| | *Iphimediella* sp | -21.7 ± 1.0 (6) | 11.8 ± 1.0 (6) | 5,8 |
| | *Pseudorchomene coatsi* | -22.7 ± 0.3 (3) | 9.3 ± 0.3 (3) | 4,7 |

| PHYLUM | Class / Species | $\delta^{13}C$ | $\delta^{15}N$ | *TL* |
|---|---|---|---|---|
| | *Waldeckia obesa* | -22.8 ± 0.9 (4) | 7.3 ± 0.7 (4) | 3,9 |
| | *Eurythenes gryllus* | -27.3 ± 1.1 (9) | 8.5 ± 0.5 (9) | 4,4 |
| | *Abyssorchomene plebs* | -26.5 ± 0.4 (6) | 9.5 ± 0.8 (6) | 4,8 |
| | *Epimeria georgiana* | -22.9 ± 1.9 (9) | 7.9 ± 0.4 (9) | 4,1 |
| | *Epimeria similis* | -25 ± 1.4 (15) | 7.6 ± 0.5 (15) | 4,0 |
| | *Leucothoe spinicarpa* | -22.7 ± 0.6 (6) | 8.3 ± 0.8 (6) | 4,3 |
| | *Paraceradocus gibber* | -23.5 ± 0.7 (12) | 5.0 ± 0.5 (12) | 2,9 |
| | **Euphausiacea** | | | |
| | *Euphausia superba* | -28.6 ± 1.1 (6) | 2.8 ± 0.4 (6) | 2,0 |
| | **Decapoda** | | | |
| | *Notocrangon antarcticus* | -23.6 ± 0.3 (4) | 9.3 ± 0.2 (4) | 4,7 |
| | *Chorismus antarcticus* | -24.0 ± 1.8 (2) | 7.4 ± 1.3 (2) | 3,9 |
| **BRYOZOA** | *Reteporella* 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** | | | |
| | *Psolus* sp. | -26.6 ± 1.4 (3) | 8.0 ± 0.8 (3) | 4,2 |
| | *Bathyplotes fusviculum* | -24.8 ± 0.3 (2) | 8.8 ± 0.7 (2) | 4,5 |
| | *Echinocucumis* sp. | -29 ± 0.3 (2) | 7.5 ± 0.2 (2) | 4,0 |
| | **Ophiuroidea** | | | |
| | *Astrotoma agassizii* | -23.9 ± 2.1 (3) | 7.5 ± 0.9 (3) | 4,0 |
| | *Ophiosparte gigas* | -27.3 ± 1.6 (3) | 5.5 ± 0.4 (3) | 3,1 |
| | *Ophionotus* 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 | | | |
| | *Champsocephalus gunnari* | -25.1 ± 0.3 (5) | 8.5 ± 0.3 (5) | 4,4 |
| | Nototheniidae | | | |
| | *Gobionotothen gibberifrons* | -24.3 ± 0.1 (5) | 9.8 ± 0.4 (5) | 4,9 |
| | *Notothenia coriiceps* | -23.6 ± 0.8 (6) | 9.9 ± 0.6 (6) | 5,0 |
| | *Notothenia rossii* | -24.4 ± 0.5 (6) | 9.2 ± 0.3 (6) | 4,7 |
| | *Trematomus bernacchii* | -19.7 ± 2.0 (2) | 12.6 ± 0.2 (2) | 6,1 |
| | *Trematomus pennellii* | -20.2 ± 0.6 (3) | 11.0 ± 0.8 (3) | 5,4 |
| | *Trematomus nicolaii* | -20.5 ± 0.0 (1) | 11.0 ± 0.0 (1) | 5,4 |
| | *Trematomus hansoni* | -21.9 ± 0.0 (1) | 10.2 ± 0.0 (1) | 5,1 |
| | *Trematomus eulepidotus* | -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 ± 3‰) (reviews in Rau et al. 1982, Fischer 1991, France 1995). Low temperature (below 2°C), low light intensity and high water [$CO_2$ (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.

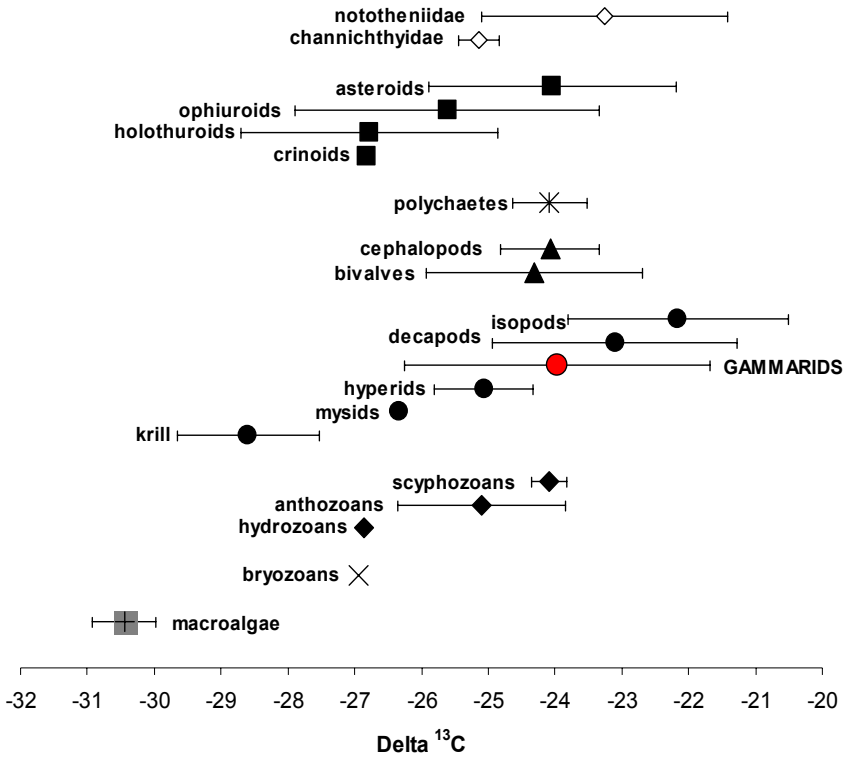
On the other hand, a considerable overlap of the $\delta^{13}C$ values is observed between groups.

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 $\delta^{13}C$ 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 $\delta^{13}C$ 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 ± 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 $\delta^{13}C$ 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 $\delta^{13}C$ and $\delta^{15}N$ values between SPOM and ice algae, generally more enriched (e.g. $\delta^{13}C$ = -18.5‰, $\delta^{15}N$ = 8.3‰, 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, $\delta^{15}N$ values clearly indicate direct feeding on POM and not on the isotopically heavier ice algae. Low $\delta^{13}C$ 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:

$$\boldsymbol{TL = (D - 0.4)/2.4 + 1}$$

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

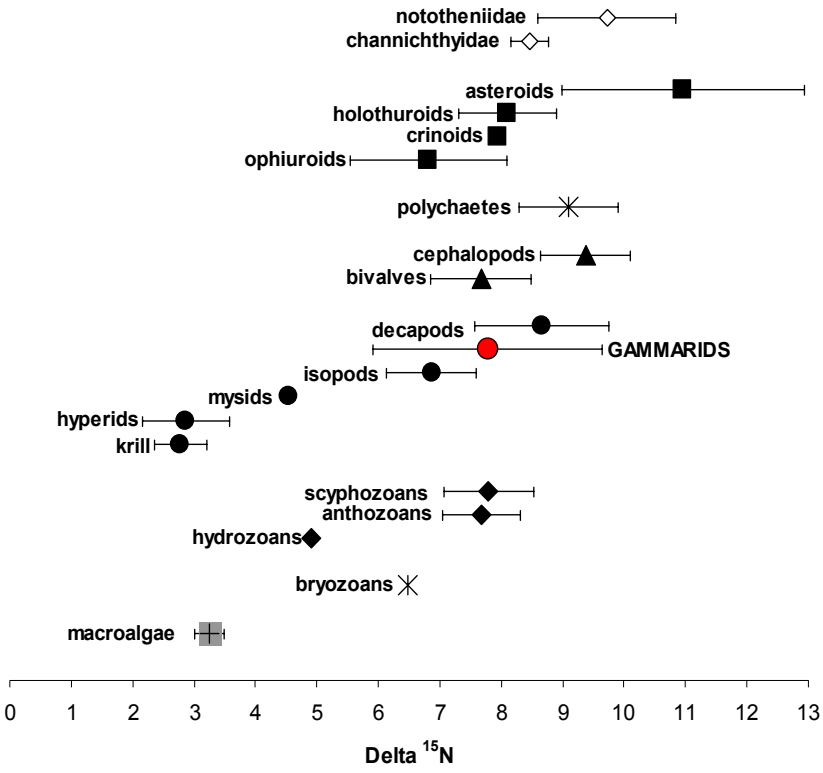
Based on the assumption that POM is the first trophic level, the range of $\delta^{15}N$ values in Antarctic Peninsula fauna reflects a food web characterized by 6 trophic levels, the highest level being occupied only by the demersal emerald

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 ($4^{th}$ and $5^{th}$ 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 $\delta^{15}N$ 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 ($\delta^{13}C$=-26.5 to -23.2‰ and $\delta^{15}N$=3.9 to 9.9‰ (Nyssen, unpublished

data). These isotopic values are also coherent with the classification of another amphipod species, *Leucothoe spinicarpa* ($\delta^{13}C$=-22.7±0.6‰ and $\delta^{15}N$=8.3±0.8‰) 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 ± 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 $\delta^{15}N$ values (4.1‰ – 5.0‰), but their $\delta^{13}C$ 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 $\delta^{13}C$ 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) $\delta^{15}N$ 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, $\delta^{13}C$ 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 $\delta^{15}N$ 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 13C-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.

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# ANNEX 1: BIODIVERSITY OF THE SOUTHERN OCEAN: A CATALOGUE OF THE AMPHIPODA

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From a combination of the checklist of De Broyer C & Jazdzewski K (1993) and the catalogue of Lowry J & Bullock (1976)

# BIODIVERSITY OF THE SOUTHERN OCEAN:

# A CATALOGUE OF THE AMPHIPODA (CRUSTACEA)

Combination of De Broyer & Jazdzewski 1993 checklist & Lowry & Bullock 1976 catalogue
+ corrections, update and complements.

Restricted to Gammaridea and Corophiidea (sensu Myers & Lowry, 2003).

Based on a complete survey of taxonomic literature to 31 Dec 2002.
"Ecological" literature may not be complete.

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*Ampelisca anversensis* Karaman, 1975e
*Ampelisca barnardi* Nicholls, 1938
*Ampelisca bransfieldi* K.H. Barnard, 1932
*Ampelisca composita* Schellenberg, 1931a
*Ampelisca dallenei* Bellan-Santini, 1985a
*Ampelisca dentifera* Schellenberg, 1931a
*Ampelisca gracilicauda* Schellenberg, 1931a
*Ampelisca hemicryptops* K.H. Barnard, 1930
*Ampelisca macrodonta* Goeke, 1987
*Ampelisca richardsoni* Karaman, 1975e
*Ampelisca statenensis* K.H. Barnard, 1932
*Byblis antarctica* Schellenberg, 1931a
*Byblis securiger* (K.H. Barnard, 1931a)
*Byblis subantarctica* Schellenberg, 1931a
*Byblisoides juxtacornis* K.H. Barnard, 1931a

### AMPHILOCHIDAE

*Amphilochella simplicarpa* Schellenberg, 1926a
*Amphilochus marionis* Stebbing, 1888
*Gitanopsilis amissio* Rauschert, 1994
*Gitanopsis denticulata* Rauschert, 1994
*Gitanopsis fucatosquamosa* Rauschert, 1994
*Gitanopsis inaequipes* Schellenberg, 1926a

*Gitanopsis pusilla* K.H. Barnard, 1916
*Gitanopsis simplex* Schellenberg, 1926a
*Gitanopsis squamosa* (Thomson, 1880a )

**ASTYRIDAE**

*Astyra antarctica*. Andres, 1997
*Eclysis similis* K.H. Barnard, 1932

**CARDENIOIDAE**
**CHEIDAE**

*Cheus annae* Thurston, 1982

**CLARENCIIDAE**

*Clarencia chelata* K.H. Barnard, 1931a

**COLOMASTIGIDAE**

*Colomastix castellata* K.H. Barnard, 1932
*Colomastix fissilingua* Schellenberg, 1926a
*Colomastix simplicicauda* Nicholls, 1938
*Colomastix sp. 1* Holman & Watling, 1983b

**CYPROIDEIDAE**

*Victorhensenoides arntzi* Rauschert, 1996

**DEXAMINIDAE**

*Atylus dentatus* (Schellenberg, 1931a)
*Atylus villosus* Bate, 1862
*Paradexamine fissicauda* Chevreux, 1906b
*Paradexamine nana* Stebbing, 1914b
*Paradexamine pacifica* (Thomson, 1879b)
*Paradexamine sexdentata* Schellenberg, 1931a
*Polycheria acanthocephala* Schellenberg, 1931a
*Polycheria acanthopoda* Thurston, 1974b
*Polycheria antarctica* (Stebbing, 1875b) s.s.
*Polycheria cristata* Schellenberg, 1931a
*Polycheria dentata* Schellenberg, 1931a
*Polycheria gracilipes* Schellenberg, 1931a
*Polycheria intermedia* Stephensen, 1947a
*Polycheria kergueleni* (Stebbing, 1888)
*Polycheria macrophtalma* Schellenberg, 1931a
*Polycheria nuda* Holman & Watling, 1983b
*Polycheria similis* Schellenberg, 1931a

**DIDYMOCHELIIDAE**

*Didymochelia edwardi* Bellan-Santini & Ledoyer, 1987
*Didymochelia spongicola* K.H. Barnard, 1931a

**EOPHLIANTIDAE**

*Cylindryllioides mawsoni* Nicholls, 1938
*Wandelia crassipes* Chevreux, 1906d

**EUSIROIDEA**

[Bousfield, 1982b, emended; Bousfield & Hendrycks 1997]

**EUSIROIDEA : CALLIOPIIDAE**

[Bushueva, (1986)] [Bousfield & Hendrycks 1997]

[genera according to Lowry unpubl. list (1998)]

*Atylopsis emarginatus* Stebbing, 1888

*Atylopsis fragilis* Rauschert, 1989

*Atylopsis orthodactyla* Thurston, 1974b

*?Atylopsis procera* Andres, 1986

*Calliopiurus excellens* Bushueva, 1986

*Gondogeneia antarctica* (Chevreux, 1906b)

*Gondogeneia bidentata* (Stephensen, 1927e)

*Gondogeneia chosroides* (Nicholls, 1938)

*Gondogeneia georgiana* (Pfeffer, 1888)

South Shetland Islands: King George Island, Admiralty Bay (KJ *et al*. 99).

*Gondogeneia gracilicauda* (Schellenberg, 1931a)

*Gondogeneia macrodon* (Schellenberg, 1931a)

*Gondogeneia patagonica* Alonso, 1986a

*Gondogeneia redfearni* (Thurston, 1974a)

*Gondogeneia simplex* (Dana, 1852a)

*Gondogeneia spinicoxa* Bellan-Santini & Ledoyer, 1974

*Gondogeneia subantarctica* (Stephensen, 1938c)

*Gondogeneia tristanensis* (K.H. Barnard, 1932)

*Gondogeneia ushuaiae* (Schellenberg, 1931a)

*Gondogeneia sp. 1* (Stephensen, 1938c)

*Gondogeneia sp. 2* (Stephensen, 1938c)

*Gondogeneia sp. 3* (Ruffo, 1949)

*Gondogeneia sp. 4* J.L. Barnard, 1972b

*Gondogeneia sp. 5* Castellanos, 1973

*Gondogeneia sp.* (= *G. antarctica* cf ) [see BK91]

*?Haliragoides australis* Chilton, 1912a

*Harpinioides drepanocheir* Stebbing, 1888

*Harpinioides fissicauda* Schellenberg, 1926a

*Lopyastis multisetosa* (Schellenberg, 1926a)

*Lopyastis signiensis* (Thurston, 1974a)

*Metaleptamphopus pectinatus* Chevreux, 1912a

*Oradarea acuminata* Thurston, 1974a

*Oradarea bidentata* K.H. Barnard, 1932

*Oradarea crenelata* Alonso de Pina, 1995

*Oradarea edentata* K.H. Barnard, 1932

*Oradarea impressicauda* K.H. Barnard, 1932

*Oradarea megalops* (Nicholls, 1938)

*Oradarea novaezealandiae* (Thomson, 1879b)

Campbell Island: Perseverance Harbour (KS 38c).

*Oradarea ocellata* Thurston, 1974a

*Oradarea rossi* Thurston 1974a

*Oradarea tricarinata* K.H. Barnard, 1932

*Oradarea tridentata* K.H. Barnard, 1932

*Oradarea unidentata* Thurston, 1974a

*Oradarea walkeri* Shoemaker, 1930a

*Tylosapis dentata* (Stebbing, 1888)

**EUSIROIDEA : EUSIRIDAE S.S.**

(sensu Bousfield & Hendrycks 1995)

[generic composition according to Bousfield & Hendrycks 1995]

*Cleonardo longipes* Stebbing, 1888

*Cleonardo macrocephala* Birstein & Vinogradov, 1955

*Eusirella flagella* Andres, 1982

*Eusiroides aberrantis* Bellan-Santini & Ledoyer, 1987
*Eusiroides crassi* Stebbing, 1888
*Eusiroides georgiana* K.H. Barnard, 1932
*Eusiroides monoculoides* (Haswell, 1879)
*Eusiroides stenopleura* K.H. Barnard, 1932

*Eusirus antarcticus* Thomson, 1880a *s.l.*
*Eusirus bouvieri* Chevreux, 1911c
*Eusirus giganteus* Andres, Lörz & Brandt, 2002.
*Eusirus laevis* Walker, 1903a
*Eusirus laticarpus* Chevreux, 1906e
*Eusirus microps* Walker, 1906c
*Eusirus perdentatus* Chevreux, 1912a
*Eusirus propeperdentatus* Andres, 1979b

*Eusirus n. sp. 1* De Broyer & Jazdzewski
*Eusirus n. sp. 2* De Broyer & Jazdzewski [AV]
*Eusirus sp. 3* Puddicombe & Johnstone, 1988
*Meteusiroides curvidactyla* (Pirlot, 1934)

*Rhachotropis anoculata* J.L. Barnard, 1962d

*Rhachotropis antarctica* K.H. Barnard, 1932

*Rhachotropis hunteri* Nicholls, 1938

*Rhachotropis kergueleni* Stebbing, 1888

*Rhachotropis schellenbergi* Andres, 1982

*Stenopleura atlantica* Stebbing, 1888

**EUSIROIDEA : GAMMARELLIDAE**

[Bousfield, 1977: 309; Barnard J.L., 1989: 701-703. See also Bnd & Bnd, 1983: 594]

*Austroregia batei* (Cunningham, 1871)
*Austroregia huxleyana* (Bate, 1862)
*Austroregia Regis* (Stebbing, 1914b)
*Chosroes decoratus* K.H. Barnard, 1932
*Chosroes incisus* Stebbing, 1888

**EUSIROIDEA: PONTOGENEIIDAE**

*Antarctogeneia macrodactyla* Thurston, 1974b
*Atyloella dentata* K.H. Barnard, 1932
*Atyloella magellanica* (Stebbing, 1888)
*Atyloella quadridens* (K.H. Barnard, 1930)
*Bovallia gigantea* Pfeffer, 1888
*Bovallia sp. 1* Monod, 1926
*Djerboa furcipes* Chevreux, 1906e
*Liouvillea oculata* Chevreux, 1912a
*Paramoera aucklandica* (Walker, 1908)
*Paramoera brachyura* Schellenberg, 1931a
*Paramoera chevreuxi* (Stephensen, 1927e)
*Paramoera edouardi* Schellenberg, 1929c
*Paramoera fasciculata* (Thomson, 1880a)
*Paramoera fissicauda* (Dana, 1852a)
*Paramoera gregaria* (Pfeffer, 1888)
*Paramoera hamiltoni* Nicholls, 1938
*Paramoera hermitensis* K.H. Barnard, 1932
*Paramoera hurleyi* Thurston, 1974a

*Paramoera husvikensis* Thurston, 1974b

*Paramoera impressicauda*

*?Paramoera incognita* Bushueva, 1986

*Paramoera kergueleni* Bellan-Santini & Ledoyer, 1974

*Paramoera macquariae* Nicholls, 1938

*Paramoera obliquimana* K.H. Barnard, 1932

*Paramoera parva* Ruffo, 1949

*?Paramoera pfefferi* Schellenberg, 1931a

*Paramoera schellenbergi* Nicholls, 1938

*Paramoera tristanensis* K.H. Barnard, 1932

*Paramoera walkeri* (Stebbing, 1906)

*Paramoera sp. 1* Shoemaker, 1945d

*Paramoera sp. 2* J.L. Barnard, 1972c

*Paramoera sp. 3* Bellan-Santini & Ledoyer, 1974 [AV *kergueleni*]

*Paramoera sp 4* Nicholls, 1938

*Paramoera spp*. Barnard & Karaman, 1991

*Pontogeneoides abyssi* Nicholls, 1938

*Pontogeneoides dubia* Ruffo, 1949

*Prostebbingia brevicornis* (Chevreux, 1906c)

*Prostebbingia gracilis* (Chevreux, 1912a)

*Prostebbingia laevis* (Thomson, 1879a)

*Prostebbingia longicornis* (Chevreux, 1906e)

*Prostebbingia serrata* Schellenberg, 1926a

*Prostebbingia spinicauda* Ren & Huang, 1991

*Schraderia acuticauda* Bellan-Santini & Ledoyer, 1974

*Schraderia barnardi* Thurston, 1974a

*Schraderia dubia* Thurston, 1974a

*Schraderia gracilis* Pfeffer, 1888

*Schraderia serraticauda* (Stebbing, 1888)

*Schraderia sp.1* Castellanos, 1973

[AV ] Frigora ascidicola Ren, 1991

**EXOEDICEROTIDAE**

*Bathyporeiapus magellanicus* Schellenberg, 1931a
*Exoediceropsis affinis* Alonso de Pina, 1997
*Exoediceropsis chiltoni* Schellenberg, 1931a
*Exoediceropsis lobata* Alonso de Pina, 1997
*Methalimedon nordenskjoldi* Schellenberg, 1931a
*Metoediceros fuegiensis* Schellenberg, 1931a
*Parhalimedon turqueti* Chevreux, 1906b

**HADZIOID GROUP**

**HADZIOID GROUP: CERADOCOPSID GROUP**

[Ceradocopsids see Barnard & Barnard, 1983: 635]

*Ceradocopsis carnleyi* (Stephensen, 1927e)
*Ceradocopsis kergueleni* Schellenberg, 1926a
*Ceradocopsis macracantha* Lowry & Fenwick, 1983
*Ceradocopsis peke* J.L. Barnard, 1972b
*Ceradocopsis tristanensis* Stephensen, 1949

**HADZIOID GROUP: CERADOCID GROUP**

[generic composition fide Lowry, unpubl. (1998)]
[ see also Ceradocid Group with different composition in Barnard & Barnard, 1983: 373, 612]

*Ceradocoides chiltoni* Nicholls, 1938
*Elasmopus bollonsi* Chilton, 1915

*Elasmopus neglectus* Chilton, 1915

*Elasmopus wahine* J.L. Barnard, 1972b

*Maera incerta* Chilton, 1883

*Maera mastersi* (Haswell, 1880a)

*Zygomaera eugeniae* (Schellenberg, 1931a)

*Zygomaera pfefferi* (K.H. Barnard, 1932)

*Paraceradocus gibber* Andres, 1984

*Paraceradocus miersi* (Pfeffer, 1888)

*Paraceradocus procerus* Andres, 1984

*Paraceradocus ramulus* Andres, 1981

*Paraceradocus stenepimerus* Andres, 1984

*Paraceradocus trispinosus* Andres, 1984

**HADZIOID GROUP: GAMMARELLA GROUP**

*Gammarella hybophora* Lowry & Fenwick, 1983

**HADZIOID GROUP: HADZIIDAE**

[Barnard & Barnard, 1983: 651]

*Zhadia subantarctica* Lowry & Fenwick, 1983

**HADZIOID GROUP: MELITIDAE**

[Bousfield, 1982b: 281; In Barnard & Barnard, 1983: 662, only Melita in MELI]

*Melita inaequistylis* Dana, 1852a

*Melita palmata* (Montagu, 1804)

*Melita tristanensis* K.H. Barnard, 1965

*Tagua aporema* Lowry & Fenwick, 1983

**HADZIOID GROUP: PARAPHERUSA GROUP**

*Parapherusa crassipes* Haswell, 1879b

**HADZIOID GROUP: HOHO**

*Hoho hirtipalma* Lowry & Fenwick, 1983

**HYALIDAE**

*Hyale campbellica* (Filhol, 1885a)
*Hyale grandicornis* (Kroyer, 1845)
*Hyale hirtipalma* (Dana, 1852a)
*Hyale macrodactyla* Stebbing, 1899
*Hyale media* (Dana, 1853)
*Hyale tristanensis* Macnae, 1953

**HYPERIOPSIDAE**

*Hyperiopsis australis* Walker, 1906a

*Hyperiopsis sp*. Birstein & Vinogradov, 1962b

**IPHIMEDIOIDEA**

**IPHIMEDIOIDEA : ACANTHONOTOZOMELLIDAE**

[acc. to Coleman & Barnard, 1991b: 257-258]

[includes Vicmusiidae]

*Acanthonotozomella alata* Schellenberg, 1926a
*Acanthonotozomella barnardi* Watling & Holman, 1980
*Acanthonotozomella rauscherti* Coleman & Jäger, 2001
*Acanthonotozomella trispinosa* (Bellan-Santini, 1972a)
*Acanthonotozomoides oatesi* (K.H. Barnard, 1930)
*Acanthonotozomoides sublitoralis* Schellenberg, 1931a
*Acanthonotozomopsis pushkini* (Bushueva, 1978)

**IPHIMEDIOIDEA: AMATHILLOPSIDAE**

*Amathillopsis charlottae* Coleman, 1998

**IPHIMEDIOIDEA : EPIMERIIDAE**

[Coleman & Barnard, 1991b: 255 ([in IPHI in B & K 91)]

*Actinacanthus tricarinatus* (Stebbing, 1883)
*Epimeria annabellae* Coleman, 1994
*Epimeria extensa* Andres, 1985
*Epimeria georgiana* Schellenberg, 1931a
*Epimeria grandirostris* (Chevreux, 1912a)
*Epimeria heldi* Coleman, 1998
*Epimeria inermis* Walker, 1903a
*Epimeria intermedia* Schellenberg, 1931a
*Epimeria macrodonta* Walker, 1906b
*Epimeria monodon* Stephensen, 1947a
*Epimeria oxicarinata* Coleman, 1990b
*Epimeria pulchra* Coleman, 1990b
*Epimeria puncticulata* K.H. Barnard, 1930
*Epimeria reoproi* Lörz & Coleman, 2001

*Epimeria rimicarinata* Watling & Holman, 1980
*Epimeria robusta* K.H. Barnard, 1930
*Epimeria rubrieques* De Broyer & Klages, 1991
*Epimeria similis* Chevreux, 1912a
*Epimeria vaderi* Coleman 1998b
*Epimeria sp. 1* Andres, 1985
*Epimeriella macronyx* Walker, 1906b
*Epimeriella scabrosa* K.H. Barnard, 1930
*Epimeriella truncata* Andres, 1985
*Epimeriella walkeri* K.H. Barnard, 1930
*Metepimeria acanthurus* Schellenberg, 1931a
*Parepimeriella irregularis* Schellenberg, 1931a
*Uschakoviella echinophora* Gurjanova, 1955b

**IPHIMEDIOIDEA : IPHIMEDIIDAE**

[See Coleman & Barnard, 1991b: 261-262.]

*Anchiphimedia dorsalis* K.H. Barnard, 1930
*Echiniphimedia barnardi* Coleman & Andres, 1988
*Echiniphimedia echinata* Walker, 1906c
*Echiniphimedia gabrielae* Coleman & Andres, 1988
*Echiniphimedia hodgsoni* Walker, 1906c
*Echiniphimedia imparidentata* (Bellan-Santini, 1972a)
*Echiniphimedia scotti* K.H. Barnard, 1930
*Echiniphimedia waegelei* Coleman & Andres, 1988
*Gnathiphimedia barnardi* Thurston, 1974b
*Gnathiphimedia fuchsi* Thurston, 1974a
*Gnathiphimedia incerta* Bellan-Santini, 1972a
*Gnathiphimedia macrops* K.H. Barnard, 1932
*Gnathiphimedia mandibularis* K.H. Barnard, 1930

*Gnathiphimedia sexdentata* (Schellenberg, 1926a)
*Gnathiphimedia urodentata* Bellan-Santini & Ledoyer, 1987
*Gnathiphimedia watlingi* Coleman,1994
*Iphimedia imparilabia* Watling & Holman, 1980
*Iphimedia macrocystidis* (K.H. Barnard, 1932)
*Iphimedia magellanica* Watling & Holman, 1980
*Iphimedia multidentata* (Schellenberg, 1931a)
*Iphimedia pacifica* Stebbing, 1883
*Iphimedia spinosa* (Thomson, 1880a)
*Iphimediella acuticoxa* Watling & Holman, 1980
*Iphimediella bransfieldi* K.H. Barnard, 1932
*Iphimediella cyclogena* K.H. Barnard, 1930
*Iphimediella dominici* Coleman, 1996
*Iphimediella georgei* Watling & Holman, 1980
*Iphimediella margueritei* Chevreux, 1912a
*Iphimediella microdentata* (Schellenberg, 1926a)
*Iphimediella paracuticoxa* Andres, 1988
*Iphimediella rigida* K.H. Barnard, 1930
*Iphimediella ruffoi* Coleman, 1996
*Iphimediella serrata* (Schellenberg, 1926a)
*Labriphimedia pulchridentata* Stebbing, 1883
*Labriphimedia vespuccii* K.H. Barnard, 1931a
*Maxilliphimedia longipes* (Walker, 1906c)
*Nodotergum bicarinatum* Bellan-Santini, 1972a
*Paranchiphimedia monodi* Ruffo, 1949
*Parapanoploea longirostris* Bellan-Santini, 1972a
*Parapanoploea oxygnathia* Nicholls, 1938
*Parapanoploea recessa* Andres, 1988b
*Pariphimedia incisa* Andres, 1985
*Pariphimedia integricauda* Chevreux, 1906a

*Pariphimedia normani* (Cunningham, 1871)

*Pseudiphimediella glabra* (Schellenberg, 1931a)

*Pseudiphimediella nodosa* (Dana, 1852a)

Stegopanoploea joubini (Chevreux, 1912a)

**IPHIMEDIOIDEA : OCHLESIDAE**

[Coleman & Barnard 1991b: 259-260; 262-263; 1991c: 269-270. Berge *et al.* 1999]

*Antarctodius antarcticus* (Watling & Holman, 1981)

*Antarctodius rauscherti* Coleman & Kauffeldt, 2001

*Curidia magellanica* Coleman & Barnard, 1991c

**LAPHYSTIOPSIDAE**

*Prolaphystiopsis platyceras* Schellenberg, 1931a

*Prolaphystius isopodops* K.H. Barnard, 1930

**LEPECHINELLIDAE**

[re-established by Andres & Brandt, 2001]

*Lepechinella cachi* J.L. Barnard, 1973a

*Lepechinella cetrata* K.H. Barnard, 1932

*Lepechinella drygalskii* Schellenberg, 1926a

*Lepechinella huaco* J.L. Barnard, 1973b

*Lepechinelloides weddellensis* Andres & Brandt, 2001

*Paralepechinella occultolongicornis* Andres & Brandt, 2001

## LEUCOTHOIDAE

*Leucothoe orkneyi* Holman & Watling, 1983
*Leucothoe spinicarpa* (Abildgaard, 1789) *s.l.*
*Leucothoe sp.* Branch *et al.*, 1991

## LILJEBORGIIDAE

*Liljeborgia chevreuxi* Stebbing, 1888
*Liljeborgia consanguinea* Stebbing, 1888
*Liljeborgia dubia* (Haswell, 1879)
*Liljeborgia eurycrada* Thurston, 1974b
*Liljeborgia georgiana* Schellenberg, 1931a
*Liljeborgia kerguelenensis* Bellan-Santini & Ledoyer, 1974
*Liljeborgia georgiensis* K.H. Barnard, 1932
*Liljeborgia falklandica* K.H. Barnard, 1932
*Liljeborgia longicornis* (Schellenberg, 1931a)
*Liljeborgia macrodon* Schellenberg, 1931a
*Liljeborgia octodentata* Schellenberg, 1931a
*Liljeborgia proxima* Chevreux, 1907a
*Liljeborgia pseudomacronyx* Bellan-Santini & Ledoyer, 1987
*Liljeborgia quadridentata* Schellenberg, 1931a
*Liljeborgia quinquedentata* Schellenberg, 1931a

## . LYSIANASSOIDEA

[Family arrangement according to Lowry unpubl. 1998]

### LYSIANASSOIDEA : ADELIELLID GROUP

*Adeliella laticornis* Nicholls, 1938

*Adeliella olivieri* De Broyer, 1975b

*Ambasiopsis georgiensis* K.H. Barnard, 1931a

*Ambasiopsis tumicornis* Nicholls, 1938

*Ambasiopsis uncinata* K.H. Barnard, 1932

### LYSIANASSOIDEA : ALICELLID GROUP

*Paralicella similis* Birstein & Vinogradov, 1960

### LYSIANASSOIDEA : AMARYLLIDID GROUP

*Amaryllis macrophthalmus* Haswell, 1879a

*Erikus dahli* Lowry & Stoddart, 1987

### LYSIANASSOIDEA : ARISTIIDAE

*Aristias antarcticus* Walker, 1906a

*Aristias collinus* K.H. Barnard, 1932

### LYSIANASSOIDEA : CYPHOCARIDIDAE

*Cyphocaris anonyx* Boeck, 1871b

*Cyphocaris challengeri* Stebbing, 1888

*Cyphocaris faurei* K.H. Barnard, 1916
*Cyphocaris richardi* Chevreux, 1905e

**LYSIANASSOIDEA : EURYTHENEID GROUP**

*Eurythenes gryllus* (Lichtenstein, 1822)

*Eurythenes obesus* (Chevreux, 1905a)

**LYSIANASSOIDEA : HIRONDELLEID GROUP**

*Hirondellea antarctica* (Schellenberg, 1926a)

**LYSIANASSOIDEA : KERGUELENEID GROUP**

*Kerguelenia adeliensis* Bellan-Santini, 1972a
*Kerguelenia antarctica* K.H. Barnard, 1930
*Kerguelenia antiborealis* Bellan-Santini & Ledoyer, 1987
*Kerguelenia compacta* Stebbing, 1888
*Kerguelenia glacialis* Schellenberg, 1926a
*? Kerguelenia palpalis* K.H. Barnard, 1932

**LYSIANASSOIDEA : LEPIDEPECREELID GROUP**

*Lepidepecreella ctenophora* Schellenberg, 1926a
*Lepidepecreella emarginata* Nicholls, 1938
*Lepidepecreella ovalis* K.H. Barnard, 1932
*Lepidepecreella tridactyla* Bellan-Santini, 1972a

## LYSIANASSOIDEA : LYSIANASSIDAE S.S.

[see Lowry & Stoddart 1997]

### Lysianassinae

*Acontiostoma marionis* Stebbing, 1888

*Aruga falklandica* (K.H. Barnard, 1932)

*Kakanui integricauda* (Stebbing, 1888)

*Kakanui punui* Lowry & Stoddart, 1983b

*Lysianopsis subantarctica* (Schellenberg, 1931a)

*Lysianopsis tieke* Lowry & Stoddart, 1983b

*Parambasia rossii* Stephensen, 1927e

*Parawaldeckia hirsute* Lowry & Stoddart, 1983b

*Parawaldeckia kidderi* (Smith, 1876)

*Parawaldeckia suzae* Lowry & Stoddart, 1983b

*Parawaldeckia vesca* Lowry & Stoddart, 1983b

*Parawaldeckia sp. 1* J.L. Barnard, 1972b

*Parawaldeckia sp*. 2 Stephensen, 1949

*Socarnoides kergueleni* Stebbing, 1888

*Socarnoides unidentatus* (Schellenberg, 1931a)

*Stomacontion acutibasalis* (Bellan-Santini & Ledoyer, 1974)

*Stomacontion bulbus* Rauschert, 1997a

*Stomacontion hurleyi* Lowry & Stoddart, 1983b

*Stomacontion insigne* K.H. Barnard, 1932

*Stomacontion pepinii* (Stebbing, 1888)

*Stomacontion pungapunga* Lowry & Stoddart, 1983b

*Waldeckia arnaudi* (Bellan-Santini, 1972a)

*Waldeckia chevreuxi* Stebbing, 1910a

*Waldeckia obesa* (Chevreux, 1905d)

*Waldeckia sp.* Takeuchi et al. 2001

**Tryphosinae**

*Allogaussia galeata* Schellenberg, 1926a
*? Allogaussia navicula* (K.H. Barnard, 1932)
*Allogaussia paradoxa* (Schellenberg, 1926a)
*Cheirimedon crenatipalmatus* Stebbing, 1888
*Cheirimedon femoratus* (Pfeffer, 1888)
*Cheirimedon fougneri* Walker, 1903a

*Cheirimedon similis* Thurston, 1974b
*Cheirimedon solidus* Andres, 1986

*Falklandia reducta* (Schellenberg, 1931a)
*Hippomedon incisus* K.H. Barnard, 1930

*Hippomedon kergueleni* (Miers, 1875a)
*Hippomedon macrocephalus* Bellan-Santini, 1972a
*Hippomedon major* (K.H. Barnard, 1932)
*Lepidepecreoides xenopus* K.H. Barnard, 1931a
*Lepidepecreum cingulatum* K.H. Barnard, 1932
*Lepidepecreum foraminiferum* Stebbing, 1888

*Lepidepecreum infissum* Andres, 1983
*Lepidepecreum urometacarinatum* Andres, 1985
*Lysianella morbihanensis* (Bellan-Santini & Ledoyer, 1974)
*? Orchomene sp.* Takeuchi et al. 2001
*? Orchomenella* (*Orchomenella*) *chelipes* (Walker, 1906a)
*Orchomenella* (*Orchomenella*) *franklini* (Walker, 1903a)
*Orchomenella* (*Orchomenella*) *guillei* De Broyer, 1985a
*Orchomenella* (*Orchomenella*) *hureaui* (De Broyer, 1973)
*Orchomenella* (*Orchomenella*) *kryptopinguides* (Andres, 1983)
*Orchomenella* (*Orchomenella*) *pinguides* (Walker, 1903a)

*Orchomenella* (*Orchomenella*) *ultima* (Bellan-Santini, 1972b)

*Orchomenella* (*Orchomenopsis*) *aahu* (Lowry & Stoddart, 1983b)

*Orchomenella* (*Orchomenopsis*) *acanthura* (Schellenberg, 1931a)

*Orchomenella* (*Orchomenopsis*) *cavimanus* (Stebbing, 1888)

*Orchomenella* (*Orchomenopsis*) *cavimana rostrata* (Schellenberg, 1931a)

*Orchomenella* (*Orchomenopsis*) *chilensis* (Heller, 1868)

*Orchomenella (Orchomenopsis) denticulata* Rauschert, 1995

*Orchomenella* (*?Orchomenopsis*) *goniops* (Walker, 1906a)

*Orchomenella* (*?Orchomenopsis*) *hiata* (Andres, 1983)

*Orchomenella* (*?Orchomenopsis*) *macrophthalma* (Birstein & Vinogradov, 1962b)

*Orchomenella* (*Orchomenopsis*) *rotundifrons* (K.H. Barnard, 1932)

*Orchomenella* (*Orchomenopsis*) *zschaui* (Pfeffer, 1888)

*Orchomenyx macronyx* (Chevreux, 1905d)

*Orchomenyx schellenbergi* (Thurston, 1972)

*Orchomenyx tabarini* (Thurston, 1972)

*Paralysianopsis odhneri* Schellenberg, 1931a

*Pseudokoroga barnardi* Schellenberg, 1931a

*Pseudorchomene coatsi* (Chilton, 1912a)

*Stephensenia haematopus* Schellenberg, 1928a

*Tryphosella analogica* (K.H. Barnard, 1932)

*Tryphosella bispinosa* (Schellenberg, 1931a)

*Tryphosella castellata* (K.H. Barnard, 1932)

*Tryphosella cicadopsis* (Schellenberg, 1926a)

*Tryphosella intermedia* (Schellenberg, 1926a)

*Tryphosella longitelson* (K.H. Barnard, 1932)

*Tryphosella macropareia* (Schellenberg, 1926a)

*Tryphosella marri* Thurston, 1974b

*Tryphosella murrayi* (Walker, 1903a)

*?Tryphosella paramoi* (Schellenberg, 1931a)

*Tryphosella schellenbergi* Lowry & Bullock, 1976
*Tryphosella serans* Lowry & Stoddart, 1983b
*?Tryphosella serrata* (Schellenberg, 1931a)
*Tryphosella triangularis* (K.H. Barnard, 1932)
*Tryphosella trigonica* (Stebbing, 1888)
*Tryphosites chevreuxi* Stebbing, 1914b
*Tryphosites sp.* Andres, 1975b
*Tryphosoides falcata* Schellenberg, 1931a

**Uristinae**

*Abyssorchomene charcoti* (Chevreux, 1912a)
*Abyssorchomene nodimanus* (Walker, 1903a)
*Abyssorchomene plebs* (Hurley, 1965a)
*Abyssorchomene rossi* (Walker, 1903a)
*Abyssorchomene scotianensis* (Andres, 1983)
*Cicadosa cicadoides* (Stebbing, 1888)
*Parschisturella carinata* (Schellenberg, 1926a)
*Parschisturella simplex* Andres, 1983
*Pseudonesimoides cornutilabris* Bellan-Santini & Ledoyer, 1974
*Uristes adarei* (Walker, 1903a)
*Uristes albinus* (K.H. Barnard, 1932)
*Uristes barbatipes* Stebbing, 1888)
*Uristes georgianus* (Schellenberg, 1931a)
*Uristes gigas* Dana, 1849
*Uristes mediator* J.L. Barnard, 1962d
*Uristes serratus* Schellenberg, 1931a
*Uristes stebbingi* (Walker, 1903a)
*Uristes subchelatus* (Schellenberg, 1931a)

## LYSIANASSOIDEA : OPISIDAE

*Podoprionides incerta* Walker, 1906a

## LYSIANASSOIDEA : PACHYNID GROUP

### Acidostomatine Group

*Shackletonia robus*ta K.H. Barnard, 1931a

### Pachynine Group

*Drummondia sculptidentata* Ren, 1991
*Ekelofia oculata* (Schellenberg, 1931a)
*Figorella macrophoculata* Ren, 1991

*Figorella tanidea* J.L. Barnard, 1962d

*Pachychelium antarcticum* Schellenberg, 1926a
*Pachychelium barnardi* Alonso de Pina, 1993
*Pachychelium nichollsi* Lowry, 1984b
*Pachychelium schellenbergi* Lowry, 1984b

### Sophrosynine Group

*Sophrosyne antarctica* Ren, 1991
*Sophrosyne murrayi* Stebbing, 1888

**LYSIANASSOIDEA : SCOPELOCHEIRIDAE**

*Paracallisoma alberti* Chevreux, 1903

*Scopelocheiropsis abyssalis* Schellenberg, 1926a

*Scopelocheirus schellenbergi* Birstein & Vinogradov, 1958

**LYSIANASSOIDEA : THORIELLID GROUP**

*Chevreuxiella obensis* Birstein & Vinogradov, 1962b

*Danaella mimonectes* Stephensen, 1925b

**LYSIANASSOIDEA : INCERTAE SEDIS**

[fide BK91]

*Gainella chelata* Chevreux, 1912a

*Stenia magellanica* Dana, 1852a

**MELPHIDIPPIDAE**

[see Barnard & Barnard 1983: 607]

*Melphidippa antarctica* Schellenberg, 1926a

*Melphidippa serrata* (Stebbing, 1888)

*Melphisubchela prehenda* Andres, 1981b

**OEDICEROTIDAE**

*Carolobatea schneideri* (Stebbing, 1888)

*Carolobatea sp*. J.L. Barnard, 1972b

*Halicreion vanhoeffeni* Schellenberg, 1926a
*Monoculodes antarcticus* K.H. Barnard, 1932
*Monoculodes jazdzewskii* De Broyer, 1980
*Monoculodes scabriculosus* K.H. Barnard, 1932
*Monoculopsis vallentini* Stebbing, 1914b
*Oediceroides calmani* Walker, 1906b
*Oediceroides cinderella* Stebbing, 1888
*Oediceroides emarginatus* Nicholls, 1938
*Oediceroides lahillei lahillei* Chevreux, 1911b
*Oediceroides lahillei polita* Schellenberg, 1931a
*Oediceroides macrodactylus* Schellenberg, 1931a
*Oediceroides newnesi* (Walker, 1903a)
*Oediceroides rostratus* (Stebbing, 1883)
*Oediceroides similis* Nicholls, 1938
*Paramonoculopsis acuta* Alonso de Pina, 1997
*?Paraperioculodes belgicae* Ruffo, 1949
*Paraperioculodes brevimanus* K.H. Barnard, 1931a
*Paraperioculodes brevirostris* (Schellenberg, 1931a)
*Paraperioculodes cystiferus* (Schellenberg, 1931a)
*Paraperioculodes microrhynchus* Ruffo, 1949
*Paroediceroides sinuatus* Schellenberg, 1931a

**PAGETINIDAE**

*Pagetina antarctica* Andres, 1981
*Pagetina genarum* K.H. Barnard, 1931a
*Pagetina monodi* (Nicholls, 1938)
*Pagetina reducta* Holman & Watling, 1981

**PARDALISCIDAE**

*Halice macronyx* (Stebbing, 1888)
*Halice profundi* K.H. Barnard, 1932
*Halice secunda* (Stebbing, 1888)
*Halice tenella* Birstein & Vinogradov, 1962b
*Halicella parasitica* Schellenberg, 1926a
*Necochea pardella* J.L. Barnard, 1962d
*Nicippe unidentata* K.H. Barnard, 1932
*Pardalisca abyssoides* K.H. Barnard, 1932
*Pardalisca magellanica* Schellenberg, 1931a
*Pardalisca marionis* Stebbing, 1888

**PHLIANTIDAE**

*Iphinotus typicus* (Thomson, 1882)

**PHOXOCEPHALIDAE**

[check Bnd & Drummond 1978]

*Cephalophoxoides kergueleni* (Stebbing, 1888)
*Coxophoxus coxalis* (K.H. Barnard, 1932)
*Fuegiphoxus abjectus* Barnard & Barnard, 1980
*Fuegiphoxus fuegiensis* (Schellenberg, 1931a)
*Fuegiphoxus inutilus* Barnard & Barnard, 1980
*Fuegiphoxus uncinatus* (Chevreux, 1912a)
*Harpiniopsis aciculum* Ren, 1991
*Harpiniopsis wandichia* (J.L. Barnard, 1962d)
*Heterophoxus pellusidus* Ren, 1991
*Heterophoxus trichosus* K.H. Barnard, 1932

*Heterophoxus videns* K.H. Barnard, 1930
*Leptophoxoides molaris* J.L. Barnard, 1962d
*Metharpinia longirostris* Schellenberg, 1931a
*Metharpinia protuberantis* Alonso de Pina, 2001.
*Microphoxus cornutus* (Schellenberg, 1931a)
*Palabriaphoxus latifrons* (Ren, 1991)
*Parafoxiphalus longicarpus* Alonso de Pina, 2001.
*?Paraphoxus latipes* Ren, 1991
*?Paraphoxus pyripes* K.H. Barnard, 1930
*?Parharpinia obliqua* K.H. Barnard, 1932
*?Parharpinia rotundifrons* K.H. Barnard, 1932
*Phoxorgia sinuata* (K.H. Barnard, 1932)
*Proharpinia antipoda* Schellenberg, 1931a
*Proharpinia stephenseni* (Schellenberg, 1931a)
*Pseudfoxiphalus setosus* Andres, 1991
*Pseudharpinia antarctica* Ren, 1991
*Pseudharpinia calcariaria* Bushueva, 1982
*Pseudharpinia cariniceps* (K.H. Barnard, 1932)
*Pseudharpinia dentate* Schellenberg, 1931a
*Pseudharpinia obtusifrons* (Stebbing, 1888)
*Pseudharpinia vallini* (Dahl, 1954)
*Torridoharpinia hurleyi* (J.L. Barnard, 1958a)

**PHOXOCEPHALOPSIDAE**

*Eophoxocephalopsis colombus* Alonso de Pina, 2000.
*Eophoxocephalopsis deceptionis* (Stephensen, 1947a).
*Eophoxocephalopsis rhachianensis* Thurston, 1989a
*Phoxocephalopsis gallardoi* Barnard & Clark, 1984
*Phoxocephalopsis zimmeri* Schellenberg, 1931a

*Puelche orensanzi* Barnard & Clark, 1982a

**PLATYISCHNOPIDAE**

*Eudevenopus gracilipes* (Schellenberg, 1931a)

**PLEUSTIDAE**

*Austropleustes cuspidatus* K.H. Barnard, 1931a
*?Austropleustes simplex* K.H. Barnard, 1932
*Mesopleustes abyssorum* (Stebbing, 1888)
*Parepimeria bidentata* Schellenberg, 1931a
*Parepimeria crenulata* Chevreux, 1912a
*Parepimeria irregularis* (Schellenberg, 1931a)
*Parepimeria major* K.H. Barnard, 1932
*Parepimeria minor* Watling & Holman, 1980
*?Pleusymtes sp 1*. Branch *et al.*, 1991

**PONTOPOREIIDAE**

[see Bnd & Bnd, 1983: 562]

*Zaramilla kergueleni* Stebbing, 1888

**PSEUDAMPHILOCHIDAE**

*Pseudamphilochus shoemakeri* Schellenberg, 1931a

## SEBIDAE

*Seba antarctica* Walker, 1906c

*?Seba georgiana* Schellenberg, 1931a

*Seba saundersii* Stebbing, 1875b

*Seba stoningtonensis* Thurston, 1974b

*Seba subantarctica* Schellenberg, 1931a

*Seba typical* (Chilton, 1884a)

*Seba sp. 1* Holman & Watling, 1983b

*Seba sp.2* Holman & Watling, 1983b

## STEGOCEPHALIDAE

[see Berge, De Broyer & Vader, 2000; Berge & Vader 2001]

### Andaniexinae

*Andaniexis ollii* Berge, De Broyer & Vader, 2000

*Andaniotes abyssorum* Stebbing, 1888.

*Andaniotes linearis* K.H. Barnard, 1932

*Andaniotes pooh* Berge 2001b

*Andaniotes pseudolinearis* Berge 2001b

*Parandaniexis dewitti* Watling & Holman, 1980

*Stegosoladidus antarcticus* Berge, 2001a

*Stegosoladidus debroyeri* Berge, 2001a

*Stegosoladidus ingens* (Chevreux, 1906e)

**Andaniopsinae**

*Andaniopsis integripes* (Bellan-Santini & Ledoyer, 1987)

**Parandaniinae**

*Parandania boecki* (Stebbing, 1888)
*Parandania gigantea* (Stebbing, 1883)
*Parandania nonhiata* Andres, 1985

**Stegocephalinae**

*Austrophippsia unihamata* (Berge & Vader, 2000)
*Schellenbergia vanhoeffeni* (Schellenberg, 1926a)
*Stegocephalus kergueleni* (Schellenberg, 1926a)
*Stegocephalus rostrata* K.H. Barnard, 1932
*Stegomorphia watlingi* (Berge, De Broyer & Vader, 2000).
*Stegocephalina pacis* (Bellan-Santini & Ledoyer, 1974)
*Tetradeion crassum* (Chilton,1883)

**STENOTHOIDAE**

*Antatelson antennatum* Bellan-Santini & Ledoyer, 1974
*Antatelson cultricauda* (K.H. Barnard, 1932)
*Antatelson rostratum* Bellan-Santini & Ledoyer, 1974
*Antatelson tuberculatum* Andres, 1989
*Antatelson walkeri* (Chilton, 1912a)
*Aurometopa aurorae* (Nicholls, 1938)
*Mesoproboloides cornuta* (Schellenberg, 1926a)
*Mesoproboloides similis* (Schellenberg, 1926a)

*Mesoproboloides spinosa* Bellan-Santini & Ledoyer, 1974

*Metopoides antarcticus* (Walker, 1906b)

*Metopoides clavata* Schellenberg, 1931a

*Metopoides crassa* Schellenberg, 1931a

*Metopoides curvipes* Schellenberg, 1926a

*Metopoides elliptica* Schellenberg, 1931a

*Metopoides heterostylis* Schellenberg, 1926a

*Metopoides lanceolatus* Rauschert, 1990a

*Metopoides latus* Rauschert, 1990a

*Metopoides leptomanus* Rauschert, 1990a

*Metopoides longicornis* Schellenberg, 1931a

*Metopoides macrocheir* Schellenberg, 1926a

*Metopoides magellanica* (Stebbing, 1888)

*Metopoides sarsi* (Pfeffer, 1888)

*Metopoides sp.1* Bellan-Santini & Ledoyer, 1974

*Metopoides sp.2* Jazdzewski *et al*., 1992

*Metopoides typicaminus* Andres, 1995

*Paraprobolisca leptopoda* Ren, 1991

*Parathaumatelson nasicum* (Stephensen, 1927e)

*Probolisca elliptica* (Schellenberg, 1931a)

*Probolisca nasutigenes* (Stebbing, 1888)

*Probolisca ovata* (Stebbing, 1888)

*Proboloides typica* (Walker, 1906b)

*Proboloides sp.1* Stephensen, 1947a [

*Proboloides sp.2* Branch *et al*.

*Proboloides sp.3* Branch *et al*.

*Prometopa dorsoundata* Bushueva, 1988

*Prometopa edentata* Rauschert, 1990a

*? Prometopa longipalma* Ren, 1991

*Prometopa tuberculata* Schellenberg, 1926a

*Prothaumatelson nasutum* (Chevreux, 1912a)

*Pseudothaumatelson cyproides* Nicholls, 1938

*Pseudothaumatelson patagonicum* Schellenberg, 1931a

*Scaphodactylus bentarti* Rauschert, 1995

*Scaphodactylus foliodactylus* (Rauschert, 1990a).

*Scaphodactylus gigantocheirus* Rauschert & Andres, 1993.

*Scaphodactylus simus* Rauschert & Andres, 1994

*Scaphodactylus sp. 1* Rauschert & Andres, 1993.

*Scaphodactylus sp. 2* Rauschert & Andres, 1993.

*Scaphodactylus sp. 3* Rauschert & Andres, 1993.

*Stenothoe aucklandicus* Stephensen, 1927e

*Stenothoe falklandica* Schellenberg, 1931a

*Stenothoe magellanica* Rauschert, 1998

*Stenothoe sivertseni Stephensen, 1949*

*Stenothoe sp.1* Bellan-Santini & Ledoyer, 1987

*Thaumatelson herdmani* Walker, 1906b

*Thaumatelsonella kingelepha* Rauschert & Andres, 1991

*Torometopa andresi* (Rauschert, 1990a)

*Torometopa angustus* Rauschert, 1990a

*Torometopa antarctica* (Walker, 1906b)

*?Torometopa bellansantiniae* (Bushueva, 1988)

*Torometopa carinata* (Schellenberg, 1931a)

*Torometopa compacta* (Stebbing, 1888)

*Torometopa crassicornis* (Schellenberg, 1931a)

*Torometopa crenatipalmata* (Stebbing, 1888)

*Torometopa crypta* Andres & Rauschert, 1992.

*Torometopa dentimanus* (Nicholls, 1938)

*Torometopa elephantensis* Andres & Rauschert, 1992.

*?Torometopa laevis* (Ren, 1991)

*Torometopa macromanus* (Rauschert, 1990a)

*Torometopa nitita* (Ren, 1991)

*Torometopa palmata* (Ruffo, 1949)

*Type specimen location*:

*Torometopa parallelocheir* (Stebbing, 1888)

*Torometopa perlata* (K.H. Barnard, 1930)

*Torometopa porcellana* (K.H. Barnard, 1932)

*Torometopa pseudoperlata* Andres, 1993.

*Torometopa serrata* (Rauschert, 1990a)

*Torometopa stephenseni* (Ruffo, 1949)

*Torometopa sp.1* Andres & Rauschert, 1992.

*Torometopa sp.2* Andres, 1993.

**STILIPEDIDAE**

*Alexandrella australis* (Chilton, 1912a)

*Alexandrella dentata* Chevreux, 1912a

*Alexandrella inermis* Bellan-Santini & Ledoyer, 1987

*Alexandrella mixta* (Nicholls, 1938)

*Alexandrella pulchra* Ren, 1991

*Bathypanoploea schellenbergi* Holman & Watling, 1983a

**SYNOPIIDAE**

*Bruzelia poton* J.L. Barnard, 1972c

*Cardenio paurodactylus* Stebbing, 1888

*Syrrhoe nodulosa* K.H. Barnard, 1932

*Syrrhoe psychrophila* Monod, 1926

*Syrrhoe tuberculata* Dahl, 1954

*Syrrhoites anaticauda* K.H. Barnard, 1930

*Syrrhoites sorpresa* (J.L. Barnard, 1962d)

*Tiron antarcticus* K.H. Barnard, 1932

**TALITRIDAE**

*Allorchestes compressa* Dana, 1852a
*Allorchestes novizealandidae* Dana, 1852a
*Allorchestes sp.1* Stephensen, 1938c
*Platorchestia platensis* (Kroyer 1845)
*? Orchestia scutigerula* Dana, 1853
*Orchestoidea tuberculata* Nicolet, 1849
*Protorchestia nitida* (Dana, 1852a)
*Transorchestia chiliensis* (Milne-Edwards, 1840)

**UROHAUSTORIIDAE**

*Huarpe escofeti* Barnard & Clark, 1982b

**UROTHOIDAE**

*Carangolia cornuta* Bellan-Santini & Ledoyer, 1987
*Urothoe falcata* Schellenberg, 1931a
*?Urothoe latifrons* Ren, 1991
*Urothoe marionis* Bellan-Santini & Ledoyer, 1987
*Urothoe oniscoides* (K.H. Barnard, 1932)
*Urothoe vemae* J.L. Barnard, 1962d
*Urothoides lachneessa* (Stebbing, 1888)

**VALETTIIDAE**

*Valettia coheres* Stebbing, 1888

**ZOBRACHOIDAE**

*Chono angustiarum* Clark & Barnard, 1987

*Tonocote introflexidus* Clark & Barnard, 1988

*Tonocote magellani* Clark & Barnard, 1986

**II. SOUS-ORDRE COROPHIIDEA**
**Leach, 1814**

**INFRAORDER COROPHIIDA Leach, 1814**

**Superfamily AOROIDEA Stebbing, 1899c**
**FAMILY AORIDAE STEBBING, 1899C**

*Aora anomala* Schellenberg, 1926a

*Aora kergueleni* Stebbing, 1888

*Aora maculata* (Thomson, 1879b)

*Aora trichobostrycha* Stebbing, 1888

*Aora typica* Kroyer, 1845

*Aora sp. 1* Nicholls, 1938

*Bemlos kergueleni* (Stebbing, 1888)

*Lembos argentinensis* Alonso de Pina, 1992

*Lembos fuegiensis* Dana, 1853 [AV genus]

*Lembos sp. 1* J.L. Barnard, 1972b

*Lembos sp. 2* J.L. Barnard, 1972b = *Meridiolembos pertinax* Myers, 1981c

*Lembos sp. 3* J.L. Barnard, 1972b
*Lembos sp. 4* Bellan-Santini & Ledoyer, 1987
*Meridiolembos acherontis* Myers, 1981c
*Meridiolembos pertinax* Myers, 1981c
*Microdeutopus sp. 1* Stephensen, 1927e

**Superfamily Corophioidea Leach, 1814**

**FAMILY AMPITHOIDAE BOECK, 1871**

**Subfamily Ampithoinae Boeck, 1871**

*Ampithoe kergueleni* Stebbing, 1888
*Ampithoe valida* Smith, 1873
*Peramphithoe femorata* (Kroyer, 1845)

**FAMILY COROPHIIDAE Leach, 1814**

**Subfamily Corophiinae Leach, 1814**

Corophinae: Tribe Corophiini, Leach, 1814

*Crassicorophium bonellii* (Milne Edwards, 1830)
*Corophium cylindricum* (Say, 1818)

**Corophinae: Tribe Haplocheirini Myers & Lowry, 2003**

*Anonychocheirus richardsoni* Moore & Myers, 1983
*Haplocheira balssi* Schellenberg, 1931a
*Haplocheira barbimana* (Thomson, 1879b)

*Haplocheira barbimana barbimana* (Thomson, 1879b)
*Haplocheira barbimana robusta* K.H. Barnard, 1932
*Haplocheira barbimana typica* Haswell, 1879a
*Haplocheira plumosa* Stebbing, 1888
*Kuphocheira emancipata* Moore & Myers, 1983
*Kuphocheira setimana* K.H. Barnard, 1931a

**Infraorder CAPRELLIDA Leach, 1814**

**Superfamily CAPRELLOIDEA LEACH, 1814**
**FAMILY CAPRELLIDAE LEACH, 1814**
**Subfamily Caprellinae Leach, 1814**

*Caprella equilibra* Say, 1818
*Caprella manneringi* McCain, 1979
*Caprella penantis* Leach, 1814
*Caprella ungulina* Mayer, 1903
*Caprella sp.* McCain & Gray, 1971
*Caprellaporema subantarctica* Guerra-García 2003a
*Deutella vemae* (McCain & Gray, 1971)
*?Eupariambus sp*. Branch *et al*., 1991
*Mayerella magellanica* McCain & Gray, 1971
*Protella trilobata* McCain & Gray, 1971
*Protellopsis kergueleni* Stebbing, 1888
*Pseudaeginella campbellensis* Guerra-García, 2003a
*Pseudaeginella tristanensis* Stebbing, 1888
*Triantella solitaria* Mayer, 1903

**Subfamily Phtisicinae Vassilenko, 1968**

*Aeginoides gaussi* Schellenberg, 1926b
*Caprellina longicollis* (Nicolet, 1849)
*? Caprellina longicollis* (Nicolet, 1849)
*Caprellinoides antarcticus* Schellenberg, 1926(to be revised)
*Caprellinoides mayeri* (Pfeffer, 1888)
*Caprellinoides mayeri* Barnard, 1930 (to be revised)
*Caprellinoides singularis* Guerra-García, 2001c
*Caprellinoides spinosus* (Pfeffer, 1888) (to be revised)
*Caprellinoides tristanensis* Stebbing, 1888
*Caprellinoides tristanensis* Stebbing, 1888 (to be revised)
*Dodecas elongata* Stebbing, 1883
*Dodecasella elegans* K.H. Barnard, 1931
*Dodecasella georgiana* (Schellenberg, 1931a)
*Paraproto* sp.
*Pseudododecas bowmani* McCain & Gray, 1971
*Pseudoprotomima hedgpethi* McCain & Gray, 1971

**FAMILY CYAMIDAE RAFINESQUE, 1815**

*Cyamus balaenopterae* K.H. Barnard, 1931
*Cyamus boopis* Lütken, 1870
*Cyamus catodontis* Margolis, 1954
*Cyamus erraticus* Roussel de Vauzème, 1834
*Cyamus gracilis* Roussel de Vauzème, 1834
*Cyamus ovalis* Roussel de Vauzème, 1834
*Isocyamus antarcticensis* Vlasova in Berzin & Vlasova, 1982

**CAPRELLOIDEA: FAMILY DULICHIIDAE DANA, 1849**

*Dulichia antarctica* Rauschert, 1988.

*Paradyopedos antarcticus* Andres & Rauschert, 1990

*Pseudodulichia antarctica* (Rauschert, 1988)

**CAPRELLOIDEA: FAMILY PODOCERIDAE LEACH, 1814**

*Neoxenodice caprellinoides* Schellenberg, 1926b

*Neoxenodice cryophile* Lowry, 1976

*Neoxenodice hoshiai* Takeuchi & Takeda, 1992

*Podocerus brasiliensis* (Dana, 1853)

*Podocerus capillimanus* Nicholls, 1938

*Podocerus cristatus rotundatus* Schellenberg, 1931a

*Podocerus danae* (Stebbing, 1888)

*Podocerus danae armatus* Bellan-Santini & Ledoyer, 1987

*Podocerus ornatus* (Miers, 1875a)

*Podocerus septemcarinatus* Schellenberg, 1926a

*Podocerus sp. 1.* K.H. Barnard, 1932

**SUPERFAMILY PHOTOIDEA Boeck, 1871**

**PHOTOIDEA: Family ISChyroceridae STEBBING, 1899C**

**Subfamily Ischyrocerinae Stebbing, 1899c**

Tribe Ischyrocerini Stebbing, 1899c

*Ischyrocerus camptonyx* Thurston, 1974a
*Ischyrocerus hortator* J.L. Barnard, 1964d
*Ischyrocerus longimanus* (Haswell, 1879b)
*?Ischyrocerus sp.1* Bellan-Santini & Ledoyer, 1987
*?Ischyrocerus sp.2* Branch *et al.*, 1991
*Jassa alonsoae* Conlan, 1990
*Jassa falcata* Montagu, 1808 s.l.
*Jassa fenwicki* Conlan, 1990
*?Jassa goniamera* Walker, 1903a
*Jassa ingens* Pfeffer, 1888
*Jassa justi* Conlan, 1990
*?Jassa multidentata* Schellenberg, 1931a
*Jassa thurstoni* Conlan, 1990
*?Jassa wandeli* Chevreux, 1906e
*Jassa sp. 1* Stephensen, 1927e
*Jassa sp. 2* Stephensen, 1947a
*Parajassa tristanensis* (Stebbing, 1888)
*Pseudischyrocerus crenatipes* Bellan-Santini & Ledoyer, 1987
*Pseudischyrocerus denticauda* Schellenberg, 1931a
*Pseudischyrocerus distichon* (K.H. Barnard, 1930)
*Ventojassa georgiana* (Schellenberg, 1931a)

Ischyrocerinae: Tribe Siphonoecetini Just, 1983

*Cerapus oppositus* K.H. Barnard, 1932
*Cerapus sismithi* Stebbing, 1888
*Pseudericthonius gaussi* Schellenberg, 1926a
*Pseudericthonius hesperidesi* Rauschert, 1997
*Pseudericthonius inflatus* Ren, 1991

**PHOTOIDEA: FAMILY PHOTIDAE BOECK, 1871**

*Gammaropsis* (*Gammaropsis*) *bennetti* Thurston, 1974b
*Gammaropsis* (*Gammaropsis*) *ctenura* (Schellenberg, 1931a)
*Gammaropsis* (*Gammaropsis*) *deseadensis* Alonso, 1981
*Gammaropsis* (*Gammaropsis*) *exsertipes* Stebbing, 1888
*Gammaropsis* (*Gammaropsis*) *georgiana* (Schellenberg, 1931a)
*Gammaropsis* (*Gammaropsis*) *kergueleni* (Schellenberg, 1926a)
*Gammaropsis* (*Gammaropsis*) *longicornis* Walker, 1906c
*Gammaropsis* (*Gammaropsis*) *longitarsus* (Schellenberg, 1931a)
*Gammaropsis* (*Gammaropsis*) *monodi* (Schellenberg, 1931a)
*Gammaropsis* (*Gammaropsis*) *purpurescens* (K.H. Barnard, 1932)
*Gammaropsis* (*Gammaropsis*) *remipes* (K.H. Barnard, 1932)
*Gammaropsis* (*Gammaropsis*) *serricra* (K.H. Barnard, 1932)
*Gammaropsis* (*Gammaropsis*) *triodon* (Schellenberg, 1926a)
*Gammaropsis* (*Gammaropsis*) *valdiviae* (Schellenberg, 1926c)
*Megamphopus angustilobatus* Ren, 1991
*Megamphopus dimorpha* (K.H. Barnard, 1932)
*Megamphopus elephantis* K.H. Barnard, 1932
*Gammaropsis* (*Paranaenia*) *dentifera* (Haswell, 1879b)
*Gammaropsis* (*Paranaenia*) *typica* (Chilton, 1884a)
*Gammaropsis* (*Pseudeurystheus*) *sublitoralis* (Schellenberg, 1931a)
*Gammaropsis* (*Segamphopus*) *blaisus* (K.H. Barnard, 1932)
*Gammaropsis sp. 1* Stephensen, 1927e
*Gammaropsis sp. 2* Stephensen, 1947a
*Gammaropsis sp. 3* Truchot, 1974
*Gammaropsis sp. 4* Truchot, 1974
*Gammaropsis sp. 5* Branch *et al.*, 1991
*Paragammaropsis prenes* Ren, 1991

*Photis coeca* J.L. Barnard, 1962d

*Photis macrocarpa* Stebbing, 1888

*Photis sp. 1* Truchot, 1974