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Trophic diversity within the eastern Weddell Sea amphipod community

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Abstract

Amphipod crustaceans form one of the most diversified animal groups within the Antarctic macrozoobenthos, both from the taxonomic point of view (more than 800 species have been recorded in the Southern Ocean) as by niche occupation and at the community level. Thus, amphipods are likely to play an important role in the organic matter fluxes that occur on the Antarctic sea floor. The dietary behaviour of these peracarids is still poorly known, and only few species have been analysed. This paper describes the trophic preferences of some dominant amphipod species of the Eastern Weddell Sea benthos, deduced from stomach content analyses and behavioural observations in aquaria. More than 1000 specimens, belonging to 40 species (representing 27 genera and 15 families) were dissected; and several thousands of individuals were kept in aquaria for 6–9 weeks and presented with various potential foods. These two approaches revealed at least eight different feeding types: suspension-feeding, deposit-feeding, deposit-feeding coupled with predation, opportunistic predation, micropredatory browsing, macropredation coupled with scavenging, opportunistic necrophagy and true necrophagy. These different behaviours cover almost all the possible feeding types with the exception of macroherbivorous browsing. Among the eight described feeding types, no particular one is dominant. In the same way, types involving microphagy and macrophagy are equally represented. Predatory types (opportunistic or exclusive) account for 64% of the species analysed, while scavenging types (facultative or obligate) account for 60%. The overlap suggests that many amphipod species have a wide dietary spectrum and are able to take advantage of different food resources.

Introduction

The Antarctic macrozoobenthos is characterized by a relatively high species diversity and richness. Several zoological groups, namely sessile suspension-feeders such as Porifera and Bryozoa and the motile endo- or epibenthic Polychaeta and Peracarida, are rich in species. Moreover, a high degree of species endemism has been recorded for many taxa (White, 1984), attaining up to 85% in the case of benthic Amphipoda (De Broyer & Jażdżewski, 1993, 1996). Some groups, however, show a moderate species richness (like Bivalvia and Gastropoda), while other groups remain either absent (Stomatopoda, reptant Decapoda) or under-represented (Cirripedia, natant Decapoda) on the Antarctic shelf bottom (Arntz et al., 1997). Circumpolarity in species distribution and extended range of eurybathy (Brey et al., 1996) are common features, as are often high levels of population abundance or biomass. Detailed information on the Antarctic zoobenthos and its diversity can be found in the recent syntheses of Arntz et al. (1994, 1997).

Within Antarctic benthic communities, Peracarida form by far the most speciose animal group (De Broyer & Jażdżewski, 1996), and are likely to be one of the most diversified in terms of mode of life, trophic types, habitat and size spectra. Southern Ocean Amphipoda, for instance, number at least 820 (>85% benthic) Antarctic and Subantarctic species, more than 320 of which inhabit the Weddell Sea (De Broyer et al., 1999). Despite their low biomass, benthic crustaceans, including peracarids and natant decapods, appear to be a dominant group in terms of energy fluxes in the Weddell Sea shelf ecosystem (Jarre-Teichmann et al., 1997). Amphipods in particular provide an important food resource to many Southern Ocean demersal and benthic fishes (see e.g. Gon & Heemstra, 1990; Kock, 1992; Olaso et al., 2000), and to a number of benthic invertebrates (e.g. Dearborn, 1977; McClintock, 1994), birds (e.g. Rauschert, 1991; Cherel & Kooyman, 1998; Jażdżewski & Konopacka, 1999) and seals (e.g. Dearborn, 1965; Green & Burton, 1987).

The ecofunctional, and specifically the trophodynamic role of these Antarctic amphipods, is still poorly known, despite the pioneering studies of Richardson (1977), Oliver & Slattery (1985), Slattery & Oliver (1986), Coleman (1989a,b,c, 1990a,b) and Klages & Gutt (1990a,b). Less than 10% of amphipod species have been studied, with very little quantitative work done. Moreover, for the most important groups of Antarctic amphipods (namely Eusiroidea and Lysianassoidea), the feeding type cannot often be deduced with certainty from feeding appendage morphology. Some necrophagous lysianassoids, however, show a particular mandibular structure, with a specialised molar process, which is a clear guide to their feeding mode (see e.g. De Broyer & Thurston, 1987).

The present paper reports analyses of trophic preferences for some 40 benthic amphipod species representing 27 genera and 15 families. All species were sampled by diverse trawling or trapping devices during three cruises undertaken in the eastern Weddell Sea. Among the studied species, more than 25 had not been previously investigated from the point of view of their feeding preferences. Trophic types were determined on the basis of both digestive tract analyses and ethological observations in aquaria.

Materials and methods

Sampling

Amphipods were collected from benthic and suprabenthic samples taken in the eastern Weddell Sea during three Antarctic summer cruises of R.V. *Polarstern*: EPOS Leg 3 (ANT VII/4, 1989; Arntz et al., 1990), EASIZ I (ANT XIII/3, 1996; Arntz & Gutt, 1997) and EASIZ II (ANT XV/3, 1998; Arntz & Gutt, 1999) (Fig. 1). All the sampling areas are located within major macrobenthic assemblages known as the “Weddell Sea Eastern & Southern Shelf Communities” (Voß, 1988).

In total, 130 catches provided amphipod material from depths of 60–2000 m. Collecting gear included Agassiz, benthopelagic and bottom trawls, dredges, epibenthic sledges, TV grabs, giant and multi– box-corers, and baited traps (±48 h deployments). Most of the specimens were caught by trawls, the mesh size of which (5 mm) did not retain very small species.

Trophic behaviour

Ethological observations (food detection and capture, mobility patterns) were performed on living specimens of more than 40 species kept in a cool container on board (mostly during the ‘*Polarstern*’ EASIZ II cruise) and afterwards in a cool laboratory at IRScNB, Brussels. Amphipods were maintained at a temperature of −1 °C (±1 °C) in 2–30 l aquaria. On board, the water was changed daily and replaced by fresh seawater taken from the sea surface (pre-cooled to 0 °C when necessary).

Aquaria were provided with different substrates, depending on the species studied (filter gauze, mixed sediment, sponge spicule mat, stones and different common sessile organisms: sponges, cnidarians, hemichordates and bryozoans). Feeding experiments were performed in these aquaria, using different living organisms (like crustaceans, echinoderms or plankton) or dead material (such as pieces of amphipods, fishes or squid) placed on the bottom or presented with forceps. Reactions to odour stimuli were tested using drops of a fluid made of crushed fresh amphipods (‘amphipod juice’).

Digestive tract analyses

Amphipod gut content analyses have been done mainly on specimens fixed (immediately after sampling) in 4% formaldehyde or, sometimes, on fresh individuals. Dissections (about 1000 individuals) were conducted under a binocular dissecting microscope (Leica MZ12), using forceps and scissors. The digestive tract was cut at the oesophagus level and extracted together with midgut glands from the body. The digestive tract was separated from midgut glands, opened and the content was spread on a micro-slide. Stains (Serva blue g, fuchsin, Bengal pink) were added depending on detected material. The whole slide surface was examined under an optical microscope (Leitz Diaplan) equipped with reflection contrast system. Some digestive tract contents (or parts of them) were explored by SEM techniques.

The amount of food in stomach (C_s) and gut (C_g), respectively, was coded with arbitrary scores (4:

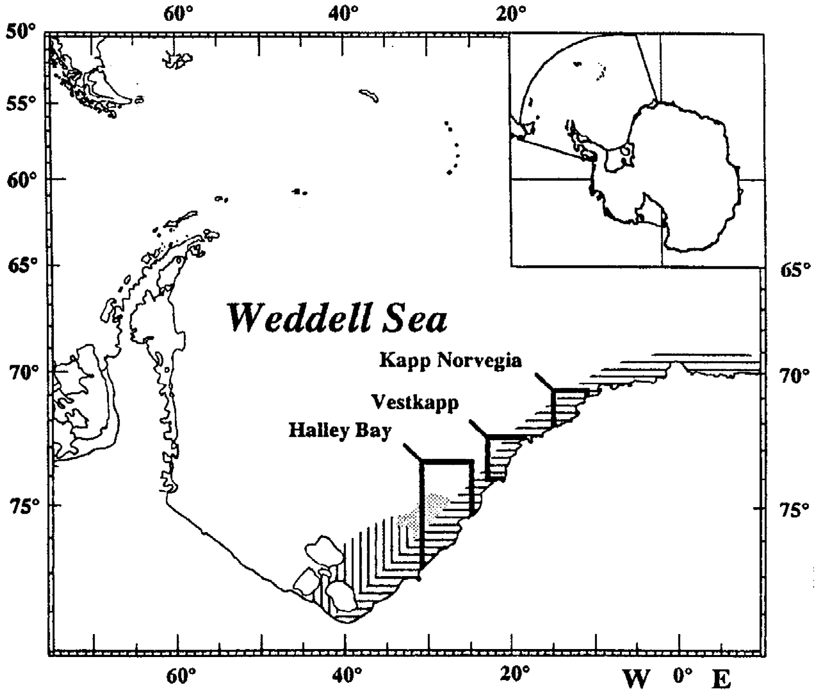

Figure 1. Map of the sampling area (modified from Voß, 1988).

75–100% of the volume is filled; 3: 50–75%; 2: 25–50%; 1: 0–25%). Every item present in the digestive tract was determined to the lowest possible taxonomic group, and its proportion was coded using a similar coefficient (P_s, P_g = 1, 2, 3 or 4). A semi-quantitative approach, related to the 'percentage points' method (Hynes, 1950; Williams, 1981), has been adopted using the formulas:

$$I(\mathrm{i}) = \sum_{n=1}^{x} C_s(n) * P_s(n) + C_g(n) * P_g(n), \qquad (1)$$

where $I(\mathrm{i})$, dimensionless, is the importance of item i in the diet of a given species, and x the number of specimens dissected;

$$R(\mathrm{i}) = \left[\frac{I(\mathrm{i})}{\sum_{n=1}^{y} I(n)} \right] * 100, \qquad (2)$$

where $R(\mathrm{i})$, in %, represents the relative importance of item i in the total diet of a given species, and y the number of different items.

These percentages must be regarded with caution as they represent somewhat of a distorsion of the real food intake. Mineral grains, and to a lesser extend diatom frustules, will be largely unchanged by digestive processes, and may have a longer residence time in the gut. In contrast, the fragments of cuticule that are sufficient to identify crustaceans, may represent less than 10% of the volume of food ingested. This possible bias cannot, however, be quantified in any meaningful way, except maybe using the stable isotope approach (Nyssen et al., 2001).

Results and specific discussion

The trophic type of any animal can be assessed in several ways, depending on the chosen approach. On the basis of food preference, distinction can be made among herbivory, detritivory or carnivory. When considering food size, it is possible to separate microphagy and macrophagy. Lastly, based on feeding mode, one can, e.g., discriminate between predation, browsing or necrophagy among carnivores, or suspension– and deposit– feeding among detritivores. An attempt to condense the different approaches on a single diagram is given in Figure 2.

Almost all different feeding types presented in Figure 2 can be encountered in the amphipod benthic communities of the eastern Weddell Sea shelf. A noticeable exception concerns macroherbivory which appears to be lacking, but which is explained by the absence of macroalgae in the ice-covered deep shelf area (Schalk et al., 1993). On the basis of both diet analyses (i.e. R(i)’s distribution in species’ digestive tract contents) and ethological observations, the following eight feeding types can be distinguished.

1. Suspension-feeding type

Amphipods of this group are typically epibenthic and feed on particulate organic material (plant or animal, dead or alive) sinking from the water column, such as plankton or micronekton or by-products (e.g. faecal pellets), and advected material. These animals are always weakly motile, or even sedentary. The most common Weddell Sea suspension-feeding amphipods exhibit distinct trophic behaviours.

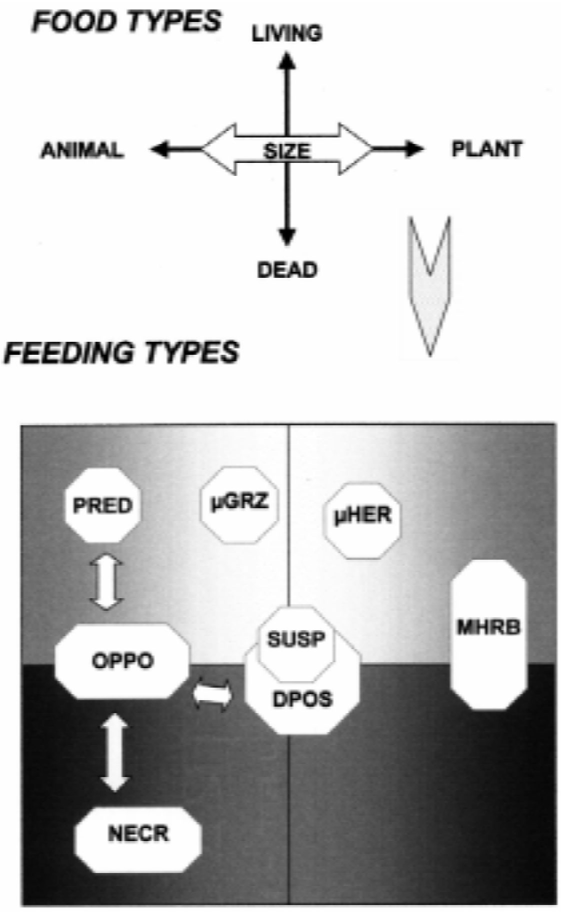

Figure 2. Characterisation of the different potential feending types according to three different gradients. Left ↔ right: animal vs plant material. Top ↔ bottom: living vs dead material. Centre ↔ lateral margins: increasing prey size. Feeding types= PRED – predators; OPPO – opportunistic predators/scavengers; NECR – necrophages; μGRZ – micropredatory grazers; SUSP – suspension-feeders; DPOS – deposit-feeders; μHER – micro-herbivores; MHRB – macro-herbivores.

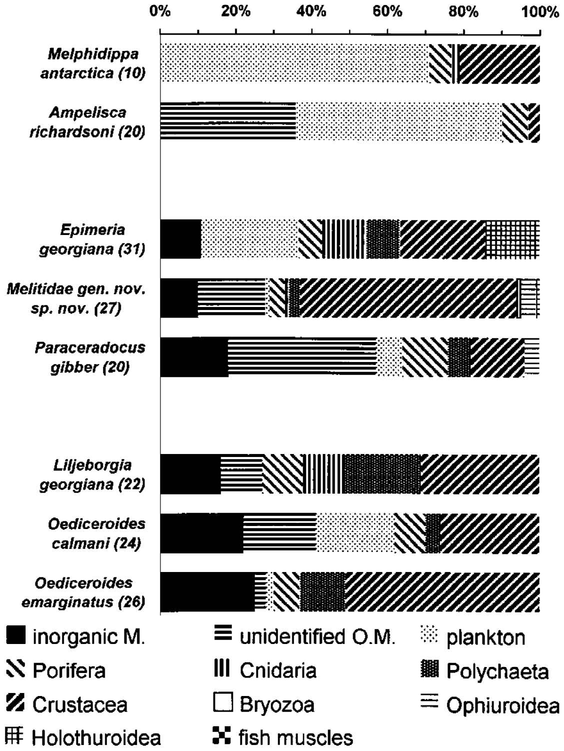

Figure 3. Mean proportions [R(i)’s] of the different food items in the digestive tract of suspension-feeding (top), deposit-feeding (middle) and deposit-feeding/predatory (bottom) Weddell Sea amphipods. Numbers in brackets are numbers of analysed specimens.

Ampelisca richardsoni *Karaman, 1975 (Ampeliscidae)*

This amphipod can reach 30 mm in length and is found in abundance (up to 25% of collected amphipods at some sampling stations) on sandy and muddy bottoms down to 550 m. The species exhibits a unusual behaviour, building a bivalve shell-like cell made of fine sediments grains conglomerated by gland secretion. In an aquarium, *Ampelisca* is first observed burrowing a kind of cradle into the sediment with its pereopods and/or pleopods. Then it builds its cell wherein it settles upside down, the antennae projecting outside. When disturbed, the animal turns round inside its cell, antennae downwards and closes it. Cells can be abandoned, however, and *Ampelisca* is quite able to swim. When feeding, the animal deploys A2 vertically, while A1 sweep the sediment. Pleopods beat intermittently, creating a water current from telson to head. Trapped food is removed from antennae to mouth by the gnathopods. The stomach is very short, and the digestive tract contents of the 20 dissected specimens look quite uniform. Food consists mainly of plankton items (mostly diatoms) embedded in unidentified organic material; some sponge spicules and crustacean remains were also noticed (Figure 3). *A. richardsoni* appears to be an active suspension-feeder, possibly completing its diet with some deposited food.

Melphidippa antarctica *Schellenberg, 1926 (Melphidippidae)*
This medium-size species (up to 25 mm) was observed to stay motionless upside-down on the bottom, with appendages (including the long uropods) directed towards the water column, as described by Enequist (1949) in *Melphidipella macra*. Antennae and pereopods are slender, elongate, and densely covered with long setae. The stomach is very short preventing any food storage (as for scavengers, see below). The main items found in the digestive tract were plankton material (a fluff of diatoms, peridinids and radiolarians) and remains of crustaceans (mainly euphausids and mysids); other items, such as sponge spicules, remains of cnidarians and holothuroid ossicles were occasionally observed (see Figure 3 for respective R(i)). Thus, *Melphidippa antarctica* can be considered as a passive suspension-feeder.

Polycheria antarctica *(Stebbing, 1875) (Dexaminidae)*
This is a small (ca. 6 mm) commensal of sponges, particularly *Crella crassa*, which makes hollows into its host's outer skin. It is found with its head driven foremost into the sponge, few appendages projecting outside and creating a water current. *Polycheria* is thus feeeding independently of its host. Food items observed in the 12 dissected specimens consist mainly of fragments of diatoms, mineral particles and unidentifiable organic debris. Other sponge-amphipod associations have been reported by Kunzmann (1996) who listed about 20 amphipod species (*Seba antarctica, Andaniotes linearis* and *Colomastix simplicauda* are the commonest), belonging to 13 families, frequently found in the atrial cavity of Weddell Sea sponges and which probably benefit from the water current.

Jassa goniamera *Walker, 1903 (Ischyroceridae)*
This amphipod (size: up to 20 mm) was observed clinging to small erected invertebrates (bryozoans, hydrozoans) by its pereopods. A1, directed forwards, and A2, almost as long as the animal body, bear very long setae organised in row, in a comb-like manner. Particles of different sizes gathered by the antennae are transferred to the mouth by the gnathopods. Food items found in the very small stomach include crustacean remains (probably copepods), diatoms and miscellaneous undefined bodies embedded in mucus.

2. Deposit-feeding type

Also typically epibenthic, these amphipods feed on a relatively large range of particles collected on the sea floor, originating either from the water column or from the breakdown of benthic biota.

Epimeria georgiana *Schellenberg, 1931 (Epimeriidae)*
This weakly motile large amphipod (up to 40 mm) can be found, sometimes in abundance, on coarse sediment bottoms or at the base of animal colonies. In aquaria, *Epimeria* refused living prey but accepted dead items (such as crushed amphipods or pieces of polychaetes) presented with a forceps. The stomach of this species is large, up to 18% of total body length (Coleman, 1991). Digestive tract analyses of 31 specimens revealed a wide variety of food items identifiable by hard remnants (Figure 3): crustaceans (mysids and amphipods), polychaetes (setae of terebellids), holothurioid ossicles and hydrozoan perisarcs; planktonic items (diatoms, radiolarians, foraminifers) also form a significant part of the diet. Finally, as for the other deposit-feeders, sponge spicules (which form a major component of bottom mats) and mineral particles complete the food, evidence of feeding on the sediment. Both these items, albeit ‘inorganic’, are likely to be of considerable nutritional value, since they may be densely coated by bacteria, the importance of which has been shown in Weddell Sea deposit-feeding nematodes (Vanhove et al., 1999).

Melitidae, gen. nov., sp. nov.
This is an amphipod of about 20 mm length, with a very short stomach. In the aquarium, it walked slowly on the floor, prospecting the sediment with the antennae. Despite many experiments (45 days of observation on 84 specimens) in different containers with various kinds of food, this species was never seen to feed, even on forceps-presented items. Injection into the aquarium of a juice made of crushed amphipods, however, seemed to arouse individual activity. Stomach contents of freshly sampled specimens were dominated by crustacean fragments (for the most part probably from *Euphausia*, and some from amphipods); less common items were pieces

of ophiuroids, holothurioids, bryozoans or cnidarians. Sponge spicules and mineral particles provide evidence for deposit-feeding (Figure 3).

Paraceradocus gibber *Andres, 1984 (Melitidae)*

This giant species (up to 100 mm, Klages & Gutt, 1990b), based on aquarium observations, seems to be unable to swim and shelters its body in crevices, with its long A1 whipping outside. Contact with food items induces capture first by A2, then by gnathopods and first pereiopods. If prey is large, the telson and uropods can participate in food retention. When outside shelter, *Paraceradocus* behaves as a side-crawler, like Gammaridae. Most of the guts were filled with unidentifiable amorphous organic material (Figure 3). This material is mixed with hard remains originating from polychaetes, echinoderms and crustaceans. Diatoms, sponge spicules and mineral particles completed the diet. It is worth noticing that gut contents presented a marked heterogeneity along the digestive tube of an individual as well as between individuals. This could reflect heterogeneity of food items on benthic substrates. Klages & Gutt (1990b) also analyzed stomach contents of 20 *P. gibber* from the eastern Weddell Sea; they found crustaceans represented 55% of the diet, with mineral particles accounting for 31%. Relying on this data and on appendage morphology, they argued that the species is a predator (an ambush-feeder), even cannibalistic. This opinion is not shared by Coleman (1989b) who observed a burrowing (owing to its size, *P. gibber* is an easy prey for fishes) and grooming behaviour. Particles trapped by A1 are cleaned away by the gnathopods. The dissected guts contained mainly detritus and sand grains. Coleman (1989b) thus considered the species to be a typical deposit-feeder, even if able to eat krill meat when suffering hunger. In addition, he showed that juveniles can leave the marsupium momentarily and participate in feeding with the female. Our assumption is closer to Coleman's concept. Probably *P. gibber* is a detritivore, but the succession of items in the gut suggests that the diet is not restricted to detrital matter, with the animal being able to feed on dead or living crustaceans.

Uristes gigas *Dana, 1849 (Lysianassoidea)*

This medium size species (up to 27 mm) was observed rarely moving in aquaria. Animals accepted and fed on pieces of fish, squid or polychaete, but no attempts at predation was noticed on living amphipods or mysids. Gut contents, when not empty (about half of the 42 dissected specimens), consisted of about one third of muscle-derived organic matter and one quarter of crustacean parts (amphipod appendages, krill ommatidia), mineral particles, broken sponge spicules and diatoms formed the remainder in about equal proportion (Figure 5). These last three items tend to suggest that *U. gigas* could be a deposit-feeder, scavenging opportunistically on dead fishes or crustaceans, as supported by the morphology of its mandibular molar process (M.H. Thurston, pers. comm.) and of its gut which is rather short, contrary to the situation usually observed in true necrophages. Moreover, *U. gigas* was only once collected in baited traps. Necrophagy thus does not seem to be the major trophic behaviour of the species.

3. Deposit-feeding/predatory type

Amphipods of this trophic type are weakly motile endo-or epibenthic forms. They feed on the same kind of items as those of the previous type, but also complement their diet with small living benthic organisms such as polychaetes and tiny amphipods. Crustacean fragments always represent a significant proportion of the gut content.

Liljeborgia georgiana *Schellenberg, 1931 (Liljeborgiidae)*

This species (up to 27 mm long) occupies a shelter. Its morphology, especially the size of gnathopods and last pereopods, suggest that *L. georgiana* is carnivorous. Feeding experiments performed in aquaria were uninformative, as the species was never seen either catching living prey (amphipods, copepods, worms or cnidarians) or feeding on miscellaneous dead material. Analyses of digestive tracts revealed a rather long stomach (about 1/4 of total tract length), nearly always empty. Main gut contents consisted of crustacean fragments (copepods, krill, amphipods), polychaete remains (Fabriciidae, Phyllodocidae, Terebellidae; Sicinski, pers. comm. and Gambi, pers. comm.), cnidarian fragments, sponge spicules and sand grains (Figure 3). These last items, the presence of setae from worms too big to be killed by *L. georgiana* and of euphausid remains suggest scavenging on deposited particles. A similar feeding behaviour has been described by Enequist (1949) for several *Lilljeborgia* species from the Skagerrak. On the other hand, capture of small living amphipods and grazing on cnidarians could contribute to the diet. Indeed, grazing has been cited as a main feeding mode for the Mediterranean species *L. brevicornis* (Bellan-Santini, 1998).

Oediceroides calmani *Walker, 1906 (Oedicerotidae)*

This is an amphipod (up to 30 mm long) which is usually found half-buried in sandy bottoms, with head and upper part of pereon emerging, A1 erected, A2 skimming the sediment, and last pereopods bent upwards. As in the previous species, neither scavenging nor predatory behaviour was observed during aquarium experiments, despite various substrates and potential prey organisms. Gut contents revealed a wide diversity of food stuffs: bottom items (mineral grains and sponge spicules), plankton (diatoms, radiolarians and copepods), some polychaete setae, and crustacean remnants (mainly from amphipods) (Figure 3). Neither aquarium observations nor gut analyses can define the position of *O. calmani* in the benthic food web. The species is likely to be non-selective, both in ingested food and foraging behaviour, and probably shifts from predatory to detritivory mode and *vice versa*, depending on food availability.

O. emarginatus *Nicholls, 1938*

This large species (up to 60 mm long) shows the same burrowing behaviour as *O. calmani*. Two months of observations in aquaria gave no information about feeding preferences: specimens remaining motionless in the sediment. Gut content analyses revealed similar items as in *O. calmani*, but in different proportions: planktonic items were less numerous, while crustacean remains (mainly from amphipods) formed about half of total items (Figure 3). As in the previous species, predatory behaviour can be suspected, but, as some food items obviously come from organisms too large to be killed by *O. emarginatus*, scavenging on the bottom must be considered.

4. Opportunistic predatory type

Amphipods of this trophic type are epibenthic and belong mainly to Epimeriidae. They feed on miscellaneous small material that they detect using antennae and capture with the gnathopods. They are weakly motile but can walk on the seafloor in search for food.

Epimeria macrodonta *Walker, 1906 (Epimeriidae, up to 35 mm long)*

Different experiments, in culture jars or in an aquarium with a natural substrate, have been carried out with about 60 individuals having various potential food (living or dead) at their disposal. Amphipods were seen walking slowly on the sediment, antennules erected and antennae directed forwards. The contact of A1 with live organisms (worm, crustacean) induced a reaction of gnathopods which move forwards, and try to catch the food. Chemoreception did not seem important in detecting food, as was shown by experiments with ‘amphipod juice’, which did not induce reaction. Gut content of aquarium animals revealed that they prey on bryozoans and hydrozoans, and also on items such as fragments of squid. Gut contents of freshly collected specimens showed a wide variety of food items: cnidarians (hydroid perisarcs, gorgonian ossicles), crustaceans (pieces of euphausiids) and pycnogonids, sea cucumbers (ossicles), and plankton (foraminifers, diatoms, ostracods); sponge spicules and sand grains completed the diet (Figure 4). *E. macrodonta* thus appears to be an opportunistic feeder, coupling microbrowsing on colonial organisms, active capture of small living prey and microdetritivory.

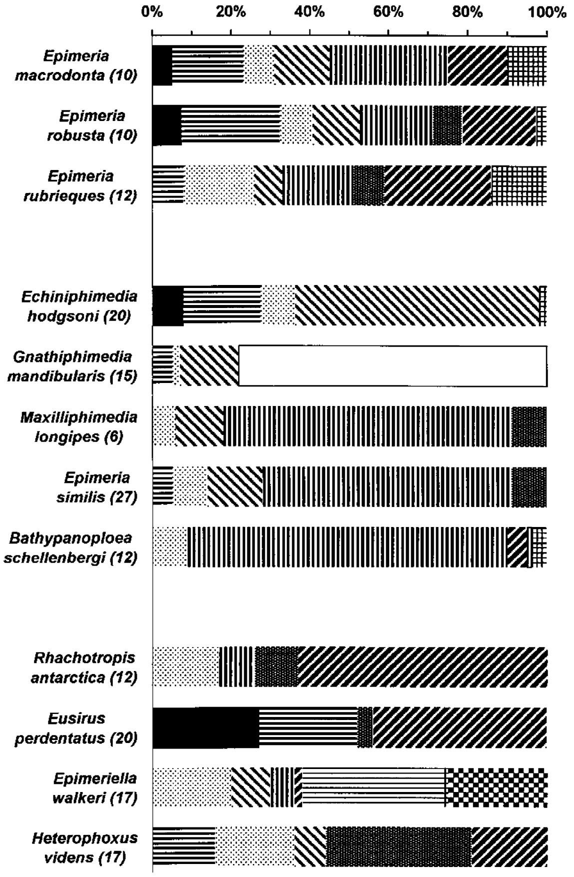

Figure 4. Mean proportions [R(i)’s] of the different food items in the digestive tract of opportunistic predatory (top), micropredatory browsing (middle), and predatory/scavenging (bottom) Weddell Sea amphipods. Numbers in brackets are numbers of analysed specimens. Same legend as for Figure 3.

E. robusta *K.H. Barnard, 1930*

This is a larger species (up to 40 mm in length). No trophic behaviour tendency could be inferred from observations, except that *E. robusta* accepted and grabbed with the gnathopods any kind of food fragment put in contact with its antennae. Klages & Gutt (1990b) observed, also in laboratory conditions, active predation on other living amphipods or on *Artemia*, and concluded that *E. robusta* behaved as a ‘sit-and-wait’ opportunistic predator of motile invertebrates. They noticed that other specimens were attracted to a feeding individual. The gut contents of our specimens are rather similar to those of *E. macrodonta*, with a smaller number of cnidarians, the presence of polychaetes, and some more crustaceans (Figure 4). Guts analysed by Klages & Gutt (1990b) were filled with miscellaneous organic matter (42%) and by polychaetes, crustaceans and holothurians in similar proportion (10% each); cnidarians were totally lacking. Differences between the Klages & Gutt (1990b) results and ours underline the problem of determining precisely the trophic position and behaviour of non-selective amphipod species. Sampling location and/or experimental conditions may be critical.

E. rubrieques *De Broyer & Klages, 1991*

This is a giant species (up to 70 mm) discovered recently in the East Antarctic. In laboratory condition, De Broyer & Klages (1991) observed *E. rubrieques* to rest for hours to days on hard substrates, the species becoming active when food (krill material or living *Artemia*) was provided close to its antennae. They concluded that the amphipod was an ambush predator. In our experiments, *E. rubrieques* did not eat pieces of food lying on the bottom, but did grasp presented items. Analyses of digestive tube contents revealed much the same items as for the other two *Epimeria* species: algal cells (diatoms), sponge spicules, cnidarian fragments (perisarcs from hydroid *Staurotheca*, spicules from *Clavularia* [J.M. Gili, det.], cnidocysts), crustacean remains (mainly from amphipods), polychaete setae, and sclerites of holothurians (*Taeniogyrus contortus*) (Figure 4). It appears that *E. rubrieques* is rather an opportunistic feeder with both scavenging and predatory behaviour, like *E. macrodonta*.

Another Antarctic *Epimeria* species, *E. monodon* Stephensen, 1947, could be linked to this trophic type. Richardson (1977) reported a dietary composition of crustacean remains (amphipods and copepods) and diatom cells, but did not provide an exhaustive list of food items or proportions.

The separation of this trophic type from the deposit-feeding/predatory type is not trivial, as the two groups behave in a different way, despite feeding on rather similar items. Comparisons of Figures 3 and 4 shows clearly that the ‘*Oediceroides-Liljeborgia* group’ has a unequivocal deposit-feeding behaviour (cfr. inorganic fractions) associated with predation (mainly on crustaceans), while the *‘Epimeria* group’ has a more widely diversified (living or not) animal-based diet and feeds more actively. Species from the latter group could also be included in the following group, as browsing obviously takes place in their feeding behaviour (e.g. on hydroids or holothurians), but they appear not to be selective in the prey items they feed on.

5. Micropredatory browsing type

Animals of this feeding type collect small food elements from sedentary organisms which are unable to flee. Browsers (or ‘grazers’) eat only part of each prey item without killing it. Macroalgae are absent, and eastern Weddell Sea browsing amphipods specialize in grazing on colonies of different benthic invertebrates. Organisms of this type are also known as ‘surface microphagous browsers’ (Margalef, 1978), ‘carnivorous browsers’ (Hughes, 1980) or ‘micropredatory grazers’ (Oshel & Steele, 1985). Grazers on periphyton (‘microherbivorous browsers’), albeit existing, cannot be easily identified on the base of gut contents, and can thus conveniently be classed among deposit-feeders. Predatory browsing behaviour has been developed in different families of Antarctic amphipods. These are typically epibenthic, and are moreover feeding preferentially on a limited selection of organisms.

Echiniphimedia hodgsoni *Walker, 1906 (Iphimediidae)*

This is a large species (up to 40 mm) that usually inhabits sponges or bryozoans in aquaria. Feeding experiments with living or detrital food were unsuccessful, and animals were never seen grazing upon their substrate. Gut contents are dominated by sponge spicules (fraction: more than 60%, size: up to 500 μm) and undetermined organic matter (maybe from sponge cells) (Figure 4). This is in very good agreement with the results of Coleman (1989a) who identified spicules from different Haplosceridae. Another *Echiniphimedia* (sp. A), less spiny and less frequent than

E. hodgsoni, but collected at the same sampling sites, was also found to feed principally on sponge material. Co-occurrence of the two species in the same biota may be related to difference in sponge prey species, although this could not be inferred from gut content data.

Gnathiphimedia mandibularis *K.H. Barnard, 1930 (Iphimediidae)*

This orange-brown species (up to 50 mm in length) is one of the few Antarctic amphipods whose diet preference has been well studied. Coleman (1989c) found that cyclostomate bryozoan remains dominated gut contents which also included some sand grains. He pointed out that *G. mandibularis* mandibles are uncommon in the Amphipoda and obviously adapted for crushing hard items. Similar crushing molar processes are known in some oedicerotids, and in some deep-sea sinopiids (e.g. in *Jeddo* and *Syrrhoites* genera, M. Thurston, pers. comm.) which feed on sponges but also on large calcareous foraminifers, known to be a major food resource for some abyssal asellote isopods (Svavarson et al., 1993). Klages & Gutt (1989b) confirmed the species' diet, and found up to 95% of bryozoan parts in non-empty guts. Our results are similar (Figure 4), despite the fact that we observed about 15% of sponge spicules, an item not mentioned by the other authors.

Maxilliphimedia longipes *Walker, 1906*

This third iphimediid has a totally different diet from the other two (Figure 4). More than 70% of gut contents consisted of cnidarian tissues, mainly represented by discharged cnidocysts (of a single unidentified variety for the six dissected specimens). As a result of the scarcity of material, no aquarium behaviour observations were performed. Nevertheless, our gut analyses corroborate the records of Coleman (1989a) on *M. longipes*, who observed, in food items, a strong predominance of nematocysts from different origins (among which spirocysts [Hexacorallia] and mastigophores [Hydrozoa or Anthozoa]). Coleman argued that the mandibles are adapted to cut large fragments of soft food, such as mucous tissues of cnidarians.

Epimeria similis *Chevreux, 1912 (Epimeriidae)*

This giant species (maximum size: 50 mm, Chapelle, pers. comm.) showed no reaction to dead organisms in aquarium experiments, despite being caught occasionally in baited traps. Most of the 27 dissected specimens had a full gut and fore-gut. Gut contents varied from white to red, and from a gelatinous mass to a suspension of cells in a liquid phase. Important items consisted of cnidocysts of various size and shape, some of them identified as from the hydrozoans *Tubularia* and *Campanula*, and others to actiniids (Gili, pers. comm.) (Figure 4). Other items observed were: planktonic cells (diatoms and foraminifers), spicules of sponges and setae of polychaetes. In some gut contents, the presence of dark red crystals could be related to the food prefences: cnidarians are iron-rich and amphipod consumers may eliminate the metal as crystals of iron compounds. Such a process has been described for stegocephalids feeding on different cnidarians (Moore & Rainbow, 1984, 1989). Finally, pieces of fish flesh were found exclusively in the fore-gut from individuals collected in baited traps. Another epimeriid, *E. oxicarinata*, was described by Coleman (1990a) as feeding on hydrozoans.

Bathypanoploea schellenbergi *Holman & Watling, 1983 (Stilipedidae)*

Gut contents of this species were dominated largely by remains of gorgonians (cnidocysts and ossicles) (73%, Figure 7). Other items included planktonic organisms and hard remains of crustaceans, bryozoans and holothurioids. Our observations are in contrast to those of Coleman (1990b) who found exclusively mucous remains with ossicles of holothurians. Unfortunately, no aquarium experiment could be performed on this large (up to 50 mm, Holman & Watling, 1983) deep-living species in order to determine its feeding behaviour and validate gut contents.

Hirondellea antarctica *(Schellenberg, 1926) (Lysianassoidea)*

Aquarium experiments performed with this species were unsuccessful, as animals did not feed on any item presented, dead or living. Examination of gut contents, when not empty, showed mainly a reddish organic mixture full of cnidocysts that were identified (Gili, pers. comm.) as belonging to hydrozoans (*Schizotricha unifurcata* and hydrocorals) or sea anemones. Cnidocysts of common gorgonians (Isididae and Primnoidae) were not found in *H. antarctica* guts. Additional items consisted of some setae and sponge spicules. Some specimens have been caught in baited traps. All of them had the digestive tract full of pieces of fish striated muscles. Scavenging is thus probably an alternative feeding mode for this species, which was sometimes collected in traps.

6. Macropredatory/opportunistic scavenging type

This trophic type, mainly predatory, embraces a large number of species belonging to various families (see further). Members of the group are endo- or epibenthic, and feed on a wide variety of prey. Prey differs from one species to another, and a site-dependent intraspecific variability is apparent. Non selective feeding is usual, but some members of this feeding type display diet preferences for particular animal groups such as polychaetes, other amphipods or ophiuroids. Different predatory behaviours (active searching, ambushingþ) are also encountered in this group.

Rhachotropis antarctica *K.H. Barnard, 1932 (Eusiridae)*

Because of the scarcity of material, no significant experiments could be performed in aquaria. The animals collected alive (12) appeared able to swim actively, but no feeding occurred in laboratory conditions. Dissection of captured individuals revealed that crustaceans (krill, copepod and amphipod exoskeletons) formed the bulk of the diet; other common items were polychaete setae, planktonic cells (diatoms, radiolarians) and cnidocysts (Figure 4). The exact trophic position of *R. antarctica* is not obvious. Its short stomach and external morphology (big gnathopods, long pereiopods, slender body) suggest predatory behaviour. This is supported by the importance of crustaceans in the diet. On the other hand, the presence in guts of plankton and krill remains could indicate a scavenging or deposit-feeding mode. It is possible that behavioural observations would help in placing the species either among this group or with the deposit-feeding/predatory types (group 3, see above and Figure 3).

Eusirus perdentatus *Chevreux, 1912 (Eusiridae)*

This giant species (up to 87 mm long) is very common on Weddell Sea bottoms down to 800 m (Klages, 1993). In the aquarium, it usually stays motionless at the top of an eminence (rock or any bump), but becomes active in the darkness, when it crawls with A1 directed upwards and A2 investigating the sediment, or even swims up to the surface. *E. perdentatus* was, with one exception, never seen preying on the different animals living in its aquarium. This could be misleading, as specimens kept in captivity soon suffer from a ‘black spot’ disease (bacteria or fungi?) that affects the eyes and antennae, thus probably lowering sensory perception. Gut contents were dominated by crustacean hard parts (Figure 4). Mineral particles and unidentified organic matter (possibly crustacean muscle fibers) each formed about one quarter of the the digestive mass, and some polychaete setae completed the diet. Klages & Gutt (1990a) found *E. perdentatus* to feed principally on live polychaetes and crustaceans (mainly other amphipods). They concluded that the species was a ‘passive’ carnivorous predator, that waited motionless for prey to approach. This is in rather good agreement with our observations and findings.

Eusirus *sp. (cf.* antarcticus)[1]

This is also a large eusirid (up to 50 mm) behaving in aquaria as does *E. perdentatus*, except that it is a more active swimmer, able to remain in the water column. The common occurrence in plankton samples suggests that *E.* cf. *antarcticus* is a benthopelagic species. In laboratory conditions, spontaneous predation (or attemps of predation) on living amphipods was observed, for instance on *Pseudorchomene coatsi*, even when this lysianassoid was burrowed in the sediment. Some other amphipod species, ostracods and polychaetes were neglected, as well as food items presented with forceps. Gut contents (20 dissected specimens) were dominated largely by amphipod remains, supplemented by a few copepod parts and bryozoan fragments. Guts of specimens caught in baited traps also contained pieces of striated muscles. *E.* cf. *antarcticus* thus appears to be a selective macropredator able to feed partially on carrion.

Epimeriella walkeri *K.H. Barnard, 1930 (Epimeriidae, up to 29 mm)*

Behavioural observations in aquarium were quite fruitless, as the 28 captured specimens did not feed at all for 53 days (except once on a fish carcass). Stomachs of freshly caught individuals were, nevertheless, full of food. The commonest items were ophiuroids (ossicles and parts of arms), striated muscle and diatoms (Figure 4). Less prevalent were sponge spicules and cnidocysts, while crustacean pieces and holothurian ossicles were infrequent. *E. walkeri* thus seems to be a predator of brittle stars and an opportunistic scavenger. The occurrence of plankton cells in the digestive tract is harder to explain. They may come from brittle star diet as many of these echinoderms are suspension-feeders.

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[1] Species status under revision (De Broyer & Jażdżewski)

Alexandrella mixta *(Nicholls, 1938) (Stilipedidae)*

As for the former species, laboratory experiments were unsuccessful, and these amphipods did not feed on any substrate. Almost all of the material found in the digestive tracts of the 16 specimens examined consisted of large fragments of brittle star skeleton. Clearly, the species is a specialized macropredator on ophiuroids.

Heterophoxus videns *K.H. Barnard, 1930 (Phoxocephalidae)*

This is a small endobenthic species (less than 10 mm) that burrows actively in the sediment for foraging. When disturbed from shelter, it digs rapidly back into the sand. Because of this behaviour, observations of feeding activity were difficult. Moreover, analysis of gut content of individuals kept in aquarium for 7 weeks revealed little evidence of feeding. Analysis of freshly captured specimens showed a relatively long foregut (about 1/3 of body length), usually nearly full. Food items were diverse: polychaetes (flesh, and setae of Syllidae, Paraonidae, Aphroditidae), crustacean parts (tanaids, copepods), sponge spicules, benthic diatoms, and other less common items such as foraminifers or nematodes (Figure 4). All these food items indicate that *H. videns* is a predator preying in the upper layer of the sediment. The size of some polychaete setae moreover tend to suggest that the species would also be a scavenger on bigger animal remains. These observations are in very good agreement with those of Oliver et al. (1982) and Oliver & Slattery (1985) who noticed the prevalence of juvenile annelids from the upper infauna (*Spiophanes* sp. and *Tharyx* sp.) associated with nematods, harpacticoids and diatoms in digestive tracts of *H. videns* from McMurdo Sound. From laboratory feeding experiments, they concluded that phoxocephalids have a significant effect on annelid larval or juvenile survival and thus regulate polychaete settlement.

7. Opportunistic necrophagy type

Amphipods of this trophic type, mainly epibenthic, are commonly found in traps baited with meat or dead fish. Analyses of digestive tract contents and observations made in aquaria show that carrion constitues only a fraction of their diet. These species are able to kill prey, the size of which ranges from copepods to small fishes. The relative importance of both feeding behaviours is likely to depend upon potential food availability, which will be spatially and seasonally dependent. All the species of this type (and of the following one – ‘*Necrophagy*’) belong to the super-family Lysianassoidea.

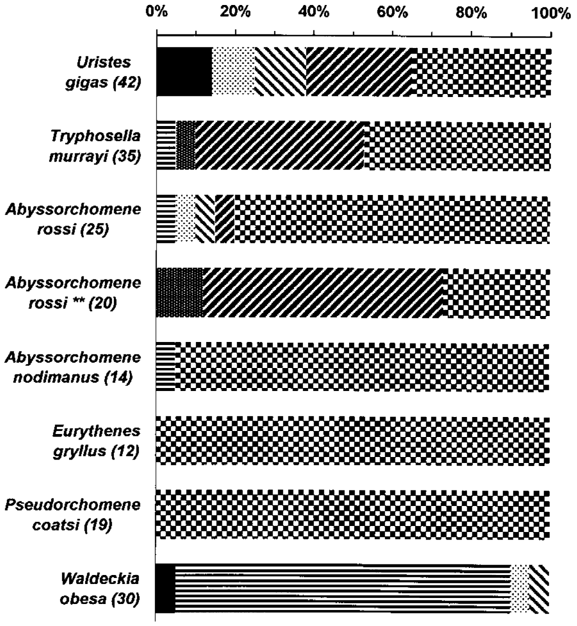

Figure 5. Mean proportions [R(i)’s] of the different food items in the digestive tract of necrophage Weddell Sea amphipods. Numbers in brackets are numbers of analysed specimens. Same legend as for Figure 3.

Tryphosella murrayi *(Walker, 1903)*

This is a rather large species (up to 35 mm) which rests on the bottom, sometimes slightly buried in the sediment with dorsum and antennae emerging. The latter move gently in the water, presumably to detect the odour of potential food. Detection induces a swimming reaction, limited to the vicinity of the bottom. In aquaria, every kind of presented carrion (crustaceans, polychaetes, squid or fish meat) is accepted, without any apparent preference. *T. murrayi* is also a predator. Four individuals were seen to kill and eat a living mysid within few minutes, while on another occasion about 150 were observed to kill a 10 cm long plunderfish (*Dolloidraco longedorsalis*), and consume it within half a day. On the other hand, a live big benthic polynoid polychaete present in the aquarium was not attacked. Such a predatory behaviour has already been described for other lysianassoids (*Abyssorchomene rossi*, Hodgson in Walker, 1907). Gut contents were dominated by two items: fragments of flesh (probably from fishes as suggested by scale or bone fragments) and pieces of crustaceans (parts of amphipods) (Figure 5). Fragments of polychaetes were sometimes observed; sponge spicules and diatoms were rare. In baited traps, *T. murrayi* is collected frequently (in 65% of trap experiments) and can reach up to 90% of all amphipods caught (>2200 in one trap). Guts of these animals are filled almost exclusively with bait. *T. murrayi* thus seems to be an opportunistic macro-feeder, both predator and scavenger. The latter behaviour had already been suggested from field collection data by De Broyer & Klages (1990).

Abyssorchomene rossi *(Walker, 1903)*

This is also a large species (up to 40 mm) which occurs in the water column as well as on benthic substrates, as shown by results from benthic, bentho-pelagic and mid-water trawls. In aquaria, *A. rossi* usually stays on the bottom, and its activity largely depends on the presence of prey and on population density. The ‘smell’ of potential preys – or of ‘amphipod juice’ – induces an active swimming reaction. When present in sufficient number in the aquarium, *A. rossi* is able to attack and kill small swimming prey. The digestive tract content varied, depending on whether the animals were collected close to the bottom or in the water column (Figure 5). Stomachs of benthic specimens were dominated by fluidish organic matter spotted with oily droplets, likely to be flesh at various stages of digestion; some other items are found, but in small quantity: sponge spicules, crustacean appendages and diatoms. Stomachs of pelagic individuals (noted ** on Figure 5) have a totally different content. While flesh was still present (about 25%), copepod remains formed the bulk (55%) of the diet; polychaete setae constitute a third, less common, item. The exact trophic position of *A. rossi* is unclear. Although an apparently selective copepod predator within the water column, it appears to be able to migrate down to the bottom to scavenge on different materials. This confirms the observations of Stockton (1982) on Ross Ice Shelf populations, who considered *A. rossi* as a facultative scavenger. No evidence was found to associate possible vertical migrations with food availability.

Abyssorchomene plebs *(Hurley, 1965)*

This is a medium-sized species (≤25 mm). In laboratory conditions, it has a behaviour similar to that of *A. rossi*. In the field, it is also collected by midwater trawls, indicating a bentho-pelagic way of life. Stomach and gut contents varied from one individual to another. Crustacean parts (eyes or ommatidia, appendages and chitinous plates) were frequent. Some individuals contained fragments of carrion (muscles), while others had ingested diatoms. The feeding behaviour of *A. rossi* and *A. plebs* could be relatively similar, with the former being more of a predator (on copepods) and the latter more of a scavenger (on krill) in the water column. It is worth noticing that *A. plebs* is found more commonly in baited traps (from 1 to 98% of attracted amphipods) than *A. rossi* (only few specimens), which could indicate a preference for scavenging. Other authors share this opinion: Rakusa-Suszczewski (1982) considered *A. plebs* as a true necrophage occuring in hordes, and Slattery & Oliver (1986) observed *in situ* scavenging on bait. In other respects, Thurston (1974) analysed museum collections, and found that *A. plebs* outnumbered *A. rossi* about 9:1, and that co-occurrences in samples of the two species were relatively uncommon.

Differences in the diet of both *Abyssorchomene* species seem, however, to depend on other parameters, such as season or geographical area. For instance, plankton samples collected in the Gerlache Strait during the austral fall, 1983, by Hopkins (1985), revealed that guts of both species contained mainly planktonic crustacean remains (copepods and euphausiids) in about the same proportion. Fish debris was present in about 50% of the guts of both *A. rossi* and *A. plebs*, the latter moreover containing a significant fraction of salp and coelenterate remains. In a study of McMurdo Sound midwater summer food web, the same author (Hopkins, 1987) found *A. plebs* to feed mainly on phytoplankton cells or aggregates and on microzooplankton, while *A. rossi* was preying mainly on coelenterates. Thus, it is likely that both species, at least those individuals feeding in midwater, are rather opportunistic and adapt their diet to local and temporal food availability.

(See also *supra: Uristes gigas*, in ‘Deposit-feeding type’)

8. Necrophagy

“*Obligate marine scavengers: do they exist?*” is the title of a recent article by Kaiser & Moore (1999). The question, to which they gave a qualified positive answer, arose in response to the paper of Britton & Morton (1994) who, in an extensive review of the ecology of marine scavengers, found no evidence for an obligate scavenging life-style, except, maybe, for two distinct animal groups: nassariid gastropods and lysianassoid amphipods. Britton & Morton (1994) argued that insufficient consistently reliable sources of food could be found that would allow specialization as obligate scavengers. However, Kaiser & Moore (1999) found some evidence to support the existence of such a behaviour for at least one lysianassoid species (*Orchomene nanus*). In Antarctic waters, environmental condition lead to a huge – but seasonal – production of organic matter which is consumed only partially within the water column. Most of this matter reaches the seafloor directly or indirectly where it becomes available to various benthic or supra-benthic scavengers, from deposit-feeders to necrophages. Moreover, the peculiar Antarctic food web provides an important amount (less seasonally dependent) of meso- (fishes and seabirds), macro- (seals) or megacarrion (cetaceans) to the benthos. 'Obligate' or at least 'preferential' scavengers should thus not be rare in these waters. The following species could be good candidates.

Abyssorchomene nodimanus *(Walker, 1903)*

This is a medium-size (≤20 mm) species frequently collected down to 810 m depth. It lives like *A. rossi*, partly buried in the sediment with antennae protruding upwards. In an aquarium, *A. nodimanus* displays a quasi predatory behaviour when present in relatively large numbers (20 or more individuals). They were able to kill and eat a 4 cm dendrochirotid holothurian, an 8 cm polychaete, an 8 cm octopus and a 15 cm fish. Prey are preferentially attacked through natural orifices, such as gill slits, anus or eyes, and are completely eaten within a few tens of minutes. *A. nodimanus* accepts and feeds on any kind of carrion. Stomachs from specimens collected by bottom trawls are almost full (at 95%) of an organic matter mixture wherein pieces of striated muscles are clearly recognizable (Figure 5). Stomachs are long (half the body length) and large, typical of scavenging amphipods (Dahl, 1979; De Broyer, 1983; Coleman, 1991; Sainte-Marie, 1992). The species is caught frequently in baited traps, where it represents from 5 to 98% of total amphipods (up to 10 250 specimens in one trap). Based on protected bait trap experiments and aquarium observations, olfaction is the major sense in detecting food. *A. nodimanus* appears to be a scavenging species. Predation observed in laboratory conditions may be an artifact resulting from overcrowding or unnatural constraint of the prey organisms.

Pseudorchomene coatsi *(Chilton, 1912)*

This is also a medium-sized species (≤25 mm) which has been collected from the surface down to about 500 m depth. In aquaria, it behaves like the three *Abyssorchomene* species. Olfactive stimulations (carrion or 'amphipod juice') trigger a quick swimming reaction. Any kind of carrion is accepted. The species was captured mainly in baited traps (40% of deployments), wherein it can represent up to 96% of total number of amphipods (one record of 24 560 specimens in one trap!). The digestive tract content of all individuals analyzed (collected either by trawl or by trap) revealed only fragments of carrion (Figure 3), indicating that *P. coatsi* is a true necrophage.

Eurythenes gryllus *(Lichtenstein, 1822)*

This is a giant (up to 120 mm in Antarctic waters, De Broyer, unpubl., but known up to 154 mm in Pacific abyssal waters, Baldwin & Smith, 1987) pan-oceanic cold-water stenotherm lysianassoid, present in both polar regions, and inhabiting bathyal and abyssal waters. *E. gryllus* is typically a pelago-benthic species, i.e. probably an almost permanent swimmer, occasionally moving down to the bottom for scavenging, at least for smaller individuals. Many authors (see reviews in Thurston, 1990, or Sainte-Marie, 1992) evidenced that *E. gryllus* can occur at considerable distances above the sea floor, even close to the surface as suggested by many records in seabirds' stomachs. Smith & Baldwin (1984) and Hargrave et al. (1994) have, moreover, shown that the vertical distribution of the species was size- and sex-related (*E. gryllus* should be an ontogenetic migrant), as well as the meal size or the lipid storage. Very few specimens (12) were caught in the Weddell Sea during the present study, all of them in baited traps. Dissection of digestive tracts revealed only fragments of bait. We could not state, however, if *E. gryllus* is a preferential or opportunistic necrophage, or if it also preys on living items within the water column. No information was obtained during observations of Weddell Sea specimens in aquaria. Abundant material (>500 individuals) was collected off Admiralty Bay, King George Island, at a depth of 800 m, during the EASIZ II cruise. In laboratory artificial conditions, *E. gryllus* from this site was seen swimming quite close to the bottom or resting or walking on the substrate. Attempts at feeding on various carrion were unsuccessful, but cannibalism occurred frequently in overcrowded jars.

Parschisturella carinata *(Schellenberg, 1926) (≤22 mm)*

This was caught almost exclusively in baited traps (3/4 of all deployments), wherein it represented from 1 to 90% of collected amphipods. This species was attracted by any bait, and showed no particular preference for one sort or another (fish, shrimp, meat). Gut of captured individuals contained only fragments of bait. In aquaria, *P. carinata* was seen to stay motionless, in a upright position, sometimes partly buried in the sediment. All dead items provided (squid, fish or polychaete fragments) were devoured.

Waldeckia obesa *(Chevreux, 1905)*

This is a large amphipod (up to 35 mm), with a wide circum-antarctic distribution (De Broyer & Jażdżewski, 1993). It occurs down to 900 m depth in the Weddell Sea (De Broyer & Klages, 1990). In aquaria, individuals stay upright motionless on the bottom or on sessile animals, with antennae slowly investigating the surrounding water. Experiments have shown that *W. obesa* is very sensitive to carrion odour, and reacts rapidly by swimming when any piece or drop of carrion is put in its container. As mentioned previously for some *Abyssorchomene* species, swarms of *W. obesa* are able to attack and eat moribund fishes (especially scaleless icefishes). Stomach content analyses were performed on specimens collected by trawl. Stomachs are long and large, able to store huge quantities of food. About one third of them were empty but the others were filled almost exclusively with organic material, hardly recognizable and variously coloured, wherein fragments of striated muscles could be distinguished (Figure 5). *W. obesa* was collected in 80% of the baited trap deployments, often in large numbers (up to 2730 specimens). The scavenging behaviour of the species was reported by Arnaud (1970) and has been confirmed by subsequent studies. The emptiness of many stomachs should suggest that *W. obesa* is rather well adapted to a discrete way of feeding, alternating periods of fasting and gluttony. Its metabolism can be regulated in response to starvation (Chapelle et al., 1994), and the species has been reported to endure fasting up to 18 months (Coleman, 1991).

Discussion and conclusion

The analyses of digestive tract content, coupled with ethological observations in a cool laboratory, revealed a wide diversity in trophic habits among the Weddell Sea gammaridean amphipod taxocœnosis. Macroherbivory excepted all the major trophic types commonly occurring in marine invertebrate assemblages have been adopted by these peracarids, and all the available food sources – from unicellular plankters to vertebrate carcasses – have been exploited.

This diversity in trophic types – for amphipods – is in a way unique if considering, following Arntz et al. (1997), that Antarctic marine fauna – and *a fortiori* Weddell Sea fauna – is part of the same immense cold-water system. Such a trophic diversity can probably be observed in areas such as the Mediterranean Sea (Bellan-Santini, 1998), but this basin is a complex of interworking ecosystems (Pérès & Picard, 1964), characterized by distinctive floral and faunal assemblages and differences in biogeochemical cycles. Other ecosystems, like, e.g., coral reefs, may have extensive trophic diversity patterns, but information about the feeding habits of the amphipod fauna inhabiting these ecosystems are unfortunately fragmentary and scattered.

What permits such a trophic diversity on the Weddell Sea bottoms? or: why are amphipod communities so diversified in Antarctic waters? Myths and realities on the high biodiversity of Antarctic fauna and of cold deep-sea fauna in general have been widely debated (e.g. Clarke, 1990, 1992; Crame, 1992; Grassle & Maciolek, 1992; May, 1992; Poore & Wilson, 1993 [and reply by May, 1993]; Gray, 1994; Arntz et al., 1994, 1997; Brey et al., 1994, 1996). Antarctic species richness is attested for several zoological groups such as priapulids, pycnogonids and amphipods, especially the families Epimeriidae and Iphimediidae, with usually a high degree of endemism (e.g. up to 90% for pycnogonids and fishes) (Arntz et al., 1997). Southern Ocean amphipods are for the most part endemic (85% of benthic species and 36.7% of benthic genera, De Broyer & Jażdżewski, 1993, 1996). The origin of the iphimediid Antarctic amphipod fauna has been discussed by Watling & Thurston (1989). They showed that the most primitive genera were distributed primarily outside Antarctica and were inferred to be relicts of a former global distribution, which is in good agreement with the third evolutionary historical model of Crame (1992). Watling & Thurston (1989) suggested that once the Antarctic Ocean 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 of Antarctic waters to act as an incubator for this 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 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, (iv) and 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 of the Southern Ocean (Chapelle & Peck, 1999). It is worth noticing that Lake Baikal, with similar physical-chemical features (cold and oxygen-rich waters), also exhibits an extraordinarily diversified fauna of (giant) amphipods (Bazikalova, 1945).

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 amphipods to adopt various life styles: epontic dwellers, (bentho) pelagic swimmers, walkers, crawlers, burrowers, borers, inquilines in/on different vertebrates or invertebratesþ This diversity in microhabitats, coupled with the variety of potential food, is likely to be a factor which has favoured the radiation of the Amphipoda and the diversification of trophic types in Antarctic waters (Jażdżewski et al., 1996).

The different trophic types described above refer only to the 40 most common species collected in our samples. Other types are likely to exist, in particular specialised ones associated with various degrees of inquilinism. Kunzmann (1996), for instance, has recorded numerous amphipod species belonging to 13 families which inhabit the atrial cavity of Weddell Sea hexactinellids and demosponges. Whether these species are simply commensal or partly feed on host tissues was not determined, except for *Seba antarctica* which is considered an ectoparasite eating the host tissues. Commensalism with ascidians was reported by De Broyer et al. (1999) for different lysianassid, stegocephalid and stenothoid species, without apparent host-specific relationships. These authors noticed also associations of some stenothoid species with hydrozoans and gorgonians (*Primnoella*). Inquilinism (in coelenterates or salps) is also common in planktonic hyperiids (about 40 species in the Antarctic region). Parasitism is observed for seven Antarctic species of Cyamidae which live and feed on cetacean skin. Finally, a specialized feeding mode may also exist for epontic species which were observed (Dieckmann, pers. comm.) supposedly grazing on phytoplankton cells which grow attached to ice platelets.

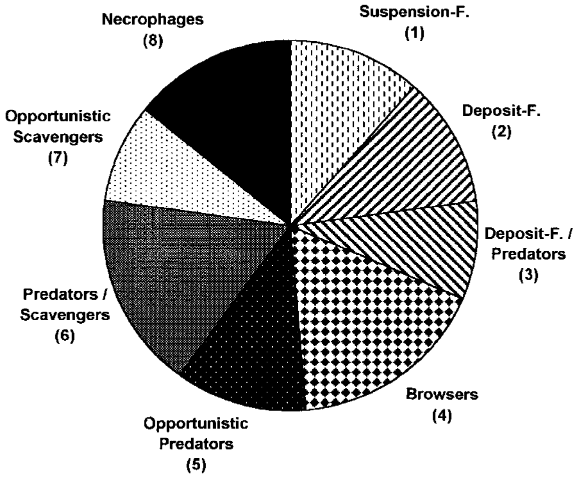

Figure 6. Distribution of the different trophic types among the Weddell Sea amphipod species analysed in the framework of this study.

The relative importance of the different trophic types described in the present paper can be analysed, bearing in mind that the 40 species examined represent only 17% of the known Weddell Sea amphipod fauna. These 40 species are moreover biased towards large size, and the inclusion of small species might well have a significant effect on the ratios presented in Figure 6. No particular type is dominant, but micropredatory browsers and predators/scavengers (both 17% of total types) are commonest.

If consideration is given not only to the trophic types as previously described, but also to food particle size, then micro- and macrophagy (types 1–4 vs 5–8 on Figure 6) are almost equally represented. On the other hand, taking into account the type of food (i.e. distinguishing among living plants, living animals and detritus), the breakdown is 11% for ‘herbivores’ (if suspension-feeders are regarded as preying mainly on phytoplankton cells, a probable overestimate), 64% for predators (accessory to exclusive, types 3–6), and 60% for scavengers (accessory to exclusive, from settled particle to carcass feeders, types 2, 3 and 6–8). There is an obvious overlap, suggesting that many

Weddell Sea amphipods have a broad-spectrum diet and take advantage of different food resources. Such a non-selectivity in prey–predator relationships (with the noticeable exception of browsers) may be related to the marked seasonal cycle in Antarctic water productivity. Spring–summer bloom conditions produce a huge yield of new organic matter which is utilized rather rapidly by water-column and bottom primary consumers. In contrast, winter conditions are characterised by a relative scarcity of fresh food resources. Opportunistic feeding behaviour thus is likely to be seen in non-specialist consumers, with a progressive shift from predation to scavenging depending on food type availability. The results presented in this paper were obtained for amphipods collected exclusively during the austral summer. A similar study on winter material (with all the sampling difficulties it would represent) should add worthwhile information for understanding the role of the amphipod taxocoenosis in Antarctic food web ecology. On another hand, coupling trophic preferences to reliable measurements of amphipod species relative abundances would allow an estimation of the impact of these peracarids on Antarctic benthic ecosystems (Dauby et al., 2001).

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Pictures of many of the amphipod species analysed in this paper can be seen on the web site: http://www.naturalsciences.net/general/sect ions/amphi.

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